FOREST ISLANDS IN AN AMAZONIAN SAVANNA OF NORTHEASTERN BOLIVIA

BY

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Acknowledgments

I dedicate this dissertation to my son, Roberto Fanor Langstroth Ugalde, who was born in Santa Cruz de la Sierra during the fieldwork period of this study. I hope that he will love the land and life of his birthplace, the Bolivian Oriente, as much as I do someday. He is certainly the most beautiful and most important product of my fieldwork in Bolivia.

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Abstract

FOREST ISLANDS IN AN AMAZONIAN SAVANNA OF NORTHEASTERN BOLIVIA

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The Amazonian lowlands of Bolivia are characterized by extensive areas of seasonally inundated savannas. These open landscapes are traversed by numerous rivers bordered by dense gallery forest on their natural levees. Within the savannas themselves, numerous forest islands dot the horizon. The objective of my research was to explain the origins of the forest islands in a selected area of the Bolivian Amazon. To achieve this goal, I engaged in an 11-month field project in 1993-94. My study area is the 2000-ha La Chacra ranch, 22 km east of the city of Trinidad. The fieldwork was funded by NSF Award SBR-9305629.

Research in Bolivia and other inundated savanna landscapes has suggested numerous factors which may lead to the formation of forest islands, including insect moundbuilding, natural fragmentation of levee forests, savanna colonization by forest species, afforestation of archaeological earthmounds, and anthropogenic fragmentation. I sampled and analyzed the vegetation, geomorphology, and soils of the forest islands and other landscape elements at La Chacra.

I describe the variety of forest island types present at La Chacra. These include higher loamy islands dominated by *Attalea* palms, low clayey islands with *Copernicia* palms, forest nuclei in the savannas, *murundu*-type islands formed by termites, pre-Hispanic artificial earthmounds, and gallery forest fragments created by recent human activity. The gallery forests on the levees of the senescent river (the Cañada de los Lagartos) revealed several major archaeological earthworks and abundant horizons of ceramics.

I conclude that the primary mode of island formation at La Chacra is the fragmentation and erosion of ancient natural levees. These islands are characterized by *Attalea* and have coarser soils than those of the wetlands. Other natural processes such as termite mound formation and tree grove establishment are common on the drier savanna, but do not create large forest islands. Midway between the pre-Hispanic gallery forest villages and the *Attalea*-type islands, lies an artificial island bedecked with largely deciduous trees. This mound was constructed by prehistoric Indians from the clayey subsoil of the adjacent wetland. Modern human activity has led to only limited instances of forest fragmentation into forest islands at La Chacra.

Preface

The following document is the result of 16 years of fascination with the land and life of the Amazonian plains of northern Bolivia. As I write these words, over half of my life has been spent in the pursuit of knowledge about the organisms and landscapes of the often flooded, often dusty, and almost always cattle-trodden, lands of the Department of the Beni.

I that knew that I wanted to work on *El Beni*[1] when I was 15 years old and made my first collection of the frogs and toads I encountered under palm logs, in swamps, and on the streets of Trinidad. I later read a book by a geographer named Denevan and learned to call this savanna-dominated region the Llanos de Moxos. This book was the only one in any language that dealt with the geography of the region; however, I clearly remember thinking "what a shame Denevan's a geographer, not a soils scientist or ecologist"!

The trick was settling in to an academic discipline and a developing a honed-down research topic. My fascination with the Moxos cattle ranching life led me to enroll as an Animal Science major at Cal Poly-San Luis Obispo, with the aspiration of becoming a veterinarian. However, my life-long interest in wild creatures soon persuaded me to change majors to the field of Environmental and Systematic Biology. Here I found that I had a knack for plants, not just creepy-crawlies. My craving for Botany eventually led me to the University of California-Davis. I never enrolled in Botany. Instead, I found a field that combined plants and cattle culture: Range and Wildlands Science. I eventually completed a B.S. and a M.S. in this field. At Davis, I finally "discovered" geography in a plant geography seminar led by Conrad J. Bahre.

I was encouraged by Bahre to pursue a Ph. D. in geography under Denevan. I thought it would be a good idea and began to take as many geography courses as I could fit into my schedule. I wrote Denevan a simple letter asking if he was still interested in savanna ecology and the Llanos de Moxos. He responded with an even simpler response: "Yes!" That was how it all began.

I came to Madison in 1990 and soon received a Latin American and Iberian Studies Program Short-term Research Grant for eight weeks of exploratory work in the Llanos de Moxos. Thus, I went to the Beni in 1991 to examine the relationships between vegetation and causeways. However, I was more impressed with the dynamic fluvial geomorphology along the Maniqui River at the edge the Beni Biosphere Reserve, where I strengthened my conviction that all so-called flood savannas were inherently dynamic landscapes.

I did not stop to examine any forest islands during this tour; however, I did take quite a few slides of termite mound islets. I also learned that the *curichi*[2] at El Sol (the ranch immediately west of La Chacra) was actually a long, weakly meandering palaeochannel, when I looked at an airphoto at the owner's home in Trinidad. Later I would learn that the *curichi* is really a *cañada*[3] around which much of my future would revolve.

It was on January 9th, 1992 that I "saw the light" and chose forest islands as my objects of focus. I was in the office of my thesis adviser, William M. Denevan, discussing a seminar paper I had written on fluvial geomorphology and vegetation in the southwestern Amazon basin. He had written a comment about whether or not one could distinguish between natural and artificial forest

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[1] The name generally used to refer to the Departamento del Beni. *Departamentos* are the first-order political divisions of the Republic of Bolivia.

[2] A general term for any localized wetland or swampy spot in the landscape. Also *curiche*.

[3] A semi-permanent wetland occupying a palaeochannel scar or recently senesced river channel.

islands from air photos. I told him that that was “a good question.” It then dawned upon me with an unusual sense of clarity that this was going to be the theme of my dissertation. I rushed out and purchased a new composition book, sat down somewhere, and began to write down my brainstorm. “The Islas of the Llanos de Moxos: Origins, Classification, and Geo-ecological Role” was at the head of the first page (actually it was “Las Islas de los Llanos de Moxos: Orígenes, Clasificación y Papel Geo-ecológico”).

Carl Troll (1936) believed (his italics) that *“one of the fundamental questions for the ecological understanding of savannas is that of which factors, in particular, determine the existence and absence of trees and forest islands.”*[4] I also believe that this is true. Thus, at least in the perspective of the founder of landscape ecology and an under-appreciated savanna geographer, forest islands are clearly important elements for understanding savanna landscapes.

At the time I decided to study forest islands, I had never really examined one up close. I still have a vague memory of visiting La Isla de los Lobos[5] at El Tajibo[6] when I was 15 years old (see Map 2). This isla was a mysterious place, far off across a swampy pampa[7]. I remember vaguely that it was high ground and, perhaps erroneously, that there was a pool of water in the center. I do remember more clearly something about eating oranges there. Now La Isla de Los Lobos is only a few hundred meters away from the Trinidad-Santa Cruz highway. I remember very well entering another isla just north of the house at El Tajibo. It was another world in that isla. It looked like a “real jungle” in there. It was shady and moist; the ground was covered with greenery and the soil was dark and organic rich. Here I saw my first wild primates, a trio of owl monkeys up in a motacú palm[8]. On the ground we recovered the skull of a sloth. I remember searching the branches and twigs around the perimeter of the isla for *Anolis* lizards. Now this island is in direct contact with the highway right of way.

By the end of 1992, I had submitted my NSF Doctoral Dissertation Award proposal. On the last day of June 1993, my wife Susy, daughter Jacqui, and I were off to Bolivia, without knowing whether or not I would actually receive funding.

On August 2, 1993, Bill Denevan walked onto the tarmac at Aeropuerto Jorge Henrich Arauz on the outskirts of Trinidad. He was returning to Moxos after more than three decades since his dissertation fieldwork. It was only then that he told me that NSF had decided to grant me the Dissertation Improvement Award. I had already chosen La Chacra as my study site.

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[4] All translations are my own, unless otherwise noted.

[5] The “Island of the Wolves.”

[6] Ranch owned by Ernesto Sanjinés and Olga Velasco de Sanjinés, 13 km E of Trinidad.

[7] *Pampa* is the term used in eastern Bolivia to denote a grassland, wetland, or savanna. The word *sabana* is not used in Bolivia. *Pampa* is in fact a word of Quechuan origin and denotes any flat, open landscape.

[8] *Attalea phalerata* Mart. ex Spreng.

Chapter 1. Introduction

General Principles of my Research

This work is not intended to be an ending point, but rather a point of departure for further research and reflection. The most basic objective of my research is to gain preliminary understanding of a place (La Chacra) and to examine the fruits of this understanding in respect to questions of broad interest regarding the development and nature of biogeographical landscapes of the South American lowland tropics.

I must admit that I am the victim of topophilia, an inescapable fascination with a place, the place being the Beni. At the lowest level, one could argue that I simply wanted to spend time in an interesting place and engage in "exploration and discovery." This is true, and it should be true of any field-oriented geographer. However, I have broader interests that extend beyond an understanding of place. These include the determinants and origins of savannas, pre-Hispanic human impacts in the Amazon, and the ecological/biogeographical role of livestock in the American tropics. So with this in mind, I decided to orient my research toward the origins and ecology of forest islands in the Moxos savannas of the Department of the Beni in Bolivia.

I firmly believe in the value of knowing one place very well, while at the same time knowing enough about other places to be able to see one's particular locale in broader perspectives. I assume that the processes that occur at La Chacra occur elsewhere, and thus my data and interpretations should contribute to general theories of interest to geographers, ecologists, and others.

Some basic tenets of my geographical perspective:

1. Landscapes are the products of complex historical factor interactions.

    The weight of the each factor is case-specific.

    Factor interactions are generally significant.

2. Biotic factors, which include human activity, can influence physical factors and thus are not simply always the *product of* abiotic variables.

3. Humans and other organisms respond and adapt to variability of other factors, including organismal interactions, over time and space.

    These responses and adaptations may alter the biophysical environment in manners which create physical features that may persist after the local extinction of the organisms which created them.

My research thus embraces a holistic approach to understanding landscape evolution, without an *a priori* bias toward the primacy of any single factor or set of factors. My bias is the attempt to consider the totality of the environment, not just a certain subset of its components. Some reviewers may criticize the broad scope of such research, but I feel that it is necessary and that it reflects an essential geographical perspective that is often lacking from other types of research.

I also have a strongly historical bias in that I believe that all landscapes reflect a unique history of discrete events and continuous processes that occur at a particular point on the earth surface, even though some of the past history may not be directly decipherable from the present landscape.

These events/processes range in temporal and spatial scales from continental drift to individual raindrop impacts. The spatial variation of past processes and events has created the landscape diversity we encounter today

I examined a sample area (ca. 20 km^2) in the region known as the Llanos de Moxos in the Bolivian Amazon basin of Bolivia. The landscape units within this area were discriminated subjectively by their vegetation cover, soils, relief, and archaeological contexts. The subjective approach has been supported by Platt (1964) and Mueller-Dombois and Ellenberg (1974:33) as "strong inference." It is illogical to apply completely "objective" random sampling designs to phenomena that exhibit non-random behavior (Kershaw and Looney 1985:29). Although I do not subscribe to Clementsian community and succession concepts, I do believe that the human mind can identify unique vegetation assemblages that have real distributions over space and correlate with suites of environmental factors. Samples within distinguishable units are representative of at least some portion of the real world, regardless of how "subjective" they are.

I used my plot samples in combination with terrestrial reconnaissance to characterize the variability of vegetation at La Chacra. I consider the observed vegetation patterns in relation to factors such as drainage, relief, soil profile type, archaeological artifacts, livestock grazing, fire history, and present human activities.

One of my goals was to contribute towards a model that explains the evolution of the modern landscape mosaic of the Llanos. I, and others (Denevan 1966, Beck 1983, Haase 1991) believe that the vegetation of Moxos largely reflects soil and drainage characteristics, which are both largely determined by topographic position, which in turn is primarily determined by the history of fluvial and human activity. I do not wish to develop wholly empirical explanations, but intend to provide as much mechanism as possible. I therefore must consider the roles of an array of environmental factors and biological and human activities as they interact and vary over time and space at La Chacra

However, to provide mechanistic explanations it is necessary to consider how each of the environmental factors exerts its influence upon the landscape and how it interacts with the other factors. Thus it will be necessary to examine and discuss the biotic responses and feedbacks in the landscape. Physiological plant ecology (autecology) and plant/plant/animal interactions (synecology) are essential in understanding why the environmental factors are indeed significant.

We must also consider the influence of the vegetation cover upon "physical" processes. I hypothesize that there are significant vegetation-geomorphology feedbacks in the landscape. For example, the establishment of a single woody plant in a floodplain environment may create a sediment trap which leads to the creation of a relief feature that promotes further woody plant colonization, which in turn leads to greater accumulation of sediments and accelerated forest island development (cf. Ponce and Cunha 1993). On the other hand, channel avulsions may lead to decreased sedimentation, decreased nutrient input, lowering of water tables, death of trees, reduced forest cover, and accelerated erosion of natural levees, all leading to the disintegration of gallery forests and the creation of discrete forest islands (cf. Adámoli *et al.* 1990, Sennhauser 1991). These two examples of vegetation/geomorphology interactions illustrate how different processes and histories can lead to similar resultant features, in this case, forest islands.

Neither of the above examples involved any type of human influence. Human activity also leads to the creation of forest islands by both "degradational" and "aggradational" process, such as forest clearing and earthmound construction, respectively.

I will thus consider the roles of these three general agents non-human organisms, geomorphic processes, and humans in an attempt to explain the evolution of the forest island landscapes of the Llanos de Moxos.

Moxos as a Cultural Landscape

In the beginning…there was neither Man nor Woman. The human species entered the Moxos plains at a date yet unknown, but in rather recent times relative to the age of the plains themselves. We do not know how similar the Moxos plains discovered by the first peoples were to the landscapes we observe today, but we do know that they were different. There were no cattle, but there may have been large native herbivores now extinct. There were no roads, but later the early inhabitants would construct a causeway system that outdistanced the roads of the present. The climate may have been different; many rivers certainly had different courses across the landscape.

We do not know whether the first Moxeños preferred the forests or the savannas or simply utilized the resources of both as they saw appropriate. At some point, these peoples began to manipulate the environment by moving and accumulating soil into a variety of structures utilized for farming surfaces, occupation sites, burial sites, hydraulic control, and perhaps transportation. Also they excavated canals to connect parallel river systems, creating east-west waterways. These activities are crucial in explaining the modern landscapes of Moxos, but remain largely neglected by the recent biological studies of the region. I, however, do not intend explain the origins and evolution of these technologies, but the description of their long-term impacts and the mechanistic integration of their landscape functions into a general model of the Moxos landscape evolution is important to my research.

The Nature of "Nature" in Amazonia

The antiquity of human civilization in the Amazon basin and the long-term impacts of human activity on the landscapes of the basin are topics germane to the flurry of research regarding the origins and maintenance (i.e. conservation) of tropical biodiversity. Field research continues to demonstrate the highly "disturbed" nature of most Amazonian ecosystems by both human and non-human ("natural") processes such as indigenous forest management and fluvial activity, respectively (Colinvaux 1987, Balée 1989, Salo 1987, Sanford *et al.* 1985, Denevan 1992b, Stahl 1994).

The central Moxos pampas may well represent one of the largest expanses of abandoned agricultural land in the world. The evidence for intensive cultivation and earthmoving is overwhelming (see Denevan 1966, Erickson 1995). The evidence is especially strong when one considers that these features have been exposed to about seven centuries of depositional and erosional activity and some three hundred years of trampling by cattle. Certainly many former agricultural surfaces remain buried under the annual flood sediments or have been lost to erosion. Erickson *et al.* (1991) found raised fields buried under more than a meter of sediments in an area far from any major modern streams in southwestern Moxos east of San Borja. Many more are hidden beneath forests which developed over the abandoned fields (Erickson 1995).

The recognition of the dynamic nature of the environment has challenged some of the previous beliefs in unchanging and undisturbed ancient forests of the Amazon. We should also keep in mind that the Amazon basin contains vegetation formations other than evergreen, perennially moist forests. A variety of highly diverse semideciduous to deciduous woodlands, savannas, parklands, and wetland formations are also present in the Amazon. These non-"rainforest" landscapes and their forest islands are the focus of my research.

Definitions

What is a forest island?

In answering this question, we must first recognize that it is a matter of scale. The most simple definition of a forest island is an isolated unit of forest. We can imagine that there are larger units of contiguous, uninterrupted “continental” forest, many hundreds of thousands, or even millions of square kilometers in area. The so-called Amazon rain forest or Amazonian Hylaea may be one such forest, broken only by rivers, *campos*[9], and artificial clearings. Within this mega-forest, we have islands of savannas and disturbed lands.

North and south of the Amazonian forest core, there are large non-forest landscapes in Colombia, Venezuela, and Bolivia, known to geographers as llanos. The llanos are bordered by forested lands of some sort on all sides. These plains are not unbroken savanna; they are penetrated by gallery forest corridors and dotted with isolated forest units of various orders of scale. These islands of forest within the savanna matrix are the objects of interest in our discussion. In the Colombian and Venezuelan Llanos these forest islands are referred to as *matas*. In the Llanos de Moxos of Bolivia these common landscape features are known as *islas* (islands). In the Pantanal and Campos of Brazil, similar islands are known as *capões*.

What is an *isla*?

As used in the savanna regions of the Beni and Santa Cruz departments of eastern Bolivia, an isla is a patch of trees or shrubs in an otherwise open landscape, often upon a slightly elevated surface. While many islas are immediately visible on the ground as discrete units of wooded vegetation, there are large islas that are recognized only by walking through them or around them (or by viewing them from the air); however, local folks are highly aware of the difference between isla forest and non-isla forests. Landscapes where islas are important are referred to as *pampa-isla* (pampa is the term used for “savanna” or “grassland” in Amazonian Bolivia). Forests, both isla and non-isla, are referred to as *monte*. Tall non-isla forests are *monte grande*.

Islas are visually important landscape elements from both the ground and the air. They are utilized at the present time by wildlife, livestock, and humans, who all take advantage of their relatively flood-free situations and the shade and fruits they offer in the otherwise treeless plains. The modern human inhabitants of the savannas use the islas as sites for *chaco* or *chacra* agriculture (small rotational slash and burn plots), benefiting from the coarser-textured soils and the organic materials contributed by the forest vegetation. In the pre-contact period, many natural islas were occupied and enlarged by indigenous peoples. Some islas are in fact wholly artificial (see Denevan 1966: 64-72).

Islas exist on many spatial scales, ranging from ant and termite mounds, to small agricultural mounds, to large natural and artificial mounds covering several hectares, extended fragments of gallery forest hundreds of meters long, and larger units many square kilometers in area. The

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[9] The Brazilian Portuguese term for open savannas or grasslands.

processes leading to the evolution and degradation of the islas are of interest and hitherto undocumented in the Llanos de Moxos.

Many islas are purported to be remnants of natural levees of abandoned channels (Braun 1961, Beck 1983, Hanagarth 1993). Aerial observation readily supports this hypothesis. Natural levee forests can be observed in various stages of fragmentation along relict channels and the discrete islas are often arranged in chain-like patterns meandering across the pampas (Fig. 1). Examination of isla soils often reveals that they are much sandier than those of the surrounding pampas, suggesting fluvial deposition (Denevan 1966: 13; Beck 1983: 21). Other possible origins include compaction ridges and fossil dunes. Compaction ridges are formed where coarser sediments (e.g., sandy channel bottoms) become topographically inverted as the surrounding structures composed of finer sediments lose volume over time. These have been identified from the Rupununi Savannas (Sinha 1968) and in the Rio Blanco forest region of Santa Cruz, Bolivia (Navarro 1992). Fossil (as well as active) dunes are common around Santa Cruz de la Sierra and have been reported as abundant in the Pantanal of Mato Grosso (Klammer 1982) and in portions of the Orinoco Llanos, but have not been identified in the Llanos de Moxos.

Another important landscape feature in the Llanos de Moxos is the *loma*[10]. Lomas and islas are not interchangeable terms. Loma refers to a topographical feature, while islas are units of vegetation, which may or may not be on elevated surfaces. Any small mound, either natural or artificial may be referred to as a *lomita*. However, the term *loma* is used solely to indicate large, often truly hill-like mounds. The local people largely recognize lomas as artificial features. Although the locals often attribute the mounds to the Jesuits, many are clearly prehistoric (see Nordenskiöld 1913). A loma may occur within an isla or within larger units of forest; however, some very large lomas are found in open savanna, and thus may form islas.

In my experience, lomas simply look artificial; they are either too high and/or too steep to fit into the range of natural relief features. While I would readily concede that all features known as lomas in the Llanos de Moxos are artificial, they are often constructed upon pre-existing natural relief features.

Denevan (1966: 64) identified three types of artificial mounds in the Beni:

1) Artificial mounds [i.e., lomas], 3-16 m high and up to 300 m long;
2) Artificial islas, 1-2 m high and 10-50 m long; and
3) House mounds, less than 1 m high and 3-7 m in diameter.

Denevan also recognized natural islas, defining them most simply as “patches of ground high enough to stand above the annual floods” (1966: 8) and “scattered patches of forest on high ground” (1966: 15).

Erickson *et al.* (1991: 72), specialists in Moxos archaeology, provide the following definitions of isla and loma (my translations):

> “Isla: Low earthen structures in the pampas of the Llanos de Moxos. They probably originate from ancient natural levee formations. Many, if not all, were utilized as domestic occupation sites (and possibly cultivation fields) by the early inhabitants of the Beni and were increased in size over the years as the result of cultural activities. Now they have dense vegetation and are sometimes utilized for *chacos* (slash and burn agriculture).

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[10] Spanish for “hill.”

Loma: An archaeological site elevated above the natural surface. Dougherty and Calandra (1984) propose that lomas are formed by [a combination of] natural (natural levee formations) and cultural (accumulations of refuse and fill) processes. Some lomas in the zone of the Mamoré River are over 10 m in height and cannot be natural features.”

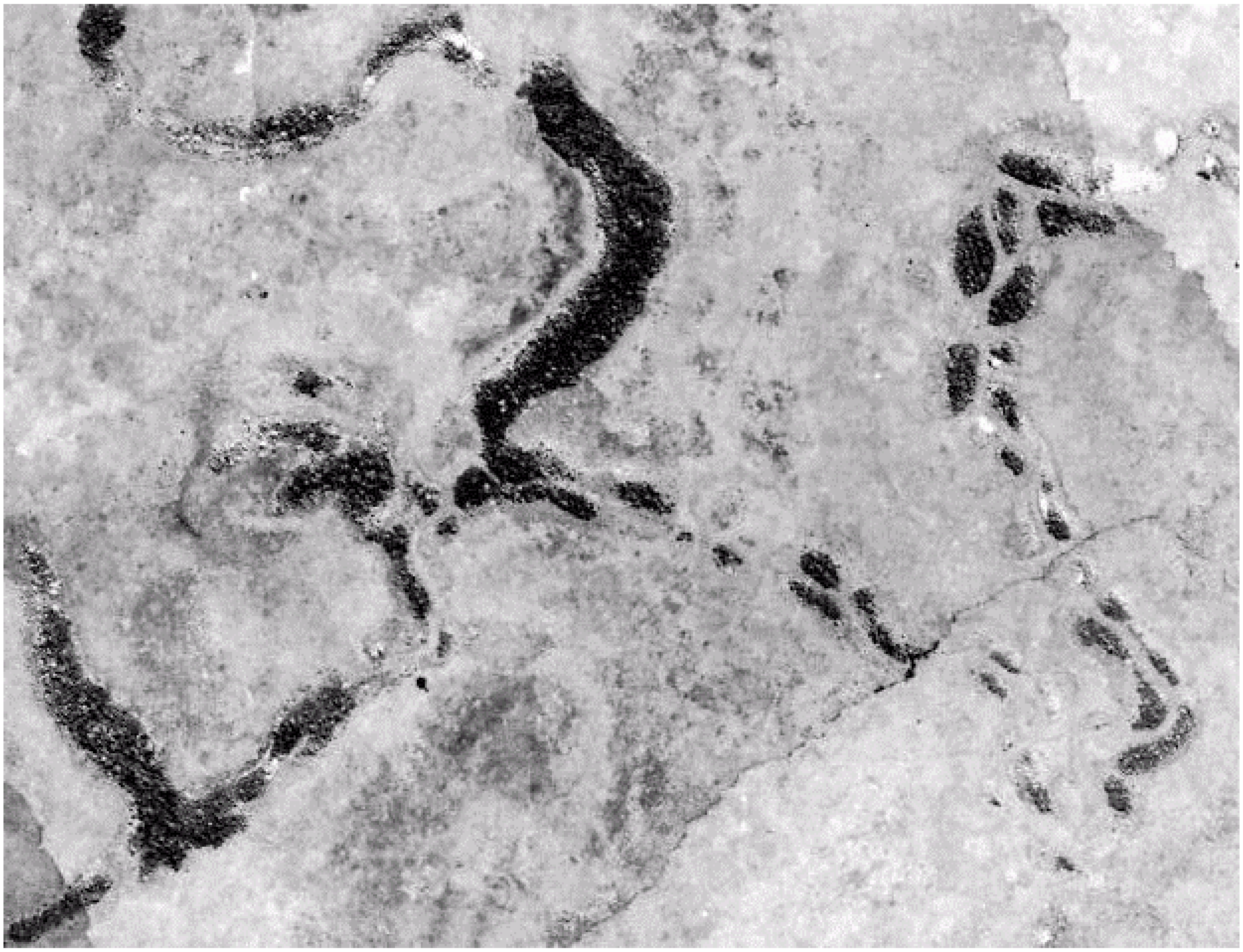

Figure 1. Digitized vertical air photo of gallery forest fragments (islas) associated with palaeofluvial system in the Llanos de Moxos, approximately 12 km west of the Río Mamoré, southwest of Trinidad. Source: Bolivia California Petroleum Company, *Mosaico preliminar*, Hoja 19-Z, 1958. Scale is approximately 1:23,530.

Pre-historic and modern human impacts

A central component of the study is the role of human activity in the origins and dynamics of the forest islands. I am not interested in the social significance or explanations for the archaeological materials which are present in many islas. I am interested in them simply as markers of human activity, specifically the temporal and geomorphological contexts of the artifacts. The essential questions are: 1) the nature of the surfaces upon which initial human occupations or activities are indicated, 2) the spatial and temporal contexts (where and when) of human activity in forest island formation, and 3) the significance of human activity as a determinant of present-day forest island ecology.

I believe that all forest islands in the Moxos region have been altered in some way by prehistoric and/or modern human activity, such as burning, agriculture, forest products harvesting, livestock, and settlement. However, human impact does not equal anthropogenic origin. Questions of the artificiality or anthropogenic nature of a given forest island will likely be answered as a matter of degree more often than by a yes or no. We can consider a forest island to be completely artificial if it can be demonstrated that: 1) either the dispersal or establishment of the trees present cannot be explained without human mediation, including the creation of raised surfaces in wetlands, or 2) the island can be demonstrated to have been created by the anthropogenic fragmentation (deforestation) of pre-existing forests.

Organization of the Dissertation

In the first section of the dissertation, I will review the pertinent ideas about the origins and ecology of tropical savannas and forest islands. Next, I will introduce the general physical geography of the Llanos de Moxos and set the context for the study site, La Chacra ranch. Chapter Four reviews the human geography and history of Moxos and the Chacra region.

Having dealt with the general background to the study, we examine the results of the field research in Chapters Five through Nine. The next task is to discuss and explain the processes and events which are responsible for the distribution of woody vegetation at La Chacra. Chapter Twelve is an analysis of the forest island components at La Chacra in the context of Neotropical phytogeography. The human impacts are discussed in the penultimate chapter. The final chapter summarizes the findings and places the results and discussion in broader contexts of the biogeography and landscape history of Amazonia.

Objectives

My research objective is to explain the origins and determinants of each forest island type identified in the study area. To do so, I will first describe the range of forest island types in a selected study area in the Llanos de Moxos. I will then examine the evidence for the possible island-forming factors as well as the determinants of the vegetation composition. Finally, I will use this evidence to make conclusions about island origins and determinants at the study site. The results of this study will contribute to the development of landscape historical and biogeographical knowledge of the Llanos de Moxos region specifically and Amazonia in general.

Methods

Site selection

I had anticipated examining three study areas in my original research proposal. After arriving in Bolivia, I decided to look at two sites. In the end, I stayed with only one, the cattle ranch known as La Chacra[11]. I had visited this site previously in 1979, 1982, and 1986; however, I knew little about it, especially about whether or not it even had islas. My most significant impression had been the shade of the tamarind trees and the abundance of their fruits in the winter season.I was more familiar with the adjacent ranch, El Sol, having visited it in 1991 during pre-dissertation exploratory fieldwork. After considerable rumination, I decided that I would accomplish the most by learning more about a single place rather than by learning a lot less about several places.

La Chacra Ranch, owned by Fernando Velasco Cuéllar of Trinidad, proved to be a convenient site for research. The ranch is only 22 km east of Trinidad, the capital of the Beni Department, and borders the 550-km Trinidad-Santa Cruz highway (Map 2). The owner was amenable to my research and tolerant of my habits and demands. The ranch workers and their families could not have been more friendly and helpful.

My first trip to the Beni during my dissertation work in 1993 was in the company of the Venezuelan savanna ecologists José San José and Rubén Montes, Venezuelan formicologist/zoologist Pedro Salinas, and my wife Susy. I had met these noted scientists at an international zoological congress in Santa Cruz de la Sierra, the largest city of the Bolivian Oriente[12] and where Susy's family lived. We traveled about in a Toyota Land Cruiser generously lent, with driver, by the Universidad Técnica del Beni. On our last day we sped by La Chacra, unimpressed by anything visible from the road and completely unaware that it would become the focus of my attention for years to come.

On our second trip to Trinidad, in anticipation of Bill Denevan's arrival, Susy and I went out to La Chacra at the suggestion of its owner, who claimed it had plenty of islas. The weather was wintry, by Beniano standards at least. We were in the midst of a polar advection event locally known as a *surazo* (see Ronchail 1989). It was on July 28, 1993, that I first entered the islas of La Chacra. The cold wind blew across the open plain as if we were in some high latitude steppe, as I pulled my hood over my chilled head. The horses plodded lethargically over the deeply hoof-pocked and cracked surface of the desiccated wetland.

The first isla we hit was baptized Isla 1 (Map 3). From there we headed in a more or less straight line toward two palm grove islas and the next forest isla in the interior of the seasonal wetland (the *bajío*). The ground was still muddy and there was standing water around some of the *Cyperus giganteus* stands, but we made it. Isla 2 was surrounded by these huge South American papyrus sedges. Around one-half of the island there was a crescent of wet ground with shallow standing water, while on the opposite side a tongue of dry, firm ground with a dense cover of low grasses extended away from the tree island. Borrow pit or channel scar? I had no idea, but I was very excited indeed.

We remained in Bolivia between July 1993 and June 1994. Susy and Jacqui lived in Santa Cruz de la Sierra, while I commuted via a 13-hour bus trip between Santa Cruz and La Chacra every few weeks.

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[11] Spanish term for a farm that produces fruits and vegetables, also refers to swidden agriculture plots.

[12] The *Oriente* refers to the eastern lowland region of Bolivia.

Vegetation studies

Plants are one of the most dominant components of the landscapes we observe in the humid tropics. In flat places such as the Llanos de Moxos, trees are generally the tallest natural structures in the landscape, towering far above the low natural relief. The contrast between forested and non-forested landscape units is strong, as is the contrast between many types of wooded vegetation.

I examined the range of vegetation types present at La Chacra by walking and riding (horses) throughout the ranch over the course of 11 months in 1993 and 1994. I believe there is no substitute for this approach. Each excursion revealed something new; some significant species were not encountered until the very last week of my fieldwork. Repeat observation of sites over the march of the seasons is essential, not just for the collection of fertile material (which still was not possible for all species), but also for the understanding of the changing environment and changes in the visual composition of the vegetation.

I examined nine vegetation plots measuring 10 x 25 m in different woody vegetation types (Map 5). All woody or suffrutescent plants 1 m high or taller were mapped and measured for diameter at breast height (DBH, approximately 1.5 m above ground) or near base of stem for smaller or multi-trunked plants. Voucher specimens were alcohol collected for each operational species identified in the field, except for easily identifiable, well-known species. Additional plants outside of the vegetation plots were collected from diverse areas of La Chacra. I estimate that the collected material represents between 25-33% of the woody species and 5-10% of the herbaceous species present at La Chacra; however, all dominant or otherwise notable species of the woody communities were collected or at least field identified.

All specimens were deposited at the Herbario Regional del Oriente Boliviano (USZ) of the Universidad Autónoma Gabriel René Moreno in Santa Cruz de la Sierra. I collected a total of 354 numbers. Identifications were made at the Herbarium by myself and the herbaria staff. Various plants were not available with fertile material and thus identifications were not possible for all species.

Most of the collected plants were shown to at least two ranch hands for identification of vernacular names. In addition, I frequently asked about the plants at La Chacra and the surrounding area in conversations over the course of the 11 months. Many shrubs could not be identified by the ranch hands, but most of the trees were known.

Topographic transects

I measured relative elevations by differential leveling using a Sokkia automatic level and rod, with the assistance of helpers (Pacho Carrasco and Armando Ruiz, both of Trinidad). We measured the depth of surface water at each rod position. Horizontal distances were measured with the stadia. Approximate compass bearings (relative to Magnetic North) of back sights were measured with a hand compass and fore sight bearings were measured with the circular angle scale of the level. This work was most gratifying, as we would rush home and crank out the calculations by candlelight and get instant results. We were often surveying in water up to our waists or cutting paths through the thickets with machetes. It was great fun. One day we ran out of daylight and I ran out of shoes and socks, staggering home barefoot and exhausted across 3 km of inundated savanna.

Archaeological surveys

I searched all areas and islands of La Chacra for archaeological remains. I accomplished this by excavating both randomly and strategically placed test pits, crawling about on hands and knees combing the surface, examining tree fall pits and the exposed roots, walking about on rainy days looking for freshly exposed materials, and examining materials excavated by burrowing animals.

Soils

I collected samples of soil materials from different forest island types, non-forest units, as well as from termite, ant, and artificial mounds. In all, 108 samples were collected from 38 sites. Basic descriptions of the soils were made in the field. I carried out particle size analyses on 18 representative samples by the pipette method at the University of Wisconsin Geography Department geomorphology laboratory. The sand fraction was analyzed by sonic sieving.

Wildlife and livestock observations

Another important component of this study is my observation of the native fauna and the introduced livestock. These organisms are all important components of the biogeographical landscape and deserve attention as such. I encountered native mammals on a daily basis during my other activities.

We will now review the most pertinent arguments and debates regarding the origins and ecology of savannas and forest islands in the Neotropics.

Chapter 2. The "Savanna Problem"

Geographers and, later, ecologists have long debated the origins of tropical savanna landscapes. The existence of a savanna in the humid tropics is often treated as an anomaly, while forests are considered the "normal" or "zonal" vegetation. However, within the savanna zones or so-called savanna climate regions themselves, the occurrence of isolated patches of forest is the anomaly. It is these forest islands which are the central theme of this dissertation. Thus, we will review arguments both for various savanna determinants as well as the occurrence and origins of forest islands within tropical savannas.

The word "savanna" was originally used by the pre-Hispanic peoples of the island of Cuba to denote a flat, open landscape. Today, this term is widely applied, yet poorly defined. Many ecologists include tree-grass mosaics of temperate North America as savannas as well; however, savannas are typically tropical formations.

Savannas are obviously non-forest formations, and in humid tropical America, almost all non-forest lowland vegetation formations, ranging from marshes to woodlands, are often considered "savannas" in the broadest sense. Another distinction can be made between "parklands" and "savannas." A parkland is a mosaic of forested and non-forested units which occur on surfaces with unique relief, drainage, and other characteristics (*sensu* Walter 1979: 75, Bucher 1982: 66)[13]. Forest islands are an inherent part of these parkland landscapes. Such landscapes contrast with savannas where the *trees are part of the savanna.* A forest island, by definition, is an entity apart from the savanna. A forest island is not a dense grove of "savanna" trees, but rather an isolated unit characterized by forest species. A clear example of this situation is provided by the hardwood hammocks of the Florida Everglades. The forested *cordilheira* ridges in the Pantanal wetlands are another example (see Wilhelmy 1958a, 1958b, Dubs 1992). Neither the Everglades nor the Pantanal are traditionally considered to be savannas; rather they are most often considered to be wetlands.

Review of Savanna Determinants

Human activity

Many savannas are popularly believed to be the result of human activity. Gerardo Budowski (1956) argued that the Neotropical savannas were largely anthropogenic. Carl Sauer (1958) envisioned the American tropics not as a New World, but rather as the home of prehistoric human cultures and argued for the extensive use of intentional burning which resulted in the savannization of considerable areas. Under Clementian perspectives, such anthropogenic savannas are considered to be "disclimaxes" maintained by repeated human disturbances where forests should otherwise dominate.

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[13] Prado *et al.*(1992:460) discussed parklands in southern Mato Grosso: "These consist of small to large islets or groves of tress, up to 50 m in diameter. The wooded areas are enclosed within a matrix of grassland consisting of *Elionurus muticus…*"

Climate

Geographers have long recognized a “savanna climate” (Köppen’s Aw) which may predispose a region towards a dominance of non-forest vegetation. Seasonality of precipitation is generally a predisposing factor for the occurrence of savannas; however deciduous tropical forests are widespread formations in all the regions of Aw climates (or at least were in the historical past).

Microclimates and soil water regimes locally override regional climate influences and allow for “azonal” vegetation types. Mean annual precipitation and its temporal distribution do not in themselves “determine” vegetation. It is the plant available moisture regime in a given body of soil which is “perceived” by plants and this is dependent upon substrate characteristics and topographic position, not regional climate.

Savannas are found in areas with less than 500 mm as well as in areas with well over 2000 mm annual precipitation. The density of trees is not mediated by water availability within the range of precipitation regimes in the Neotropical savannas; forests occur in tropical regions with as little as 500 mm annual precipitation (Walter 1979: 70).

Fire

Fire does indeed promote savannization, but fires are not necessary for the maintenance of all savanna types nor are they always involved in savanna origins. The apparent rarity of natural fires in many areas of the humid tropics does not mean that natural savannas were unlikely, only that fire may not have been a proximate causal factor.

The antiquity of fires in the Neotropical savannas is demonstrated by the evolution of a myriad of plant adaptations and responses to burning, many more than could be expected to have evolved during the last 10,000 years or so (i.e., the period of human influence in tropical America). Certainly it may be argued that many features may be useful in response to fire, but evolved in response to other factors such as drought or herbivory (i.e., they are “exaptations” to fire, not adaptations; cf. Lacey, Walker, and Noble 1982).

Regardless of the frequency of prehistoric or pre-European fires, anthropogenic fires have become a background condition for most of the world’s savannas and certainly are highly important determinants of composition and structure. Such fires have also led to the expansion of savanna at the expense of forest formations and in many sites are responsible for maintaining pyrrhic “disclimaxes” or stable states.

Soil chemistry and nutrients

Soil toxicity (especially Al) and low nutrient availability have often been implicated as favoring savanna over forest, especially in the Brazilian Cerrado (Eiten 1982, Furley and Ratter 1988). However, the recent research has not shown this to be at all consistent (see Haridasan 1992).

The Llanos de Moxos gallery forests and forest islands are favored sites for present-day swidden agriculture due their more favorable physical and chemical characteristics relative to open herbaceous sites. Numerous studies demonstrate the prevalence of “better” soils (e.g. higher OM, higher base saturation and pH, better physical properties) under trees and forest than under adjacent grasslands (Kellman 1979, Isichei and Muoghalu 1992). Frequently, the enhanced soil properties are a product of the trees themselves. However, Blackmore *et al.* (1990) examined nutrient-rich woodland patches in a South African savanna and concluded that they are indicators of Iron Age human occupation sites.

G. Scott (1978) has demonstrated that anthropogenic tropical montane grassland soils in Amazonian Peru undergo rapid compaction, erosion, and nutrient loss after deforestation; however "these differences are not significant enough to inhibit the development of arboreal species in grassland given a long fire-free period." Eden *et al.* (1991) and Eden and McGregor (1992) also find that forest can readily recolonize abandoned agricultural and pasture lands in the Rio Branco savannas of Brazil.

As argued by Haase (1992), soil nutrient status does not limit tree growth in Bolivian savannas. Furthermore, D. Scott *et al.* (1992) have demonstrated that on "very nutrient-poor soils" in the Brazilian Amazon, rain forest productivity is not constrained by low nutrient levels nor do the tree species exhibit especially nutrient-stingy strategies. Low nutrient status is essentially a background condition in the Neotropical landscapes, not necessarily a primary determinant of savanna/forest boundaries (cf. Medina and Silva 1990).

Soil nutrient status, while not determining vegetation structure, may have, however, a much stronger role as a determinant of species composition. Species “adapted” to low-nutirent environments, being displaced by nutrient-hungry weeds on richer soils: *Curatella* is an example of a nutrient-stingy sclerohyll that is ubiquitous on poor savannas, yet absent from rich flood plains

Drainage

While regional climates may indeed be predisposing factors, local drainage and soil moisture regimes are often highly important in determining actual positions of savanna/forest boundaries in the field (i.e., the “real world” as we can perceive it from the ground or air). The effect of 1500 mm of rainfall upon deep sandy profiles is quite different from that upon shallow claypan profiles. Likewise, a given quantity of rainfall has rather different consequences on a ridgetop than in a local depression. Thus, soil drainage, mediated by both edaphic and topographic factors, is of primary importance in determining the distribution of individual plants species and the formations these comprise.

We should first recognize that “floods” in themselves are not inimical to forests. Flooded forests are widespread in both temperate and tropical regions of the world. In Amazonia, various types of seasonally flooded *igapó*[14] and *várzea*[15] forests occupy extensive areas. In these forests, flood depths often exceed 10 m and flood durations may last over six months. So why would shallow ponding of water for only two or three months promote savannas in other localities?

Oxygen content and temperature of floodwaters are important in determining plant survival. Cooler, well-oxygenated water is much more favorable than hot, poorly-oxygenated (or even anoxic) water. Flowing river water is rather different than stagnant, ponded water. The latter is typical of seasonally-inundated savannas, while the former is more typical of flooded forests.

Beard (1953) argued that the alternating periods of prolonged flooding and drought which characterize many American savannas is a sufficient cause for the existence of natural savannas due to the relatively small number of woody species which are able to tolerate this combination of

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[14] Brazilian term for blackwater floodplain forest.

[15] Brazilian term for whitewater floodplain forest.

physiological stresses. This argument is not strictly climatological, as topography and soils have major roles in determining the water regime of a particular site.

Bucher (1982) described quite well the factors which control the balance between woody and herbaceous vegetation in the Gran Chaco. His discussion is rather applicable to the Llanos de Moxos as well. He notes the existence of edaphic grasslands and the significance of present and past alluvial processes. Then he discusses the role of fire and the impacts of overgrazing, with the latter leading to "the fast invasion of grasslands by woody vegetation." Bucher observed that "true savannas…are rare and locally restricted in the Chaco" and that "the predominant vegetation type is that of a parkland" (p. 66). The same could be said about the Llanos de Moxos. As in Moxos, "true savannas" in the Chaco are found where micro-topography provides patches of elevated ground upon which woody vegetation grows in an herbaceous matrix. However, this situation could be thought of as a micro-scale parkland where the herbaceous vegetation and the woody vegetation occur on distinct surface units (e.g. termite mound islets).

Heinrich Walter (1979: 75) discussed the occurrence of parklands. The *mbuga* of Tanzania are characterized by alternately wet and dry black clay soils underlain by a hard layer of iron concretion at a depth of 50 cm. The summer rains take months to drain away from the inundated grasslands of the *mbuga*. Trees grow upon slightly elevated areas with a thick, red, sandy loam. Although Walter did not explicitly define the term "parkland," he did indicate that parkland is a "mosaic of two different plant societies" (here in reference to African "termite savannas"). Walter also mentioned the *matas*, which are small scattered woods, of the Llanos del Orinoco. These are equivalent to islas (see Sarmiento 1984: 6, 80). They frequently occur where *arrecife* (indurated lateritic pans) is absent and tree roots have a greater rooting depth, not necessarily on relief features.

Sarmiento and Monasterio (1975: 240) indicated that the patchy occurrence of perched water tables above impermeable soil layers such as iron hardpan is responsible for the "complex vegetation of forest groves in a savanna matrix, leading some authors to believe that this parkland physiognomy is evidence of a formerly contiguous forest recently reduced by man's action." Sarmiento and Monasterio believed that the distribution of forest islands is not at random, as they would expect if the islands were relicts of human-destroyed forest. I must, however, disagree with this latter point. Human activity is rarely, if ever, truly random, especially activities associated with land clearing for agriculture or pastures.

Riezebos (1984) promoted a holistic approach to understanding the origins and maintenance of savanna landscapes, emphasizing that one should not rely upon the primacy of any single factor as *the* determinant of a given savanna, let alone savannas in general (cf. Hills 1969). Riezebos viewed savanna maintenance as a reflection of "an existing equilibrium between the system components." The components include geomorphological processes that may or may not be independent of the vegetation. He also provided further evidence that savannization can occur independently of climate change, suggesting the weakness of simplistic Pleistocene Refugia theories based on widespread climate-induced savannization.

Explanations for the Moxos savannas

The Llanos de Moxos as a region is essentially defined by the occurrence of extensive seasonally inundated savannas in Amazonian Bolivia, primarily in the Department of the Beni. The correlation between areas subject to inundation and the savannas is highly significant.

In 1845, the renowned scholar and traveler Alcides D'Orbigny (1992: 89-90, 110) noted that the vegetation of Moxos was less varied than other regions due to the extent of seasonally flooded *bañados* (low-lying depressions) which are dominated by graminoids. He described Moxos as "a collection of plains upon which, here and there, isolated forests can be seen, these occupying the highest ground, where the annual flood waters do not reach." D'Orbigny also noted that the "small prominences which normally separate streams are completely foreign to the region." He then challenged the "overly systematic geographers who want there to be a mountain range between every channel of water" to explain the lack of apparent watershed divides in the Moxos plains.

Agronomist Otto Braun (1961: 2) rejected fire as being the primary agent responsible for the existence of the Moxos savannas. Instead, he proposed that the poor drainage of the heavy clay soils may be the causal factor:

> "The combination of a relatively dry and impermeable subsoil allow the shallow cover of water to only slowly infiltrate or evaporate after each rainstorm, this fact perhaps explaining the hostility of the *pampa* [savanna] for the plant species of the *selva* [forest]."

Denevan (1966: 16-17) believed that fire is important in determining vegetation species composition, noting that all *pampa* and *arboleda* (scrub savanna and woodland) tree species are fire tolerant. Denevan suggested that much *arboleda* is on former forest sites degraded by annual burning and estimated that at least 25 % of *isla* forest is secondary. He concluded, however, that the degree of flooding as determined by local relief is more important than fire regimes in determining the basic pattern of vegetation (i.e. spatial distribution of forest islands).

Plant taxonomist and ecologist Stephan Beck (1983) is one of the foremost authorities on the Moxos flora, having spent considerable time in the field and at the Herbario Nacional in La Paz since 1979. Beck's doctoral dissertation was a detailed phytosociological study of the non-forest vegetation of the Estancia Espíritu, located in central Moxos just south of the Yacuma river.

Acknowledging the work of Nordenskiöld (1913) and Denevan (1966), Beck (1983: 28) noted that "large areas of the flood savannas were covered with small raised field and ditches, as well as by causeways and canals." However, he did not discuss the potential impacts of such human activity upon the vegetation formations he described. Nevertheless, he also found that "it is reasonable to suppose that a fundamental transformation of the vegetation distribution had already begun in pre-Columbian times."

Beck (1983: 29) considered that "it is likely that there was much more forest in the Beni lowlands (Moxos) prior to settlement than there is today," since he could find no satisfactory combination of natural factors that could "hinder the growth of trees in large areas of the flood savannas, if not for the fact that the inhabitants and their domesticated animals had already been at work for hundreds or perhaps even thousands of years."

Beck (1983: 29-30) summarily discredited the abiotic constraints of seasonal flood stress, seasonal drought or extreme water table fluctuations, and the presence of rocky substrate or lateritic horizons as being responsible for the lack of trees on the open plains. We shall presently discuss these factors and refute Beck's conclusions.

In terms of flood stress, Beck (1983: 29) noted the existence of seasonally flooded *várzea* forests and the abundance of flood-tolerant tree species. However, the drainage and aeration of várzea and pampa differ greatly. The Moxos pampas are expansive plains underlain at very shallow depths by an impermeable compact and clayey horizon, while the *várzeas* occupy deeper and coarser overbank deposits of whitewater rivers (Pires and Prance 1985). However, flooded forests are also found on shallow, clayey soils in some Peruvian Amazonia floodplains (Oliver Coomes 1991, pers. comm.), so we must also consider the duration of floodwaters, seasonality of precipitation, soil and water nutrient levels, among other factors. Two important features of the pampa waters are their stagnation and high temperatures, in contrast to forest floodwaters, resulting in low oxygen and physiological heat stress.

Similarly, seasonality and drought stress are not directly comparable among regions without consideration of substrate differences. We know that trees are abundant in much “drier” (less annual precipitation) and more “seasonal” (greater range in temperature and/or moisture regimes) environments than those of Moxos, but Beck again did not compare specific sites with comparable soil and drainage conditions. Few woody species tolerate the combination of prolonged inundation followed by drought. Heavy clay soils, such as those of the Moxos pampas, offer little plant available water during the dry season. Beck noted an absence of underlying rock or laterite barriers to tree roots in the Moxos pampas. He is correct; however, dense clay pans and anaerobic conditions can also inhibit root penetration.

We could enumerate other biological and physical phenomena which can exclude woody vegetation, negating the need to invoke human activity as the primary determinant of savanna occurrence. For example, competition with dense grasses can also prevent the establishment of woody plant seedlings in both tropical and temperate savannas (Medina and Silva 1990, Momen *et al.* 1994). Nevertheless, Beck (1983: 30) preferred to argue that “numerous factors support the hypothesis of large-scale deforestation in pre-Spanish times, above all:

> [1.] the clearing and continual cultivation of raised-bed agricultural fields,
>
> [2.] the wood requirements for house construction and cooking,
>
> [3.] the millennia of hunting for game with the aid of large-scale, systematic, intentional burning, [and]
>
> [4.] the endeavor to keep the surroundings of settlements free of forest and bush in order to prevent the encroachment of uncontrolled fires.”

I consider Beck's suppositions concerning the extent of pre-settlement forests and the role of human impact to be speculative for the following reasons:

1. Beck's first line of support for human influence is erroneous. Raised field agriculture was not practiced on forested, better-drained sites, but rather in seasonally-flooded basins that are free of woody vegetation. Denevan (1966: 94-95) suggested that raised field agriculture in wet grasslands may have been more efficient than clearing forests without the benefit of metal axes;

2. The requirements for fuelwood and construction materials in Amazonia have certainly not led to massive deforestation, even in modern times (although in other parts of the world they have led to devegetation of semiarid landscapes);

3. Over thousands of years, the cumulative “erosion” of forests edges by repeated burnings certainly may be significant, however the data are lacking to demonstrate this. In fact, after thousands of years, we might suspect that fire-resistant vegetation would have developed in the forest/savanna ecotone. Modern grass fires for forage management do not severely affect forested areas and there is no evidence for greater impact in the past. Forested islas surrounded by annually burned grassland persist on cattle ranches throughout Moxos. Troll (1956) commented that the boundaries between grassland and moist forest are very sharp

> in the Llanos del Mamoré (Moxos), the Pantanal, and several African flooded savannas since the regularly occurring savanna grass fires cannot penetrate the moist forests without grassy undergrowth. Fire penetration into pre-Columbian forests was likely significant only during exceptionally dry years, as is true today.
>
> We must keep in mind that burned forests do not simply disappear or become anthropogenic savannas unless high-intensity tree-killing burns are repeated at some minimum recurrence interval or long-term management systems are introduced which preclude the redevelopment of forest plants. However, the prehistoric raised field peoples mostly were not farming the forests; they were farming the wet pampas. Also, slash and burn agriculture in the forests does not lead to a retreat of the forest boundary. The swiddens are cut from the interior of the forest, not the edge (cf. Eden 1986). Beck's postulated widespread deforestation in Moxos cannot be attributed to slash and burn agriculture in either the past nor the present, although local deforestation has certainly occurred; and
>
> 4. Clearing around home sites is certainly probable, but of limited spatial extent. We should also recall that many home sites were on artificial mounds, some within the gallery forests, some within the savannas, but not at the forest/savanna boundaries.

Haase (1992) described soils from lowland savannas in the Department of La Paz and concluded that the spatial variability of the soils was largely the result of the vegetation, not that soils determined vegetation patterns. He cited the Blydenstein (1967) and Askew *et al.* (1970) to corroborate his conclusions, however I cannot agree with this interpretation. To conclude that two soils are "the same" or "similar" on the basis of USDA taxonomic classifications is likely to obscure differences that may be ecologically significant. Haase noted thus that "the same soil class or even subdivision was found to support both gallery forest and grassland." However, I cannot see how it is at all possible to claim identical soil environments on well-drained natural levees and poorly-drained floodbasins. Haase believes that grasslands on the better drained soils of his study area are the "consequence of deforestation, grazing, and frequent burning." Thus, we may conclude that any forest islands on the same better-drained soils are true forest fragments.

Haase's primary conclusion, however, is that the water regime is the primary determinant of soils and natural vegetation patterns. He then concludes that the water regime was "closely related to topographic position." We may thus conclude that topography is a primary determinant of soil and vegetation patterns in the savannas of the Bolivian Amazon. To understand the landscape, it is thus necessary to understand the determinants of the topography. We may then postulate that where the vegetation does not fit the topography/water regime, anthropogenic causes are suggested.

Forest islands

The literature on forest islands in tropical savannas is rather limited. There are no general reviews which examine these phenomena on a intercontinental scale. We will review ideas related to forest islands in Neotropical savannas in terms of the processes credited as the primary determinants of forest island origins.

Reports of islands in flooded savannas in Moxos and the Pantanal date to early Spanish chroniclers of the 16th and 17th centuries. Cabello Balboa (1600-1604?, in Jiménez de la Espada

1965:2:115) observed that the Llanos de Moxos (Paitití) was “a province populated as copiously as claimed by the reports of that archipelago it contains, being called as such because its greater part is known to be lakes with well-populated islands.” Recio de León reported in 1623 that in the land of Paitití there was a “great lake, caused by all the rivers in very flat lands, and that therein are many islands populated by infinite peoples” (in Maurtua 1906:11:250-251). Today these islands are largely uninhabited, but many yield abundant archaeological evidence to support these reports of once-great populations (cf. Nordenskiöld 1916, Denevan 1966, Dougherty and Calandra 1984). Holmberg (1969: 3), who researched the Sirionó peoples in the forests east of the Chacra region between 1940 and 1942, mentioned that “the extensive llanos of Mojos, located from the Río Blanco west to the Rio Mamoré, are dotted with the island forests once occupied by Indian groups.”

Erland Nordenskiöld (1916) reported that indigenous peoples in Moxos built numerous mounds for protection during the flood season; however, he speculated that these were probably agricultural and ceremonial (i.e. burial sites) in origin, noting that the effort required to create such large mounds was not efficient just to create dry living space. Nordenskiöld presented no definitive evidence for exclusively artificial origins of these mounds, except that they are often right-angular in shape, associated with cultural horizons, and adjacent to depressions interpreted as borrow pits. These allegedly artificial mounds were distinguished from the islas (forest islands), which he interpreted as natural elevations.

Alleged Origins of Neotropical Forest Islands

Termite and ant mounds

Termites and ants are renowned as earth-movers and mound builders in a multitude of environments. Termites are especially important in tropical savannas.

Carl Troll (1936) discussed the phenomenon of *Termiten-Savannen* in Africa and South America. He wished to show by his examples that (his italics) “*the soil differences that are brought about by the geological activity of termites and leaf-cutter ants can control the distribution of forest and bush islands in savannas.*”

Troll distinguished between *Trocken-savannen* (dry savannas) and *Überschwemmungssavannen* (flood savannas), where there are significantly different ecological relations between forest islands and their surrounding herbaceous formations in each case. “Dry savannas and flood savannas offer at first sight, a very similar park landscape with gallery forests and scattered forest islands;” however, Troll noted, they are actually very different. In the case of the drier and sandier Pampa de Santa Cruz near the southernmost edge of the Amazon Basin, gallery forests are restricted to the narrow river valleys of the Piraí River and its tributaries. The forest islands here occur where there are moister soil conditions. The islands are forests of low, predominantly deciduous trees and, on the drier parts, candelabra-type cacti. The gallery forests, however, are tall and contain numerous rain forest species.

In the flood savannas, however, these relationships are reversed. The gallery forests in the north of Santa Cruz (to the immediate south of Moxos) are restricted to the better-drained surfaces created by natural levee formation and the forest islands are found (Troll's italics) “*not in depressions, but rather on flat soil prominences.*” Here Troll first cites the local terms *isla* and *pampa isla* in reference to the flood savanna landscapes. *Islas* support dense moist forest on their "more favorable, lighter, aerated, sandy soils." These islands have an average diameter of only 6 to 8 m.

In some areas, they are only 30-40 m apart. Each island contains the nest of leaf-cutter ants and the open trails of these ants radiate outward from all sides. These islands contain common trees such as ambaibo (*Cecropia* spp.), motacú (*Attalea phalerata*), totaí (*Acrocomia aculeata*), bibosi (*Ficus* spp.), and bombacaceous species (*Pseudobombax* and *Chorisia*). The edges of the islands are dominated by melastomataceous shrubs, as also observed by Beck (1983) in Moxos. Troll believed that "most of the islas of the Llanos del Mamoré [Moxos] owe their existence to leaf-cutter ant nests," although he never actually saw these islands in person (the botanist Werdermann, who had collected extensively in Moxos, personally confirmed this to Troll).

Troll (1936) fully recognized both the importance of natural islas for traditional cultivation and cattle ranching and the existence of pre-Hispanic earthworks. He believed that the ancient human inhabitants of Moxos may, in part, have owed the idea of artificial mound construction to the even more ancient inhabitants of the flood savannas, the leaf-cutter ants.

Herbert Wilhelmy (1958b) described the Pantanal of Mato Grosso, Brazil as a "genuine flood-savanna" where forest islands are "a clear sign that the land rises above the average flood level." He investigated dozens of circular forest islands (*capões*) in the middle of open *campos* and invariably concluded that they were overgrown termite mounds. He observed that abandoned termite mounds become flattened and resemble the artificial mounds (*aterrados*) constructed by indigenous people in some parts of the Pantanal and in the flood-savannas of Marajó Island.

Wilhelmy repeatedly observed that the development of woody vegetation upon old termite mounds followed a similar succession: the first colonist was the carandá palm (*Copernicia alba*), followed by the strangler fig (*Ficus* sp.). Eventually the palm dies while the fig remains as a "mighty, widely-spreading tree," in whose "shadow the cattle gladly rest at midday." Wilhelmy considered that the only example of "true *termite* flood-savannas in South America are those of the southern Pantanal." In the northern Pantanal, he observed that the flat mounds (*murundus*) were created by leaf-cutter ants (*Atta*) as in the Pampa of Santa Cruz. The Pantanal ant mounds are not grown with *Copernicia* palms, but rather with irirí palms (*Mauritia flexuosa*).

In the humid Lamto Savanna of the Ivory Coast, weathered termite mounds serve as protected sites where forest species may become established due to the absence of fire and the concentration of soil nutrients (Menaut and Cesar 1982).

Bucher (1982: 67-69) discussed the edaphic influences of ants and termites in the Gran Chaco. The mounds of *Atta* (leaf-cutter ants) were found to be highly calcareous, low in organic matter, and unsuitable for agricultural use. Abandoned and flattened *Atta* mounds provide the only suitable sites for tree establishment in parts of the eastern and central Chaco. In the western Chaco, *Atta vollenweideri* mound density averaged 2.9 per ha, of which 0.85 were active. Diameters averaged 5.5 m and heights 0.4 m. An average of 1100 kg of soil per ha was turned up by the ants each year. In the central Chaco, nest density is even greater. *Camponotus* ants create mound densities of up to 2500 per ha in the periodically flooded grasslands of the eastern Chaco. Termites construct conical mounds about 1 m high by bringing fine materials from subsurface horizons.

Eiten (1982: 37-39) noted that the hillside wet campos in Brazil are often characterized by the presence of numerous round earth hummocks, occupying up to 80% of the wet campo area. These mounds are usually several meters in diameter and 0.3 to 1.5 m high. They may be as small as 1 to 2 m diameter and 10 to 20 cm high. Each hummock is topped by one or more termite mounds, although the very small ones may lack them. Eiten noted that there was yet not a geological or biological explanation for these hummocks. Whether the termites create the platforms or merely take advantage of them is still a subject of debate. The hummocks generally bear typical Cerrado vegetation, except for those near gallery forests. Eiten also describes hummocks of several meters diameter from the Pantanal; however, these are only 10 to 15 cm high.

In the flood savannas near Espíritu, Bolivia, Hanagarth and Sarmiento (1990) did not find termite mounds, but rather leaf-cutter ant (*Atta* sp.) mounds, as predicted by Troll (1936). These mounds, according to Hanagarth and Sarmiento, only add to the relief or expand the area of pre-existing forest islands, not creating large islands *de novo*. Hanagarth and Sarmiento believed that termites and ants create small forest islands "only in exceptional cases," and these largely on high, unflooded *pampa*.

Termite mounds, however, are actually rather abundant in many parts of the Moxos savannas (Denevan 1966, Beck 1983, Hanagarth 1993). Oliveira-Filho (1992a, 1992b) has presented new evidence to support termite origins for Brazilian *murundus* (wooded or forested mounds in seasonally-inundated herbaceous formations). Oliveira, however, recognizes that distinct combinations of numerous biotic and abiotic processes create morphologically and vegetationally similar earthmounds in Brazilian savannas. He (1992a) outlines three broad classes of *murundus*: 1) those of valley-side campos, which are the result of differential erosion, 2) those of "floodplains" where deposition by floodwaters is minimal, and 3) those "formed by running water deposition…where strong currents may be associated with the much larger hillocks [of the lower Gran Pantanal] locally known as *capões* and *cordilheiras*."

Oliveira (1992b) examined the "island effect" on plant communities of termite *murundus*. He found that only a small portion of the surrounding woody *cerrado* vegetation is able to colonize the earthmounds and suggests that the shallow rooting depth above the seasonally-flooded herbaceous *campo* is major limiting factor

Dubs (1992: 443-445) reports on termite mounds created by *Cornitermes snyderi* and *Rotunditermes bragantinus* in Pantanal forest islands. *Armitermes euamignathus* creates abundant 35 cm high cone-shaped earthen nests in herbaceous wet savanna

Ponce and Cunha (1993) have recently commented on "vegetated earthmounds" in the savannas of Central Brazil. They conclude that the larger earthmounds are largely created by differential flood deposition, while the small mounds are the result of termite activity and/or differential erosion. Ponce and Cunha describe a symbiotic relationship between the earthmounds and their vegetation. This is an important perspective, where a reciprocal relationship between plants and their substrate is seen. However, it is erroneous to assume that the earthmound/vegetation unit is eternal once established. Earthmound forest islands can represent shrinking habitats as well as expanding ones. Sedimentation regimes are controlled by numerous dynamic processes which may well change over time, especially in highly dynamic, low-gradient environments where some flood savannas are found.

Natural levee remnants

Waters draining from the Andes and the Brazilian Shield create numerous rivers in the Moxos plains. Many of these rivers are highly dynamic, and the landscape is marked by the scars of past avulsions (channel abandonment events) and meander migrations. Satellite imagery reveals gallery and meander belt forests as prominent indicators of active and abandoned rivers.

Wilhelmy (1958a) considered the crescent-shaped forested ridges (*cordilheiras*) of the Pantanal in western Brazil to be levee remnants which border the flooded *baías* (shallow seasonal lakes). Likewise, he interpreted the more extensive *terra firme* (upland) surfaces of the Pantanal as being derived from sequentially deposited laterally migrating levees and the planation of formerly higher and narrower levees.

Braun (1961: 3) was perhaps the first person to suggest that the Moxos islas are relicts of former gallery forest:

> "The existence of forest islands in the middle of the pampas is very easy to explain by observing them from an airplane. They almost always have the shape of a half-moon [i.e., crescent-shaped], as do the *curichis*, which indicates that they are remnants of ancient gallery forests."

The "curichis" Braun referred to are palaeochannel scars which accumulate rainwater and form local swamps. Braun was clearly implying that the forest islands correspond to relict natural levee or point bar deposits.

Denevan (1966: 13) considered some Moxos islas to be relicts of natural levees, as evidenced by their coarser surface soil textures, ranging from loams to fine sands which contrast with the typical clay loams of the pampa surfaces.

Dougherty and Calandra (1984), Argentinean archaeologists, concluded that most of the islas and even the higher lomas of Moxos are largely fluvial in origin. They described those near the Mamoré River as "mixed-growth mounds, not deliberately built, but growing upwards after aggregation of cultural debris and sediments of diverse origin (flood-borne clays, decayed vegetation)." However, these authors did not provide or refer to any geomorphological data to substantiate their hypotheses.

In the first self-proclaimed "geo-ecological" study of a Moxos landscape, Hanagarth and Sarmiento (1990) further supported the argument that islas are largely relics of natural levees or terraces; however, they also acknowledged the existence of pre-Hispanic artificial islands. The work of Hanagarth and Sarmiento does not provide any quantitative estimates of the areal significance of the different island types, however it does indicate that these *alturas* (higher surfaces) cover no more than 2% of the Espíritu area. Another type of island indicated by these authors are those of relict *semialturas* (intermediate surfaces), which support more open vegetation formations dominated by species with adaptations to more xeric conditions, such as *Copernicia alba*, *Machaerium hirtum*, *Tabebuia heptaphylla*, and *Tabebuia aurea*. I find it most likely that some islands of semialtura represent the later stages of natural levee degradation, as suggested by Beck (1983: 22-23), who demonstrated that some semialtura surfaces are likely the exposed B horizons of former forest island soils.

Ponce and Cunha (1993) conclude that fluvial deposition is responsible for the origins of many of the larger forest islands in the Pantanal. However, this deposition is believed to create isolated mounds *de novo*, not natural levees which later become fragmented into islands.

I do not believe that many, if any, of the trees in most of the forest islands have persisted as individuals or even as descendants of the trees of the former gallery forests. Numerous post-fragmentation/isolation/insularization processes interact to alter the composition of the former gallery forest remnants (cf. Adámoli *et al.* 1990, Sennhauser 1991). It is the presence of the elevated surface and the coarser textured soils that are important here.

Topographic inversion of channels / compaction ridges

Palaeochannel bed sediments are coarser than the sediments of either the adjacent levees, point bars, or floodplain deposits. Over time, these former channel beds may become topographically inverted, that is that they become the local high spots instead of the low spots. This may occur as the result of 1) bed armoring[16] which leads to differential erosion or 2) differential compaction of coarser and finer textured deposits. Such compaction ridges have been identified in the Rupununi savannas of Guyana (Sinha 1969) and are suggested for the Río Blanco forests of Bolivia (Navarro 1992).

Woody plant establishment in savannas

In some cases, isolated patches of forest may simply occur in the midst of a grassland or savanna on surfaces without any appreciable topographic or substrate difference from that of the surrounding matrix. Frequently in such situations, the balance between woody and herbaceous vegetation is largely a factor of fire and/grazing regimes. In these cases, trees may become established anywhere within the savanna or grassland matrix since they are not limited to restricted substrates or topographic positions. Such situations occur where seasonal inundation and drought cycles or soil resource patchiness do not limit tree establishment and growth in the herbaceous matrix. This is typical of subtropical and temperate savannas, but not tropical wet savannas.

Ecologist John Blydenstein (1962, 1967) examined forest islands in both the Venezuelan and Colombian Llanos. He distinguished between *relict forests* and *developing tree groves*. Relict forests were often "distinguished by their elongated shape parallel to the prevalent wind direction, due to the action of recurrent fires." The combination of predominantly northeasterly tradewinds and west to east drainage patterns result in the preservation of relict forest islands to the south of the larger rivers, which act as natural firebreaks. Consequently, the relict forests in the Colombian Llanos were most abundant in the most highly dissected regions. It should then follow that expansive poorly-drained savannas without significant topographic firebreaks should be more susceptible to frequent and widespread fires.

Developing tree groves were characterized by generally rounded shapes and outer margins of fire-resistant species. Blydenstein described a facilitation model of forest island development, where "a number of pioneer grove species…prepare the way for the establishment of tree species typical of the groves but never found in the open savanna."

Similarly, Kellman (1979) later suggested that pioneer savanna trees in Belize may significantly enhance soil conditions which favor establishment of other woody species. Such autogenic forest islands, independent of other factors, have not been suggested in the literature for Moxos.

Blydenstein (1962) believed that these *matas*, started by savanna trees, could develop into forest islands up to a hectare in area, dominated by trees such as *Copaifera*, *Vochysia*, and *Xylopia* which indicate more humid conditions. However, he could not find any evidence for growth in area of individual matas over an 11-year period, concluding that fires limit the expansion of the matas. Blydenstein never mentioned termite or ant mounds in his discussions of Llanos groves and islands; however, he did note that *Curatella* often occurred on a type of mound.

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[16] Shielding of the riverbed by a layer of coarse texured sediments which protects the surface of the abandoned channel bed from erosion.

Tectonic processes.

A remarkable feature of the Moxos landscape is the presence of numerous oriented lakes, which are often markedly rectangular in shape. Plafker (1964, 1974) and Allenby (1989) present evidence to suggest recent tectonic activity along orthogonal fractures in the underlying Brazilian Shield as the causal factor for the lakes and other linear and oriented surface features. River channels and savanna forest boundaries frequently demonstrate patterns consistent with those of the lakes. Local subsidence is believed to be responsible. Subsidence on the order of a few centimeters would have profound effects upon the flow of surface and ground water in the flat plains of Moxos. Large scale forest/savanna boundaries in Moxos may be locally explained by the drainage regimes resulting from this tectonic activity. Hanagarth (1993) believes that the origin of many seasonally flooded basins in the central Moxos plains are the result of such neotectonic processes. Forests would potentially develop on the resulting better-drained surfaces adjacent to the zones of subsidence.

Other natural origins

In upland or dry savanna landscapes, as noted by Troll (1936), forest islands may occur in topographic depressions or concavities where increased soil moisture availability during the dry season favors trees [e.g. Colombian Llanos (Brunnschweiler 1972), Surinam (Riezebos 1984)]. In Moxos, depressional areas with sodic soils are often dominated by xerophytic thickets known as *tusecales* (groves of *Machaerium* spp. usually in association with *Copernicia* palms). These localized forest island types are distinguished from better-drained and more mesophytic islas.

Gleason and Stone (1991) report on two types of tree islands from peatlands in the Florida Everglades. One type, dominated by *Persea borbonia* (Lauraceae), is believed to form by the grounding of floating peat islands. This hypothesis is certainly possible in the immense *Cyperus giganteus* wetland formations in permanently inundated basins of the Beni where floating islands with small trees (*Tabebuia nodosa*) are known to occur. The other type is a low, elongate island dominated by a holly bush and ferns which develops when woody plants become established on elevated microsites created by tussocks of fern rhizoids (somewhat analogous to the low mounds created by *Cyperus giganteus* rhizomes).

Human impacts

There are two principal mechanisms by which human activity may create forest islands: 1) the destruction of existing tree cover, which creates forest fragments; and 2) the promotion of tree establishment and growth, which creates forests on previously treeless sites, especially by the creation of raised surfaces and fire suppression.

Anthropogenic fragmentation of forests

Perhaps the image of most people when they think of forest islands is that of a *forest fragment* which is the result of historic human activity. Such forest islands are ubiquitous features in temperate agricultural landscapes. The biological consequences of forest fragmentation in Amazonia has been studied near Manaus in a massive experimental landscape where islands of varying sizes were created by clearing forests (see Bierregaard *et al*. 1992 for a summary). These islands bear little resemblance to most forest islands the Neotropical savannas, yet are invaluable for understanding the effects of the modern human transformation of forested landscapes.

Although swidden farmers are sometimes blamed for contributing to the fragmentation of forests, the research does not clearly demonstrate this. For example, Eden (1986) has shown that forest islands in Guyanan savannas did not demonstrate areal changes over a 30 year period, even in the face of increasing population and agricultural pressure. This maintenance of forest island boundaries is due to the fact that swiddens tend to be created within the forests, not along the edges. Forest islands in the Llanos de Moxos frequently demonstrate “hollowing” under swidden agriculture, but with the persistence of the forested edge.

Enhancement of tree establishment and survivorship

Human impacts which favor the establishment or growth of woody vegetation in savannas are numerous. Livestock grazing and/or reduction of fire intensity and/or frequency is responsible for woody plant increases in subtropical savannas (Morello 1970, Bucher 1982, Archer 1990) and in the Llanos of Moxos (Beck 1983, Erickson 1995). However, the primary human impact which has fostered forest island development in the Llanos de Moxos and other flooded savannas of the American tropics is the creation of better-drained surfaces.

Grazing and fire management

The introduction of Old World livestock into the Americas led to profound changes in vegetation. Shrub and tree increases are produced by grazing under two scenarios: 1) where grazing reduces water use by herbaceous plants or 2) where grazing reduces standing phytomass (fuel loads) and thus fire intensity. Where fire itself is suppressed, this may be sufficient to allow woody plant invasions in the absence of grazing. The Gran Chaco has allegedly experienced extensive tree and shrub invasions (Bucher 1982) due to the interactions of altered fire and grazing regimes, as has the subtropical Lower Rio Grande Valley of Texas (Archer 1990). Livestock have become key dispersal agents for many New World savanna trees (Archer 1990, Brown and Archer 1987, Janzen 1988, Janzen and Martin 1982).

On large scales, the post-contact decimation of indigenous peoples across the New World led to the widespread decline of land use/management practices, of which annual burning was an important component. Changes in savanna/forest and cerrado/forest boundaries noted by Furley (1992) and Ratter (1992), respectively, may well be attributable to this change.

Creation of artificial raised surfaces

Denevan (1966: 70-72) considered some Moxos islas to be wholly artificial. He characterized artificial islas as low mounds which rise up to 2 m above the flooded savanna surfaces and are commonly 10 to 50 m in diameter. Excavations of allegedly artificial islas have revealed horizons of snail shells along with broken pottery. Some allegedly artificial islas are adjacent to depressional areas which are assumed to be borrow pits. The often circular forest patches are frequently found several kilometers away from other high ground. The pre-Hispanic earthworks provide better drainage and some degree of fire protection which fosters the establishment of woody vegetation (forest islands) upon the abandoned structures.

Archaeologist Clark Erickson has found forests growing upon blocks of raised fields near the Río Apere (Erickson 1995). He has also observed islas which appear to have been formed by the accumulation of materials at the intersections of causeways. This latter observation suggests that some causeways which appear to be running between islas may actually be the causes of the islas themselves.

The *apêtê* model

Anderson and Posey (1989) have presented what they consider to be evidence for the intentional planting and management of artificial forest islands (*apêtê*) in Brazilian savannas. *Apêtê* photographed by these authors are identical in their gross morphology to many of the smaller islas I have observed in Moxos. In addition, Moxos islas and Brazilian *apêtê* often contain some of the same widespread savanna species, such as *Casearia sylvestris*, *Curatella americana,* and *Hymenaea courbaril*.

Parker (1992) recently reported on *apêtê* at the same sites studied by Anderson and Posey. Parker could not substantiate their claims and interpretations and concluded that "*apêtê*, in the form described by Posey, do not exist" (Parker 1992). I, likewise, have many concerns about Anderson and Posey's interpretations. For example, the observation that a species is *reported as being* useful or *considered* plantable in no way implies that the species actually *is* used or planted in the present or past. Useful and plantable organisms can be found in both highly managed and little-disturbed environments. The presence, or even absolute abundance of useful and plantable species in forest islands does not necessarily imply artificiality or management. Many useful and potentially plantable species do exist in the Moxos islas; however, this observation does not inform us at all about the origins of the islands.

Conclusions

Both savannas and forest islands in savannas are typically inadequately explained by single factor models. They more often each have many, often interacting. possible determinants. While there are useful generalizations, the occurrence of a particular forest island or savanna is always the result of a unique site history and abiotic conditions. Forest islands are convenient phenomena as they are readily identifiable, discrete entities in the landscape. Their existence provides a ready-made geographical question: why are these features present where they are? I will consider this and other questions in the context of the landscape of La Chacra ranch in the Llanos de Moxos region of Bolivia, whose general geography is discussed in the next two chapters.

Chapter 3. Location and Physical Setting of La Chacra and its Surroundings

La Chacra is a 2,000 ha cattle ranch, located 22 km east of the city of Trinidad, Provincia Cercado, Departamento del Beni, Bolivia (14°52'S, 64°43'W, 160 m above sea level, Maps 2 and 3). The ranch is located along a senesced river known as the Cañada de los Lagartos, whose waters ultimately flow out to the Amazon via the Mamoré and Madeira rivers. La Chacra lies in the eastern zone of the region known as the Llanos de Moxos (also Mojos).

The Llanos de Moxos is a 160,000 km^2 expanse of seasonally-inundated wetlands, savannas, woodlands, and forests between 10 and 18 degrees southern latitude. It is an extremely flat lowland plain in the Beni-Mamoré sub-basin of the Madeira River Basin. Mean elevations are on the order of 150-160 m and the range is from about 135 m in the north to near 210 m near the Chapare region to the south (see Hanagarth 1993: 8). Moxos lies between the Brazilian Precambrian shield to the east and the Andes to the west and south. Moxos is part of what is often referred to as the Upper Amazon and more specifically, the Southwestern Amazon basin.

Geology of Southwestern Amazonia

The southwestern Amazon basin drains two principal structural units: the Andean Cordillera and the Brazilian Precambrian Shield. The extreme southern limits of the Amazon Basin lie in the northern Gran Chaco of southeastern Bolivia.

Around 200 million years ago, the Nazca plate began its subduction under the South American plate, initiating the Andean orogeny at the western edge of the Precambrian shield (James 1973). Between 100 and 60 million years ago, Gondwana split into South America and Africa and there was increased Andean mountain building. Throughout the Tertiary, erosion of the young Andes created sediments which were deposited over the Brazilian Shield to the east. There was a major period of uplift during the Pliocene and early Pleistocene, followed by the erosional phase which has created the deep Quaternary sediments in many low basins, such as the Llanos de Moxos.

The Andean sediment mass has been accumulating above the western margin of the Precambrian shield, causing a flexing downwards associated with possible upwarp to the northeast (Allenby 1988). The regional surface thus appears to dip toward the northeast.

The lowland region immediately eastward of the Andean front has been called the Sub-Andean Sedimentary Basin (Irion 1989) or the Andean Foreland Basin (Salo and Räsänen 1989). This zone is generally considered to be part of the Upper Amazon Basin (Sioli 1984). Sioli (1984: 135, 137) characterized the principal rivers of the upper Amazon as having "endless meanders, and frequent oxbow lakes," while "the whole land adjacent to the rivers is in constant and rapid process of dismantling and rebuilding, a process which can be observed on a time-scale of a few decades."

Räsänen *et al.* (1991) note that in the Pastaza-Marañón-lower Ucayali flood basin of northeastern Peru “vertical accretion by annual basinal flooding also gradually masks the relief of the abandoned meander belts, promoting a drowned wetland landscape from which the remains of meander and scroll patterns become less evident.” Such activity may have once been important in the Moxos basin where relict meander and scroll patterns are rare except in the active zones along the Beni and Mamoré rivers.

The largest of the sub-basins of Southwestern Amazonia is that of the Upper Madeira. This basin drains an area of over 850,000 km^2, primarily in Bolivian territory (Roche and Fernández Jáuregui 1988). There are four major tributaries: (from west to east) the Madre de Dios, the Beni, the Mamoré, and the Iténez (called the Guaporé by Brazilians). The Madeira itself flows northeast through the western arm of the Brazilian shield into the Amazon River downstream of the Rio Negro (ca. 130 km east of Manaus).

Stratigraphic Studies, Chronologies, and Explanatory Theories

The surficial deposits of the Llanos de Moxos are fine grained, with fine sands important only in present and former lateral accretion deposits. The soils of the plains are heavy, usually with an impervious claypan at shallow depths.

Two drilling sites west of the Río Mamoré revealed sediment depths of 813 m (El Perú) and 436 m (La Esperanza) (Plafker 1964). None of the sediments were sufficiently consolidated to allow recovery of cores; however the electric logs revealed that about 25% of the sections were clay, the remainder sand and silt without coarser particles. Seismic profiles indicated that the sediments reach as much as 3,000 m thick near the Andean foothills. Plafker considered the sediments to be of Quaternary and possibly Late Tertiary age. No other deep stratigraphic sequences for the Bolivian Amazon lowlands have been reported in the literature.

Campbell and Frailey (1984) described a sequence of Holocene sediments which rest uncomformably upon Late Miocene (Huayquerian) strata in northern Bolivian and southeastern Peru. Radiocarbon dates from Holocene wood samples ranged from ca. 10 to 5.5 thousand years before present. The absence of Pleistocene strata was interpreted as evidence for repeated flood events between 10-5 thousand years before present. They proposed a lowering of Andean snowlines and increased snowpack, which resulted in increased summer flooding. Campbell and Frailey believed that these conditions corresponds with Kutzbach's (1981) model where global solar radiation receipt was decreased 9% in January at 9,000 years before present. Campbell and Frailey interpreted the present phase to be an erosional cycle which began sometime after 5,000 BP, during which the modern channels and topography were incised.

Campbell *et al.* (1985) reported on fieldwork on the Río Beni, from the Andean foothills downstream to the confluence of the Madre de Dios at Riberalta. Along the northernmost (i.e., downstream) section of the Beni ("Monte Depositional Realm"), they observed the three members of the Iñapari Formation previously described on the Río Acre. The Beni members were presumabed to overlie Tertiary strata, although these were not observed. The southern 195 km section was not well described, although banks revealed a consistent 2 m of "Recent" alluvium, except within about 15 km of the foothills where three "Sierra Depositional Realm" members are found. The definitions of "Quaternary" and "Recent" were not made clear. The Monte Realm sediments are supposedly of Peruvian Andes origin, while the Sierra Realm sediments are of Bolivian Andes origin.

Later work revealed wood dating back to 35,000 years before present in the basal member of the postulated Holocene age formation (Frailey *et al.* 1988). Frailey *et al.* (1988) reinterpreted the former middle member of the formation as lacustrine in origin. They postulated that a vast inland sea, “Lago Amazonas,” would have covered the entire Amazon Basin below ca. 150 m, as well as the Casiquiare-Orinoco Basin. The lake was hypothetically blocked from Atlantic drainage to the east by the upwarped Gurupá arch, thus draining into the Caribbean through the Orinoco.

At Cachuela Esperanza there is a thick conglomerate of Brazilian shield clasts up to 30 cm, diminishing eastward, indicating late Pleistocene downwarping of the Bolivian Amazon lowland basin (Frailey *et al.* 1988). The conglomerate is overlain by the Madre de Dios / Solimões Formation (Tertiary age). Upper basin (220-260 m) sediments deposited during the last active uplift phase have possibly been uplifted by isostatic rebound (Frailey *et al.* 1988). The relationship between “Lago Amazonas” and “Lake Beni” (which allegedly would have covered the Llanos de Moxos, see map in Frailey *et al.* 1988) was not discussed. According to these authors, the lakes might have drained as recently as ca. 2,500 BP. In contrast, Grabert's (1984) hypothetical “Beni lake system” would have drained by ca 10,000 BP when the drainage shifted from the Purus Gap to the Madeira gap. Grabert's evidence for the lake or lakes is not stratigraphic or even geomorphological. Rather, Grabert proposed the lake to explain the evolution of blind river dolphins which Grabert believes must have occurred in a turbid water lake.

Campbell *et al.* (1989) described a possible meteor impact structure west of the Río Beni in the northern La Paz department (12°35'S, 180-190 m). The meteor supposedly fell into the center of a finger delta which would have formed in the Pleistocene Lake Beni. Campbell *et al.* suggested that lacustrine deposition in the region probably ended ca. 11,000 BP., when drainage shifted from the northeast and opened the Madeira gap. The underlying sediments comprise at least two Pleistocene "horizons," with the basal horizon yielding fossil tree trunk radiocarbon dates from ca. 32 to 36 thousand years before present. Supposedly, these horizons can be traced from the edge of the Brazilian Shield westward over 600 km to the Andean foothills. The less than 45 m thick Pleistocene sediments overlie Late Miocene sediments as reported previously (Campbell *et al.* 1985). The open pampa containing the deltaic features occur has a NE-SW trend (see Fig. 3 in Campbell *et al.* 1989), as do most Bolivian Amazon lowland rivers and oriented lakes, suggesting structural control (see Plafker 1964).

Räsänen *et al.* (1990) critically evaluated the hypotheses based upon supposed widespread, synchronous lake sediments in southwestern Amazonia. They emphasized that stratigraphic similarity in no way implies correlation without adequate age control, which is largely missing in the Amazon basin. According to their interpretations, the surficial deposits of the *terra firme* surfaces have resulted from diachronic aggradation, not widespread lacustrine deposition. Thermoluminescence dating of cutbank sediments 8 m above the Madre de Dios at Laberinto, Peru provided an age of 176,000 BP, substantially older than the dates of Campbell, Frailey, and associates. A tree trunk from the Río Tambopata provided an infinite radiocarbon date. These dates do not support the Campbell-Frailey Holocene flooding hypothesis.

Rates of deposition have not been documented, but Hanagarth (pers. comm. 1991) obtained a radiocarbon date of ca. 2,500 BP from a wood sample found at 9 m in a well coring at El Porvenir, a site away from any present major rivers. Erickson has identified raised fields buried under a meter or so of sediments in the alluvial plains of central Moxos. The fields Erickson dated elsewhere in Moxos were largely abandoned ca. 800 radiocarbon years before the present.

Campbell (1992:70) discussed islands of savannas and/or low canopy forest in the taller Amazonian forest in Bolivia. He believes that these vegetation patches are found upon old lake bottoms within palaeodelta systems. In the southern edge of the basin, the savanna islands appear to be as reported by Campbell; however, the surrounding alluvial ridge forests are not necessarily deltaic features. They may be more of the nature of Pantanal *Dammuferseen* as described by Wilhelmy (1958a), where enclosed basins are created by networks of intersecting natural levee formations.

Campbell lacks the physical data to prove his suppositions, which are basesd solely upon interpretation of remote sensing imagery. In fact, Hanagarth (1993) reports that the bird's-foot deltaic forest patterns are in some cases created by the presence of gallery forest in incised channels and narrow valleys *below* the level of the savannas, precisely the opposite of what would occur in a delta environment.

Evidence for regional and local subsidence in the Moxos plains

Plafker (1964, 1974), Allenby (1989), and Hanagarth (1993) all suggest that there are major neotectonic influences on the drainage patterns in the Beni basin. Many bajíos and curichis are allegedly formed by local subsidence due to faulting in the underlying Precambrian shield. Air photos of the Llanos de Moxos demonstrate right-angle and linear vegetation, lacustrine, and fluvial features which are highly suggestive of tectonic control to some observers (e.g. Plafker 1964, Denevan 1966, Allenby 1989, and Hanagarth 1993). There are, however, no geophysical data to support these hypotheses.

Foreland shortening of the Bolivian Andes during the last 12 million years has been ca. 100 km, with 15-20 km during the last 3 million years (Isacks 1988), which can be linked with the hypothesized neotectonic activity responsible for the formation of the Moxos oriented lakes as suggested by Plafker (1964, 1974) and Allenby (1989). Examination of satellite imagery of the region suggest that the tectonic activity may be oldest to the southeast and most recent in the northwest. Lakes have been filled in by lateral channel migrations in the extreme southeast (W. Hanagarth, pers. comm. 1991). The oriented lakes are most evident in the central plains, while west of the Beni River the savannas occur in oriented depressions with fingered margins. Westward into Peru, the irregular savannas disappear, but long, straight-sided depressions of similar width and orientation appear, vegetated by extensive *Mauritia* palm swamps (aguajales).

A most notable feature of the Llanos de Moxos is the occurrence of large numbers of shallow (1-2 m), oriented, angular lakes, streams, and savanna/forest boundaries (Plafker 1964, 1974; Allenby 1988). These features are primarily oriented along a SW-NE axis. La Chacra ranch itself falls between four of these oriented lakes: Laguna Cernández, Laguna Santa Rosa, Laguna Perotó, and Laguna Suárez (Map 2). Local tradition holds that the infamous rubber baron Nicolás Suárez had the lake bearing his surname constructed. However, Laguna Suárez is identical in all characteristics to the hundreds of other oriented and aligned lakes of the Moxos plains. Erickson (1980) suggested that the oriented lakes may had been constructed as reservoirs by indigenous peoples of the past.

Plafker (1964, 1974) set forth a tectonic model for the origins of these lakes and other “lineaments” in the Beni basin. He believes that orthogonal fractures in the underlying Precambrian shield are responsible for the angular surface patterns and alignments. Allenby (1989) and Hanagarth (1993) essentially support Plafker’s tectonic model.

Campbell *et al.* (1985) concluded that a catastrophic flood event was the causal agent responsible for the oriented lakes and other lineated features of the Llanos de Moxos. The flood supposedly resulted from the failure of an ice dam retaining glacial Lake Titicaca. The flood waters would have descended rapidly down the Alto Beni gorges and shot out of the narrow gap (the Angostura del Bala) in the foothills near the present town of Rurrenabaque, scouring the alluvial plains to the northeast. Campbell and his associates claimed that even the so-called raised fields are really nothing more than "ripples" left by the flood. Although the authors presented some interesting data concerning the various depositional realms of the Bolivian Amazon, their theory is not plausible in light of other evidence.

A quick perusal of any recent map showing the broader extent and distribution of oriented lakes in eastern Bolivia (e.g., Map 2) will reveal that it is physically impossible for a high velocity flow from a single point near the base of the Andes to have scoured out the oriented lakes across such a wide area, especially without a systematic divergence of the angle of orientation. For example, oriented lakes occur to the east of Trinidad, due east of the proposed outlet. How then could it have been possible to scour a northeast trending lake without waters emanating from the southwest? Also, how does catastrophic flooding account for the striking quadrangularity of many of the lakes?

Clapperton (1993) disagrees with both Plafker and Campbell *et al.* (1985). He discounts Plafker's model for the lack of any known mechanism to translate bedrock fractures or faulting through hundreds or even thousands of meters of unconsolidated alluvium. He then more substantially discredits Campbell and colleagues by denying the existence of physical evidence for the alleged glacial lake and ice dam (Clapperton himself was in the field with Campbell in the Bolivian Andes). Clapperton (1993: 196-198) concludes:

> "Thus it is possible that these oriented lakes are palaeo-deflation basins associated with drier climatic periods, and may have been developing during a recent interval of the Quaternary, most probably the last global glaciation maximum. The orientation of the basins and other features reflects the dominance of stronger winds from the NW and NE. As in the Pantanal, the distribution of many basins may have been influenced by palaeocourses of rivers emerging from the Bolivian Andes, like the Río Beni."

Physiography of the Beni-Mamoré basin

The Bolivian Amazon corresponds to an essentially well-defined physiographic region (Map 1). The eastern boundaries are defined politically by the river frontier with Brazil; however, hydrologically includes the drainage of the Iténez / Guaporé enclosed by the plateau divides of the Precambrian Brazilian shield in the Rondônia and Mato Grosso states of Brazil. The southern limit is the rather weak watershed divide of the Amazon and La Plata-Paraná systems, which runs roughly SW-NE across southeastern Bolivia from the Andean foothills (20°S) to the Brazilian shield of Mato Grosso (16° 30'S). The western limits of the region correspond to the divide between the endorrheic Altiplano basin and the eastern ranges of the Andean Cordillera, The lower foothills comprise a series of parallel folded Appalachian-type valleys and ridges trending NW-SE north of the Bolivian Orocline "elbow." The "Bolivian basin" extends into extreme eastern lowland Peru, encompassing the Madre de Dios drainage basin and physically separated from the rest of Peru by the divides of the Ucayali and Acre-Purus river systems. The northern limit (10°S) of the region is the Acre-Abuna divide which is formed by the low westward arm of the Brazilian shield, which only relatively recently has been traversed by the upper Madeira River (Grabert 1983).

The Bolivian Amazon can be subdivided into several physiographic regions**.** The humid uplands on the Andean slopes correspond to the *Yungas*. Further to toward the interior of the Andes, there are drier valleys and canyons of the *Valles* region. The Amazon basin truly extends to the rim of the *Altiplano*, which is dramatically demonstrated at La Paz. The eastern Andes bend from a roughly NW-SE trend to a roughly N-S trend around 18°S, southwest of Santa Cruz de la Sierra. This is very approximately where the southern Amazonian plains are differentiated from those of the *Gran Chaco*. Tectonically, the "Elbow Line" (Schlatter and Nederlof 1966) or "Ichilo Line" (Rod 1960) marks this same boundary, albeit somewhat to the north.

Pereira and Salinas (1982) divided the Beni/Moxos lowlands into four major physiographic regions. The southern piedmont and alluvial fans comprise the largely forested unit denominated the "Sub-Andean Plateaus." Immediately to the north lie the "Plateaus of Beni," which they consider to be equivalent to the Pampas of Moxos. The pampas are bordered to the north by the older and dissected "Plateaus of Guayaramerín," which are largely forested. To the east of the alluvial "plateaus" rise the "Plateaus of the North Brazilian Shield." I agree with this separation of units; however, I find the use of the term "plateaus" problematic, except for the Shield region. “Plains” would be a much more accurate term. North of the Beni River, the forests are contiguous with those of the Madre de Dios Department of Peru and the States of Acre and Rondônia, Brazil.

Definition of the “Llanos de Moxos”

The Llanos de Moxos correspond to the predominantly savanna-covered plains of the Bolivian Amazon basin lowlands (i.e., the Plateaus of Beni unit of Salinas and Pereira). The first accurate delineation of the region was done by Denevan (1966:7). Later, satellites would reveal the surprising accuracy of Denevan’s map, which was based on partial air photo coverage and his own air surveys (compare with maps in Beck 1983, Hanagarth 1993).

Hanagarth (1993) maps and discusses subunits of the Beni plains based on various criteria. He identifies a “Bala-Rogagua Line” which divides the region into a “Southern Beni Region” and a “Northern Beni Region.” This line, roughly corresponding to the watershed between the Beni and the Mamoré, runs to the northeast from Rurrenabaque near the Andes in the southwest to the northeast, cutting through the large lakes and crossing the Mamoré near rapids of Cachuela Envidia. Hanagarth implies that this line is highly significant to the biogeography of the Beni region and that it is linked to tectonic phenomena. He notes that the line is parallel to the Pisco Deflection (see Loczy 1970) which Grabert (1983) suggested is a transcurrent fault.

North of the Bala-Rogagua Line, the drainage is primarily northwards into the Beni River and the topography is rather dissected. There are also abundant lateritic nodules or crusts on these surfaces. Fluvial flooding is limited in extent. The northernmost savannas have a vegetation much more closely related to the Brazilian *campos cerrados* than to the typical Moxos savannas (Killeen *et al*. 1993:9). South of the line is what should most properly be assigned to the Llanos de Moxos. Here, the rivers generally flow to the northeast into the Mamoré or north into the Iténez.

West of the Beni River there are numerous savannas in the Department of La Paz, including the Pampas del Heath, which are the westernmost units of the Moxos savannas, *sensu lato.* These savannas extend just into the Republic of Peru (Denevan 1980).

The Mamoré River is the centerpiece of the Llanos de Moxos, into which most of its rivers and streams flow. The Mamoré itself originates in the plains at the confluence of the Ichilo and Chapare rivers, the former being the primary tributary. These rivers flow northwards and drain Andean slopes which run roughly east-west and receive great amounts (over 6000 mm mean annual precipitation at some localities, Roche and Rocha 1985) of orographic rainfall produced by the forcing of warm and humid air by the dominant northerly winds from the Amazonian lowlands.

Hydrology and Hydrography of the Bolivian Amazon

River basins of the Bolivian Amazon

The entire Beni/Moxos Basin drains northward into the Madeira River, then into the Amazon and out into the Atlantic Ocean. There are four principal subbasins, each named for its principal river: the Madre de Dios, the Beni, the Mamoré, and the Iténez/Guaporé. The Madre de Dios, Beni and

Mamoré are born in the Andes, while the Iténez originates in the Precambrian shield. Each of these rivers and their basins are rather different in their characteristics. The Madre de Dios and Beni Basins are not directly linked to the region of La Chacra.

On a finer level, we can break the basins down somewhat further (Map 1). In far northern Bolivia in the Department of Pando, there is actually a very small area of the Río Acre/Purus drainage. Also in this region is the Abuná drainage, which contributes directly to the Madeira River. The Orthon basin feeds into the Beni River downstream of the Madre de Dios, whose basin occupies part of northernmost La Paz and southern Pando departments.

The basin of the Río Beni proper, lies entirely within the territory of Bolivia and largely within the Department of La Paz, not the Department of the Beni. The name of the department is not an adequate reflection of the actual and historical significance of the Mamoré River relative to the Beni River!

The Río Yata drains much of the northern Beni plains north of Hanagarth's Bala-Rogagua Line and east of the northern Beni basin. The Yata basin contains the large Rogoaguado lake complex, as well as the Río Tapado. Hanagarth (1993, p. 25-26) believes that the Yata once drained the Río Beni in palaeo times. The Yata feeds into the lower Mamoré, only some 15 km above the mouth of the Beni. The Yata and Beni Basins do not belong to my stricter definition of the Llanos de Moxos, although they do contain considerable areas of savanna.

The Mamoré Basin, in the broadest sense, also includes the Iténez basin; however I will exclude the latter here due to its considerable differences in nature. The Mamoré basin, in the broad sense, also includes the Grande and Ibare basins. In the strictest sense, which I will use here, the Mamoré basin includes the watersheds of the easternmost *serranías* of the Andes in the southernmost Department of the Beni and the Chapare-Ichilo region of the departments of Cochabamba and Santa Cruz. Almost all of the water comes from the west side of the Mamoré, directly from the Andean slopes north of the "Elbow" (the point where the Andes "bend") and from the plains themselves. This basin (plus the Ibare) corresponds to my strict definition of the Llanos de Moxos and is the area of the greatest concentration of agricultural earthworks. La Chacra is located within the small portion of this basin east of the Mamoré River itself, wedged between the watersheds of the Ibare and the Machupo rivers.

The primary eastern tributary of the Mamoré is the Río Grande, whose drainage basin includes a large area of semi-arid Andean valleys. The Río Grande enters the lowlands far to the south of Moxos in the Subandean zone of the Chaco, where there are three important depositional realms (Iriondo 1993). The northernmost is the fan of the Río Grande, followed by that of the Parapetí to the south. The southernmost is that of the Pilcomayo. The Amazon/La Plata watershed divide lies somewhere between these last two. The Grande and Parapetí watersheds contribute to the eastern Moxos plains, via the Mamoré and San Pablo rivers respectively. The Río Grande exits the Andes after flowing to the southeast, draining the rather dry valleys of the Cochabamba, Chuquisaca, and westernmost Santa Cruz departments. The Grande is sediment rich and massive quantities of sand are deposited in the Santa Cruz lowlands. However, by the time the Grande reaches the Mamoré, it is no longer a significant source of coarse sediments and is a rather narrow, deeper, meandering river. At El Pailón, due east of Santa Cruz de la Sierra (Map 1), the major bed of the Río Grande is composed of very fine sands (Iriondo 1993). It is not as "grande" as the name may imply, erroneously depicted as the source of the Mamoré on many maps. The Parapetí river likewise dumps much sand onto the plain, with a 25,000 km^2 aeolian sand plain extending southward

(Iriondo 1993). Waters from the Parapetí flow into the Paraguay river via the Río Timané during the rainy season.

The Río Ibare is the Mamoré's only other eastern tributary of note, discharging just northwest of Trinidad. It is a pampas river whose watershed lies in the plains sandwiched between those of the Grande and San Pablo rivers. The Ibare basin is where the first large mounds were identified by European scholars (Nordenskiöld 1913); however, only a very limited area of agricultural earthworks have been identified here (at Naranjitos-San Carlitos (Map 2), see Erickson *et al.* 1991).

The final set of basins are those which feed into the Río Iténez. The streams of the northern Precambrian shield region all flow into the Iténez. This collection of numerous small watersheds forms a major zone of inundation in the Baures region, much of which is flooded forest, not savanna (Hanagarth, pers. comm.). This region has incredible earthworks in the form of village mounds with moats and causeways, yet agricultural earthworks have not been identified. The Iténez river itself is a "clearwater" or more precisely, a "greenwater" river, quite unlike the "whitewater" Mamoré.

The Itonamas-San Miguel-San Pablo-Parapetí basin collects water from the southernmost limits of the entire Amazon basin, beginning in the souther Andean foothills of the Gran Chaco. The San Pablo river runs in the easternmost alluvial plains of Moxos along the western edge of the Precambrian shield zone. It is believed that the Río Grande once flowed north into the Iténez through this path (Werding 1977, Hanagarth 1993, Iriondo 1993).

Almost immediately east of the Mamoré and just northeast of La Chacra lies the Machupo basin, which includes the Cocharcas and Ipurupuru rivers. This area is was important in the Jesuit period as the administrative center (San Pedro Mission) and site of a bell foundry fed by the iron-rich lateritic concretions common in the soils of portions of this basin. The Ipurupuru is connected to the Mamoré by a pre-Hispanic artificial canal (Nordenskiöld 1916, Denevan 1966: Plate 10). Each of the sub-basins of the Bolivian Amazon, which I have only briefly discussed above, has unique sedimentological, geomorphological, and cultural characteristics that remain to be adequately examined.

General Hydrological Patterns

The alluvial plains are of extraordinarily low relief, with abandoned natural levees and point bar deposits creating the primary natural relief features. The rivers of the Llanos de Moxos all converge into the Río Madeira to the north, creating a roughly triangular basin. The regional base level is determined by the section of the Brazilian Precambrian shield which is cut across by the Madeira in the northern tip of the basin. The Río Madeira at its confluence has an annual discharge of 536 billion m^3, of which 256 billion m^3 are contributed by the Río Mamoré (Roche and Fernández J. 1988). The gradient of the entire lowland basin is very low, approximately one foot per mile (Denevan 1966:8). Hanagarth (1993: 9) reports that the gradient for the Mamoré between Trinidad and Guayaramerín is 6 cm per km, which is equivalent to 3.8 inches per mile. Almost all of the savannas and much of the forests are flooded annually.

The area east of the Mamoré is not as prone to fluvial flooding and has much less evidence of ancient agricultural earthworks than the plains west of the Mamoré. Roche and Fernández (1988) demonstrated that the Andean waters contain much higher concentrations of cations than do the waters of the acidic Precambrian shield streams. I hypothesize that these relative nutrient loads may have been important in determining the distribution of raised field and other forms of hydraulic agriculture in the Llanos de Moxos. As a result of the lack of streams flowing westward into the Mamoré, pre-Hispanic peoples constructed several canals which run east-west and connect the western and eastern regions (Nordenskiöld 1916; see maps in Pinto Parada 1987).

On the margin of the Precambrian shield, Laguna Huachi and other smaller lakes appear to have been formed through the natural damming of valleys. The margins of the lakes have the appearance of flooded valley reservoirs. These lakes show no signs of orientation. The large lakes in the northernmost zone of the Moxos savannas (Rogaguado, Yajchaja, Guachuna, etc.) similarly appear to be formed by the blockage of large, broad valleys. I have examined airphotos which reveal the presence of forested islands within these lakes (not yomomo-type floating islands).

The Cañada de Los Lagartos Basin

The Chacra region is traversed by a senesced river with lethargic wet-season flow known as the Cañada de los Lagartos (the slough of the caimans). This weakly meandering, shallow, flat-bottomed, 60-100 m-wide channel runs roughly to the west-northwest, parallel to the Trinidad-Santa Cruz highway, from wetlands near Laguna Perotó. Just west of El Tajibo ranch, the cañada turns northward, eventually running into two minor eastern tributaries of the Mamoré, the Mocoví and Matiquipiri rivers (Map 2). During the dry season, the cañada dries out completely,. except for a few ponds created by road-causeways. Meander cut off (ox-bow) lakes are absent in the region of La Chacra except within the Mamoré-Ibare floodplain. Reports of a deep lake north of Ibiato suggest an isolated meander cut off lake far to the east of La Chacra, probably formed by the Río Cocharcas.

La Chacra actually lies near the edge of the watershed divide between the Mamoré and Iténez sub-basins. The Cocharcas belongs to the Iténez system, the Matiquipiri and Mocoví to the Mamoré. The watershed divide lies within only a few kilometers of the Mamoré itself in the zone just north of San Javier northwards to San Pedro Viejo and not far from La Chacra itself in the northeast direction. South of La Chacra lies the Ibare watershed. The Cañada de los Lagartos is actually the longest and easternmost tributary of Mamoré north of the Ibare basin. The Lagartos basin occupies a narrow wedge between the Cocharcas (i.e., upper Machupo) and Ibare basins.

The Río Mocoví begins in the bajío west of Laguna Cernández, northeast of Trinidad. The stream flows westward, crossing under a bridge at the Trinidad-San Javier road. At this point, the river flows in an incised channel 4-5 m deep and perhaps 30 m across the top. The gallery forest here is largely on the inner slopes of the incised arroyo-type "valley." Also at this point, water is added to the system by a recently constructed drainage canal excavated along the road from Trinidad. It is thus now possible to navigate by canoe from Trinidad to Laguna Cernández via the canal, the Mocoví, and the canoe trail across the bajío. West of the road, the Mocoví trends to the northwest, and is briefly parallel to the Ibare at a distance as close as 2 km. The Mocoví flows into an old meander cutoff known as Laguna del Siquero within the meander belt of the Mamoré.

The Río Matiquipiri was the lower reach of the Cañada de los Lagartos for some time in the past, at least indirectly until the early 1990s. Channel scars linking the cañada and the Matiquipiri are clearly visible on air photos. The present-day Matiquipiri is a much longer stream than the Mocoví and is apparently much more sinuous. The stream drains the wetlands northwest of Laguna Cernández, and previously the "Lagartos basin" as well. The Matiquipiri passes about 3 km south of San Javier then continues roughly northwards into the meander cutoff Laguna Verdún.

According the IPGH Map of the Americas 1:250,000 sheet, the Matiquipiri once went directly into the Mamoré via another lake just northwest of Laguna Verdún.

The Río Cocharca is the first major stream northeast of La Chacra. This river is a tributary of the Machupo and Iténez. Downstream, the Cocharcas joins the Ipurupuru as it flows to the northwest toward the Mamoré. Curiously, the Ipurupuru never hits the Mamoré, as it is deflected to the north-northeast just a few kilometers before reaching the big river. Prehistoric folk, apparently not pleased with the overland portage, constructed a canal connecting the Ipurupuru and the Mamoré. This canal is still visible today (Denevan 1966: pl. 10). These conjoined rivers flow into the Machupo and pass through the San Ramón-San Joaquín region. The region of the Cocharcas is not really comparable to the true “Moxos” plains to the southwest, across the Mamoré. Jesuit records indicate that the Canichana and Itonama peoples occupied the region north of the present site of San Pedro, not Moxo peoples.

The separation of the Machupo and Mamoré basins might be expected to be somewhat delicate. Hanagarth (1993) believes that the Mamoré may have once flowed through the channel of the Machupo, but this is only conjectural. Nordenskiöld (1916) observed that the water of the Mamoré entered the mouth of the canal and he believed that the river might eventually cut through and exit via the Ipurupuro/Machupo. However, there is no indication that this is happening in the present. Nordenskiöld also observed that the canal is higher than the dry-season river levels and that it is thus usable only during the high-water periods.

There is a rather interesting corridor of gallery forest running from the area south of Villa Bánzer, north to Casarabe, the roughly northwest to El Cerrito, north of San Javier, and on to the Mamoré. This is a massive corridor of forest with many important villages and ranches upon it. Whether this marks a major palaeofluvial system is not known, however its SE to NW path is typical of the streams of the region. On the other hand, this forest corridor more or less marks the Ibare/Machupo and Mamoré/Machupo watershed divides. It may thus indicate a palaeo-alluvial ridge feature or a structural feature related to the underlying Precambrian shield. There is another broader, but shorter forest corridor beginning in the pampas between San Juan de Aguadulce and Arroyo Ibiato. This forest runs almost due north, just west of the Cocharca in the northernmost segment. Numerous large loma-type mounds have been constructed upon these forested ridges, such as the ones at Casarabe, El Cerrito, Cernández, and those I observed at La Mónica in 1991 during pre-dissertation fieldwork.

Dougherty and Calandra (1984) observe that "very numerous remnants of a very old and important fluvial activity are easily seen in the landscape east of the Mamoré to the San Pablo River," the very region where La Chacra lies. Near Casarabe, they observed sand lenses and gravels of fluvial origin in deep cuts made by the Servicio Nacional de Caminos. Likewise, numerous well records demonstrate even cobbles and boulders at depth in the region of La Chacra (i.e. between Trinidad and Casarabe; Lee and Bottega, pers. comm.). These findings of large rock fragments are rather significant in terms of palaeogeography, as they suggest a former dominance by rivers born in the Precambrian shield region to the east rather than of Andean origin. The longer distance and lower gradient from the Andean front does not allow the transport of such coarse particles by any means (except by barge!). The base of the Loma Alta of Casarabe is 3 m above the adjacent savanna; Dougherty and Calandra believe that this relief was a pre-existing natural feature of the landscape. However, I find this rather unlikely in light of the range of natural relief features.

Hydrology of the Chacra Region

The regional base level control is the Mamoré River, into which all surface water in the Lagartos basin ultimately drains. North of the mouth of the Ibare, the next river is the Mocoví, which enters into a cutoff lake instead of the main channel. Further north is the Matiquipiri River, into which the Cañada de los Lagartos has drained in the recent past.

The rivers that flow directly into the Mamoré, theoretically, have the greatest potentially for incising their channels. The Río Mocoví has a rather deeply incised channel with forest covering the inner slopes, without any levee deposits. Given that both the Mocoví and the Matiquipiri terminate in channel cut-off lakes, neither of these rivers are controlled directly by the base level of the Mamoré.

The Cañada de los Lagartos once flowed into the Río Matiquipiri, as observed on 1979 air photography. However, around 1991 or 1992, human activity led to a change of course. The residents of Cernández, a village situated upon an artificial, pre-Hispanic *loma* near Laguna Cernández, cleared a canoe trail through the dense *junquillar* (*Cyperus giganteus*) marshes. This trail connects the lake with the Río Mocoví, which is south of the Matiquipiri. The opening of this path created increased flow into the Mocoví, lowering the level of the lake and incising a channel across the pampa and across the cañada. Thus, the waters of the Cañada de los Lagartos were diverted into the Mocoví. The lowering of the lake led to massive fish kills during a subsequent *surazo*, when strong southerly winds blew many fish right out of the shallow lake (R. Bottega and others, pers. comm. 1994).

An “arroyo” flows out of Laguna Santa Rosa and northwest into Laguna Cernández. This stream is free of levee deposits and was not more than a meter deep late in the wet season[17]. Unlike the Cañada de los Lagartos, this watercourse is open and has little aquatic vegetation. Like Laguna Santa Rosa, this slow-moving stream is also full of yellow-bellied piranhas (“palometas,” *Serrasalmus nattereri*). The local use of the word “arroyo” has no implication of any channel incision; an arroyo is simply an active watercourse of lesser magnitude than a river (i.e., a “río”).

Fluvial deposition and flooding

There is a great degree of misunderstanding regarding the nature and extent of overbank flows (i.e., floods of fluvial origin) in the Llanos de Moxos. The term "flooding" is too vague to be of much use, as it can denote both fluvial overbank events as well as the direct ponding of rainwater. Large areas of the Beni savannas are free from fluvial floodwaters and, hence, from annual flood deposits. Only limited areas adjacent to the larger rivers of Andean origin experience significant fluvial deposition at the present time (Hanagarth 1993: 52). The widespread persistence of raised fields and shallow oriented lakes attests to this lack of deposition. The lack of present day flood deposition limits the formation of new alluvial surfaces as well as any annual deposition of nutrient-rich sediments on the savanna surfaces.

Flooding from the cañada is of very limited extent, but does leave some fine mud coatings on the vegetation as the waters recede. There is a true floodplain along parts of the cañada, perhaps 10 cm below the low ‘terrace’ and some 5-10 m wide. The flooded gallery forest areas can be considered floodplain forests of a sort, although much of the water that accumulates in the mini-basins is overland flow off of the altura levees themselves.

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[17] Tamayo (1961: 31) reported this type of savanna stream from the Venezuelan Llanos, where it is known as an *hilero*.

Rainwater ponding

In contrast to the limited areal extent of fluvial overbank flows, the accumulation of rainwater in depressions (or simply over flat areas) is the principal mechanism of "flooding" in the region of La Chacra. On a larger scale, “rainwater flats” account for the occurrence of hyperseasonal savannas in interfluvial uplands, terraces, plateaus, and other surfaces free from the influence of modern streams or rivers. The combination of impermeable soil horizons at shallow depth and low relief create large areas of imperfect drainage.

Saline ponds or salt-encrusted dry lakes have not been described from the Beni, however they are common in the Chaco and the Pantanal. Nevertheless, sodic soils are documented for numerous localities in the Beni savannas (Hanagarth 1993). There has not been any process-oriented study to determine whether these salt accumulations are products of past climates or whether they form today in the highly seasonal rainfall regime. I have identified $MgSO_4$ crystals (up to at least 4 mm in length) from the heavy clays of a semialtura island soil during the dry season. According to local experts (long-time water well drillers K. Lee and R. Bottega), sodium is virtually unknown from subsurface water in the region of La Chacra. Recently excavated semialtura subsoil often turns white with crystals upon drying (observed at El Sol after excavation for artificial pond in 1986). On the semialturas there are occasional small depressions (probably created by hoof action and deflation) where there is no external drainage and salts accumulate in the upper portions of the soil.

The general lack of surface salt accumulations suggests that most of the seasonally-inundated basins are drained externally. This drainage, however, is very slow. The slowly flowing waters of the nearly level plains can neither carry nor deposit exceptional quantities of sediments. The greatest source of sediments is likely the churning of the heavy soils by cattle. Fine particles are thus entrained and transported. The net results of this have not been documented, but are likely significant locally.

Migration of the principal rivers

Hanagarth (1993: 30) concludes that the Mamoré has been relatively static, being confined to a elongate depression that runs from the "Elbow Line" to the Madeira. (Plafker plotted parallel faults on both sides of the river in his 1964 map.) Hanagarth also attributes tectonic control as a contributing factor. Nevertheless, I had concluded that the Mamoré appears to be moving slowly to the west, given that most of the ancient meander relicts lie to the east of the river today. However, Hanagarth has concluded that it is actually migrating eastward, cutting into the presumably higher and older surfaces upon which lie Trinidad and La Chacra.

The waters of the Lagartos basin drain into the Mamoré via the Mocoví, (Matiquipiri prior to 1991 or 1992). Oxbow lakes or meander scars have not been recognized from air photos or satellite images of the Lagartos basin region, except those created by the Mamoré and the Ibare, far to the west. This attests to at least the lack of meander activity in these plains.

Climate of the Llanos de Moxos

The mean annual precipitation at Trinidad, ca. 20 km west of La Chacra, is approximately 1800 mm (Fig. 2). For the period 1946-1960, 82% of the mean annual precipitation fell between the months of October and April, of which each month averaged above 125 mm of rain. Between May and September, when average monthly rainfall of all months was less than 95 mm, only 18% of the mean annual precipitation was accounted for. Under a non-seasonal regime, the same period should average 42% of the mean annual rainfall.

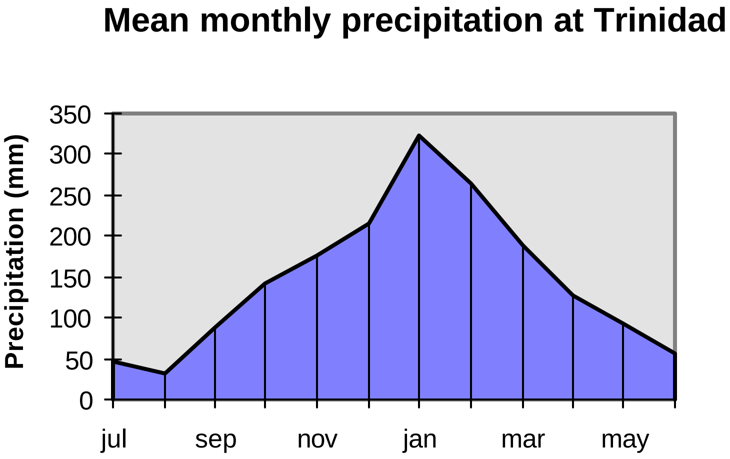

Figure 2. Mean monthly precipitation at Trinidad for the period 1946-1960.

Data from Denevan (1966:10).

Mean annual temperature at Trinidad is approximately 27°C. During the low sun season between June and October, temperatures may plunge as low as 6°C, but average lows during this period are on the order of 15°C. This period is characterized by occasional polar advections known as “surazos,” which bring these low temperatures and often high winds and thunderstorms. However, on the days without extratropical air mass incursions, the daily highs are often 35° or above. During the rainy season, temperatures are moderated by the increased cloud cover and the weather is much less oppressive than one might imagine. Extremely high temperatures (i.e., above 40°C) are very rare indeed. Relative humidities are generally high, but even during the wet season there is sufficient evaporative potential to dry out the soil surface where it exposed. During the dry season, forest frogs will desiccate to death if left exposed to the air overnight, as I have witnessed when frogs are trapped inside the house.

The climate of Trinidad and La Chacra is certainly characteristic of the Aw climate type, which is popularly known as the “savanna climate.” However, let us not forget the dominance of forest cover on all surfaces that are not exposed to the extremes of wet season inundation, shallow rooting zones, and dry season desiccation.

Quaternary climate change in central South America

The Quaternary climate history of the Amazon basin has been a subject of considerable discussion by both physical and biological scientiests during the past three decades. Servant and Villarroel (1979) proposed a model for postulated Quaternary arid periods in the Bolivian Andes and their forelands. They suggested that the strengthening and the westward migration of the South Atlantic Anticyclone would draw the Amazonian Low southward into the Bolivian Andes, creating strong surface convergence and increased precipitation in the Andes, while creating dry conditions in the Bolivian lowlands under the influence of the anticyclone.

The model suggests increased precipitation in the Bolivian lowlands during the periods of warming. Conversely, periods of cooling (increasing latitudinal temperature and pressure gradients, strengthening of meridional flow aloft) would be characterized by lowland aridity and increased Andean snowfall, contributing to the formation of the glaciers. Unfortunately, no estimated dates for the scenario were proposed by the authors, but they do specify that it is for "more important low temperature periods of the Quaternary.” The southerly shift of the southern hemisphere Westerlies at ca. 18,000 BP predicted by the National Center for Atmospheric Research general circulation model (Kutzbach and Guetter 1986), however, should tend to cause a similar poleward migration of the subtropical anticyclones.

Klammer (1982) developed a climatic scenario to support his interpretations of Pleistocene arid-climate landforms in the Pantanal of the upper Paraguay basin, which lies to the southeast from Moxos, across Precambrian shield and the low watershed divide between the Amazon and La Plata basins. The majority of the features Klammer interpreted as fossil dunes have either north-northwest or north-northeast orientations. He considered this to be evidence for year-long influence of the South Atlantic High circulation, with some influence of the continental low during the southern hemisphere summer. These conditions, he noted, are not different from the modern patterns.

Servant *et al.* (1981) presented evidence for two periods of Holocene aridity (7,.000-4,000 years BP and 3,000-1,400 years BP) in the southern Bolivian Amazon at Santa Cruz de la Sierra. Their interpretations were based on a combination of biostratigraphic, lithostratigraphic, and pedostratigraphic observations. The dates for the arid periods are based on radiocarbon dating of charcoal found in the stratigraphic sequences. Periods of terrace incision and deposition of coarser sediments are interpreted as arid. Periods of soil formation are interpreted as humid. The second arid period is marked on the surface by north-northwest-south-southeast oriented sand dunes, which corresponds to dominance of north-northeasterly winds under a prolonged anticyclonal influence. Destruction of the humid-phase forests is attributed to both cooler temperatures and increased aridity, as present-day Bolivian Amazon forests are not especially prone to forest fires under humid conditions.

Hanagarth and Sarmiento (1990) proposed that the sodic soils and surficial salt crusts of the Bolivian Amazon plains must have developed during the Holocene arid periods proposed by Servant *et al.* (1981) for the Santa Cruz region. However there is no indication that such soils could not have formed under the modern seasonally-dry climate. The poor drainage, fluctuating water tables, and seasonal water deficit of the current environments should certainly foster salt accumulations.

Elsewhere in Amazonia, Saldarriaga and West (1986) and Sanford *et al.* (1985) reported increased charcoal abundance after 6,.300 BP in forest soils in Venezuela, both authors linking the increase to possible arid episodes and/or human activity. Other authors point to various mid to late Holocene dry periods in the Amazon (Absy 1982, Van der Hammen 1982, Markgraf 1989), which correlate with both the Bolivian and the Venezuelan data. The results of the NCAR GCM for the period between 12,000-6,,000 BP also predict greater aridity around 6,000 BP due to weakened monsoonal flows (Kutzbach and Guetter 1986).

Soils of the Llanos de Moxos

The literature on Bolivian soils in general is extremely poor. A few generalizations are in order. In contrast to much of the Orinocan Llanos, the Moxos plains are not underlain by “arrecife” or other indurated “lateritic” structures. Oxisols are uncommon. Instead, Entisols, Inceptisols, Aquolls, and Aqualfs dominate. The northernmost savannas, however, do contain significant areas where iron-rich, indurated nodules (*cascajo*) are prominent on the soil surface (see Hanagarth 1993). These “lateritic savannas” are very different from the more recent alluvial pampas of central and southern Moxos.

The soils of the seasonally inundated interfluvial plains are generally rather shallow (to an impervious Bt) and drainage is restricted by gleyed clay horizons. The plains soils generally have black or dark gray epipedons, with yellow to gray subsoils usually with red and orange mottles. In the Yacuma-Maniqui interfluve, mineralogically the soils are mostly quartz particles, illite, and kaolinite (Hanagarth and Sarmiento 1990). The floodplain and natural levee soils associated with the more active fluvial systems are largely Entisols and Inceptisols.

Lugo López *et al.* (1981) examined seasonally inundated Aquic Tropudalfs under forests at two sites near La Chacra. Neither site is subjected to fluvial influences, which helps explain the well developed, 36-cm deep A horizons At San Carlitos, the B horizons (36-80 cm) had up to 96% silt and clay content and was underlain by a sandier (16%) horizon (80-107 cm), followed by another fine (95% silt and clay) horizon which they designated as the C. The C contained 44% clay, the maximum for the profile. At Villa Bánzer, sand decreased to 15-18% between 13-118 cm and then increased abruptly to 56% at 118-150 cm. The Alfisol classification may not be expected for tropical forest soils, but we should keep in mind that the alluvial sediments of the Llanos de Moxos region are relatively young and that these soils are generally not well-drained internally.

In the wetland savannas, Aquolls can be found where there has been enough stability and time for the development of the mollic epipedon. Histosols are highly likely from the less disturbed wetlands as well, but they have not yet been described.

Soils of the dissected and densely forested surfaces north of the Moxos plains are highly weathered Oxisols (Lugo López *et al.* 1980), described as Tropeptic Haplustox in the Riberalta area (11 S, 139 m). These soils have formed on surfaces which are much older and much more stable than those of the alluvial plains of Moxos.

Just as much as the vegetation that is the focus of this study, the soils are products of multiple interactions of abiotic, biological, and human processes. There are some general correlations between soils and vegetation; however, these are tenuous and do not necessarily imply that either is a cause of the other. Rather, they are both closely linked to the drainage conditions caused by the topography and are both highly sensitive to past and present human activities.

We have now considered some of the more salient aspects of the physical setting of the Llanos de Moxos in general. As our survey demonstrates, there are few studies of the physical geography of Amazonian Bolivia overall or the Llanos de Moxos in particular. The geological, climatological, and hydrological histories are all important to our understanding of the present landscapes and their forest islands. In the next chapter, we examine the human history of Moxos and in the region of La Chacra.

Chapter 4. Human Geography and History of Moxos and the La Chacra Region

We will now review the basic patterns of human activity and culture across the Amazonian lowlands of the southernmost Upper Amazon. As I have argued previously, the human history of the Llanos de Moxos has not been without consequence for the vegetation, local topography, and hydrology.

Archaeology

The Llanos de Moxos is an archaeologically rich, yet still poorly investigated, region. La Chacra itself lies between several documented (i.e., reported in the literature) archaeological sites and many others which are known locally, yet which remain unexamined by professional archaeologists. To the east are the Loma Alta of Casarabe and the mounds around Ibiato. To the west are the numerous mounds along the Mamoré and Ibare rivers.

Erland Nordenskiöld (1913, 1916) was the first archaeologist to enter Moxos. He described mounds, canals, and other earthworks from several sites, primarily to the southeast of La Chacra in the zone of the Río Ibare (Loma Hernmarck, Loma Velarde, and others).

Geologist George Plafker (1963) first reported on the occurrence of extensive raised fields in the western Moxos pampas. He observed these on air photos used for petroleum exploration, as well as on the ground.

However, it was geographer William M. Denevan who was particularly responsible for bringing Moxos to the attention of the English-reading scholarly population. His dissertation (1963), revised as a monograph (1966; Spanish version, 1980), addressed the “aboriginal cultural geography” of Moxos, with an emphasis on the raised field agricultural systems. Denevan has proposed population estimates for pre-contact Moxos (1966, 1976, 1992) which exceed the historical and present rural populations. The 1992 census data for the Beni Department provide an estimated population of 276,174 or 1.29 persons per square kilometer (INE 1993). Of these, 182,748 live in towns and cities of 2,000 inhabitants or more. 57,328 people lived in Trinidad in 1992. Denevan’s (1966: 117) estimates for Moxos in 1690 range from 100,000 to 150,000 based on Jesuit records. Potential yields from the surviving, extensive raised field agricultural complexes could have supported 97,000 people (Denevan, pers. comm., 1995).

Kenneth Lee, born and raised in rural Texas, has lived in the Bolivian Amazon since 1957. A well driller and mechanical wizard by profession, Lee was perhaps the greatest living repository of information on the earthworks and landscapes in Moxos[18]. Lee is responsible for the theory that the raised field agriculture of Moxos was sustained by a combination of “white water” management and mulching with water hyacinths. I spent much time conversing with Kenneth about islas and other topics germane to Moxos research.

Dougherty and Calandra, Argentinean archaeologists funded by both the Smithsonian Institution and the National Geographic Society (1984) provided the first radiocarbon dates from Moxos *lomas*. These dates range from 2775 ± 80 BP to 640 + 60 BP.

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[18] Kenneth Lee passed away February 9, 1999.

Rodolfo Pinto Parada (1987) cleverly discusses both the history of archaeological research and the pre-history of Moxos in two-in-one novel entitled *Pueblo de Leyenda*. In alternating chapters, Pinto narrates the adventures of a real-life personage, Kenneth Lee, and the somewhat speculative, yet insightful, story of a fictional prehistoric Moxeño named Yucu. Pinto, a civil engineer by profession, is a native of Trinidad and a leading member of the local intelligentsia.

Archaeologist Clark Erickson (1980, 1995) is the latest North American scholar to examine the earthwork cultures of Moxos. Erickson *et al.* (1991: 52-57) obtained the first radiocarbon dates for raised field sites in the Llanos de Moxos. The oldest date from the basal unit of canal sediments is 2790 ± 170 radiocarbon years BP That sample is assumed to pre-dates the construction of the agricultural earthworks. The latest date was 800 ± 70 BP from canal sediments, indicating abandonment of the site by 1150 AD at the latest. It has been suggested that the 800 BP date may be associated with a drought period which could have led to the abandonment of the flood-water dependent raised-fields (Beck 1983:28). Few of the many earthworks in Moxos can be attributed directly to the tribes encountered by the Jesuits, except for the palisaded and moated island villages of the Baures peoples.

Pre-Hispanic Earthworks

Here we will briefly review the principal types of earthworks created in prehistoric times in the Moxos plains. Further details on earthworks as they relate to the forests of La Chacra are presented in later chapters.

Canals and ponds. The prolonged low-sun season droughts make water scarce in areas away from perennial streams and rivers. The present residents of La Chacra depend on water collected in a cistern and in artificial ponds excavated in the semialturas. It is logical to assume that earlier inhabitants of the region would construct water-holding structures, be it for drinking and bathing, irrigation, pisciculture, or other uses. The dead-end channels which penetrate the gallery forest at La Chacra were likely constructed for such purposes.

Causeways. These are linear earthworks that may have performed multiple functions, including transportation, hydraulic control, and boundary markers. I examined air photos which reveal that causeways surround the larger mound complexes in the Lagartos region (i.e. Monovi, Perro Muerto, etc.) In 1991 I identified large causeways on the ground at La Mónica and Naranjitos. An informant reported one from the bajío of La Chacra; however, I later learned that he was referring to curving relict levee features which appear between some of the islas. I have identified several smaller causeway type features at La Chacra, all linked to Loma Complex 1.

Mounds (Garbage piles or middens, House mounds, Burial mounds). These are the most abundant earthworks found in the area east of Trinidad, especially around Casarabe. The gallery forests of the Arroyo Agua Dulce, the Río Cocharca, and the San Pablo forest are full of large mounds or "lomas" (Wendy Townsend, Mario Villca, pers. comm.). I observed forest mounds with funeral urns and bones at Estancia La Mónica, northeast of El Cerrito, in 1991. One of the mounds was cultivated with bananas which grow especially well on these culturally-enriched soils.

Raised fields. Elongate rectangular raised fields (*camellones*) are known from Naranjitos-San Carlitos, some 15 km due south of La Chacra (Erickson *et al.* 1991: 18-23); however, these features are relatively rare east of the Mamoré. West of this river these fields are nearly ubiquitous features. I have speculated that raised field agriculture was uncommon east of the Mamoré due to the lack of more nutrient-rich "white" waters of Andean origin. Small flat round mounds are common in the savannas and gallery forests in the Lagartos region; however, the evidence seems to indicate termites, not humans as the constructors.

Cultural Groups at the Time of Jesuit Contact (1680s)

A salient characteristic of pre-Hispanic Moxos was the considerable linguistic and ethnic diversity of its human inhabitants. The Moxo and Baure languages are Arawak in origin, but others are of Panoan, Guaranian, Chiquitoan, and Mosetenan (related to Aymara) origins. We should begin by noting that most of the tribes could be classified as either forest tribes or savanna tribes. The latter were most rapidly assimilated into the Jesuit and post-Jesuit Hispanic culture, while the former tended to retreat deeper into the forests and remained isolated until rather recently.

There were six principal savanna tribes at the time of Jesuit contact: the Moxo, the Movima, the Cayuvava, the Canichana, the Itonama, and the Baure, each of which occupied a rather discrete territory (Denevan 1966: 41). These territories largely correspond to somewhat distinct eco-physiographic regions. In the forest regions which surround the savannas lived tribes such as the Chimane (southwest), the Yuracaré (south), the Sirionó (southeast), the Guarayo (east), and the Chácobo (north). All of these tribes have surviving remnants.

The Moxo people occupied the territory on either side of the Mamoré between the Río Apere to the west and the San Pablo Forests, just to the east of the modern village of Casarabe. Their northern boundary very roughly corresponds with the northern limits of the zone of oriented lakes. To the south, the Moxo did not extend much beyond the confluence of the Chapare and Mamoré rivers., where their territory abutted the zones occupied by the reputedly more “warlike” forest tribes such as the Yuracaré. Their northern neighbors, the Movima west of the Mamoré and the Canichana east thereof, were also supposedly less pacific folk than the Moxo. The Moxo tribe thus did not occupy the entire area of the “Llanos de Moxos,” only its southernmost extension.

The Chacra region lies entirely within the historical territory of the Moxo tribe, but it is also near the western frontier of the once-nomadic Sirionó. The Sirionó have received significant attention from anthropologists. Holmberg’s *Nomads of the Long Bow* is a widely read account of his experience in the forests not far east of La Chacra during the 1940’s. Allyn Stearman (1987) followed up on the Sirionó with her book *No Longer Nomads.* I visited the Sirionó in 1994 at their principal settlement, Ibiato, site is only about 30 km east-northeast of La Chacra.

European Settlement of the Region of La Chacra

The first Spanish town in the Bolivian Amazon lowlands was Santa Cruz de la Sierra, founded in 1561, near the edge of the northernmost Gran Chaco. Penetration northwards into Moxos was a slow and difficult process.

Loreto, the first Jesuit mission of Moxos, was established on the shores of Laguna Azere near the east bank of the Mamoré in 1682, some 50 km south-southwest of La Chacra. Soon thereafter, Trinidad was founded in 1686. Both of the modern towns bearing these names have moved away from the sites of the original missions due to flood problems. Historian David Block recently (1994) published an important book on the Jesuit period of Moxos.

La Chacra lies within close proximity to these earliest European settlements in Moxos. We can safely speculate that the inhabitants of the region were either rapidly incorporated into the missions or were forced to move further into the hinterlands to the east of the missions. It is thus likely that the forests and savannas of La Chacra were abandoned by their indigenous inhabitants over three centuries before the present.

The Jesuits were the first to call the Moxos forest islands “islas,” as evidenced by the following extract from a report on the extent of mission territories written in 1715: “Desde esta línea comprende la jurisdicción de la Trinidad las *islas* y campiñas, los montes y arroyos que caen hacia el sur…[19]” (Padre Antonio Garriga, 10 October 1715 in Chávez Suárez 1986: 267). This statement also likely indicates that the islas were considered useful as resources to be exploited by the missions.

The area east of the Mamoré was said to be a zone of open savannas followed by the “Guarayo Forest”, which corresponds to forest zone presently beginning just east of Casarabe (Map 2). The Jesuits never did successfully establish missions in the forests due east of La Chacra. Only much later did the Franciscans establish missions in the Precambrian shield region between the Jesuit provinces of Moxos and Chiquitos to the southeast.

Introduction of Livestock to the Moxos savannas

Cattle were first introduced to the Moxos savannas at the Loreto mission in 1686 by Cipriano Barace, a Basque Jesuit priest from Isaba de Navarro, Spain. Barace is honored by Trinidad’s newest and most notable statue, at the northern terminus of the avenue which bears his name. Barace journeyed northwards from the city of Santa Cruz de la Sierra with a herd of 200 cattle, of which only 86 arrived at the mission of Loreto. These cattle were likely of Andalusian stock bred in the missions of Argentina and Paraguay.

For over two centuries these criollo cattle bred freely in the pampas and forests of Moxos, subject only to natural selection and occasional harvesting by cattle hunters. These animals soon adapted to the wet conditions, which are not altogether different from the Andalusian *marismas* (coastal marshes and estuary environments in southern Spain). Only in the 20th century were Zebu (*Bos indicus*) breeds introduced to Moxos. The present cattle of Moxos are largely Criollo/Zebu hybrids or pure Zebu. Pure criollo cattle are rare today, except on a few ranches where they are selectively bred. This relict breed is known as the *Criollo Yacumeño*.

The Jesuit mission herds rapidly expanded and the plains around each mission undoubtedly underwent vegetation changes under new fire and grazing regimes. The numbers of feral cattle which roamed the plains will never be known with certainty, but all reports suggest that the herds were rather immense. Even in the early 1900’s, the wild cattle posed considerable inconveniences on travelers on the savannas as evidenced by the accounts of the well-known explorer Percy Fawcett. I will discuss the impact of livestock and fire on the Moxos landscapes in considerable length in later chapters.

The Jesuits were expelled from Spanish America in 1767. Thereafter, the missions of Moxos were run by secular priests and governmental administrators. Only recently have the Jesuits returned to Moxos (see Jones 1991).

An important period in the history of Amazonian Bolivia was the Rubber Boom between 1886 and 1912. Major changes in the population structure of Amazonian Bolivia occurred as the result of two processes: 1) the influx of Spanish Bolivians from Santa Cruz de la Sierra and 2) the forced

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[19] “From this line, the jurisdiction of Trinidad includes the forest islands and prairies, the forests and streams, which lie to the south…”

movements of indigenous male laborers. Many of the Spanish families of the Beni originated with the migration of ambitious men from Santa Cruz into the Beni. The most dramatic event, however, was the depopulation of savanna villages and indigenous communities as their men were rather forcibly recruited for labor in the rubber districts.

After the crash of the Bolivian rubber industry, many of the *cruceño* capitalists remained in the Beni as ranch/plantation owners and urban entrepreneurs. Much of the land immediately east of Trinidad as far as El Tajibo (10 km west of La Chacra), was once part of the Suárez Brothers cattle empire, whose headquarters was situated atop a massive prehistoric mound on the Río Ibare now known as Loma Suárez.

La Chacra Ranch

The site occupied by La Chacra ranch has long been an important place in the region. Pinto Parada (1978: 114) noted that to reach the Sirionó mission of El Eviato (i.e., Ibiato) in the 1930s, one followed the trail that went from Trinidad to La Chacra, then continued through the Bajío de Totaí (the bajío of La Chacra), through a ranch of the Suárez Brothers to El Cerrito, and so on. La Chacra was founded in 1955 by an uncle of the current owner. Beyond La Chacra, there are numerous ranches to the north, northeast, and east. However, with the exception of the small villages of Cernández, El Cerrito, and San Juan de Agua Dulce, there are no significant centers of populations beyond the road.

La Chacra is a ranch with excellent accessibility throughout the year due to its location along the Trinidad-Santa Cruz Highway (finished in 1985). All-year road access to La Chacra increased the utility of the ranch and expanded its range of economic activities. In addition to beef on the hoof, chickens, eggs, and young hogs are sent to Trinidad for sale. Tamarind fruits are collected from the trees around the house. Small quantities of grapefruits and sweet bananas (*guineo*) are produced in an orchard immediately adjacent to the house.

The ranch is approximately 2000 ha (20 km^2) in area. Only a few hectares immediately around the house have been cleared for plantations, pastures, corrals, living areas. The ranch owners live in Trinidad, but visit frequently to manage the livestock operations. The human population of La Chacra varies from time to time, but there are generally 14-16 people living there, including the small children. The ranch workers do not hunt for necessity, although they will occasionally hunt for pacas or armadillos just for the sport of it or to vary the menu. The only firearm on the ranch is a vintage 22-caliber rifle. In spite of its name (a chacra is a swidden garden), little effort is put into fruit or vegetable production. Most of the day’s activities are spent on maintaining the infrastructure, herding and livestock care, cooking, collecting firewood, and other tasks directly related to running a cattle ranch.

During my fieldwork period, the cattle herd was approximately 1,300 head, which calculated to a rather high stocking rate of 1.54 ha per animal. This number does not include the 30 or 40 horses which also roam the range (the horses tend not to stray far from the corrals, however). At times in the recent past, herd numbers have been considerably higher during periods when animals were moved from other ranches west of the Mamoré where fluvial flooding is often severe.

La Chacra continues to be an important as a crossroads point for the ranches of the northern interior. The trail across the bajío is well trodden, even in the rainy season. During the dry season trucks, jeeps, and motorcycles traverse the parched bajío, but in the rainy season travel is restricted to horseback, muleback, or oxcart. (I did not observe the use of the riding ox or *buey-caballo* around La Chacra, although I saw it elsewhere in the Beni during my fieldwork.)

Establishment of Modern Villages (Casarabe, Somopae, Elvira, etc.)

East and southeast of Trinidad, there are several minor villages inhabited largely by mestizos and indigenous peasants (Map 2). These villages are based on slash and burn agricultural production from swidden fields in the adjacent forests. These villages are located on roads constructed during the 1950s and 1970s. However, many of the villages predate the modern roads, as they lie along the old trails to Santa Cruz or other points.

The first settlement east of La Chacra is the roadside village of Elvira, the site of a highway checkpoint and a few food stands. Somopae is built around a large prehistoric earthmound in a stretch of forest south of the Cañada de los Lagartos, near Laguna Perotó. Further down the road lies Casarabe, the site of an “Indian School” used to “incorporate” the Sirionó during the 1930's-40's (see Pinto 1978 and Holmberg 1969). La Chacra lies at the halfway point between Trinidad and Casarabe. East-northeast of La Chacra and west-northwest of Casarabe lies El Cerrito, yet another village built on and around prehistoric mounds.

The “school” at Casarabe was founded in 1937, 12 leagues (60 km) east of Trinidad. Ethnologist Stig Rydén (1941) visited Casarabe in 1938. The first trail to Casarabe (initiated in 1939), however, was not routed through La Chacra, but rather to the southeast of Trinidad, past Laguna Suárez to Sachojere, then back north-northeast to Somopae and Casarabe.

The Sirionó frequently ventured into ranches and chacos to steal metal tools which they could not obtain otherwise (Wilson Melgar, pers. comm., Sirionó informant from Ibiato). It is thus highly probable that they made excursions through the area of La Chacra in earlier days. However, Sirionó impact on forest islands has likely been negligible, except for modern cultivation and unintentional seed dispersal.

The Trinidad-Santa Cruz Highway

The Trinidad-Santa Cruz highway forms the boundary of La Chacra on its southwest-facing edge (Map 3). In 1978 , a 200 m wide right-of-way was cut through the extreme southern part of La Chacra, running roughly parallel to the Cañada de los Lagartos. The opening rapidly was filled by spiny mimosa shrubs and other ruderal woody plants. I first traveled to La Chacra from Trinidad on horseback along this trail in June 1979. However, we did not use the right-of-way all the way to La Chacra. Instead, we followed the old trails through the forests. From El Tajibo, we took the *camino real* trail through the gallery forest and woodlands along the Cañada de los Lagartos.

The highway more or less follows the high ground of semialturas and alturas through woodlands and forest. However, there are several which traverse open bajíos as well. At El Tajibo the road approaches the Cañada de los Lagartos and crosses a tributary which flows out of a bajío from south to north. This tributary has also long been known as the Cañada de los Lagartos and was always a difficult crossing until the completion of the road. Today, however, this old cañada is barely visible and flows under the road through corrugated tubes. In the "old days" this crossing was even too deep for oxcarts and had to be crossed by floating in *pelotas* (oxhide rafts). One informant reported that the trail along this part of the cañada was covered with white sands which burned his bare feet during his youth (perhaps some 30 years prior). The road then follows southeast some 500 m or so from the weakly meandering cañada. The cañada gets closer and closer to the road and crosses beneath it at a point I have never clearly identified after tens of trips across it. Eventually, the road hooks up with the older road from Trinidad via Sachojere, Somopae, and Perotó from the south and continues to Elvira, Casarabe and points eastward (Map 2).

The Santa Cruz-Trinidad highway was completed in 1985, with only six km of asphalt heading east of Trinidad. However, upon my departure from La Chacra in 1994, work had begun for the asphalting of the road between Kilometer 6 and Casarabe. The road work camp was built upon a large loma just off the highway near the northward bend of the Cañada de los Lagartos (Map 3). One negative consequence of the highway has been the fragmentation of landholdings by the selling of small "farms" to well-to-do Trinitarios who want a weekend home in the country (*el campo*). This fractionization of properties has increased the population density along the highway and increased the destruction of semialtura woodlands and gallery forests.

In the Llanos de Moxos we can identify landscape features which date to three major periods of human history: 1) the pre-human era, 2) the pre-Hispanic period, and 3) the post-contact/modern period. Quite often we find a superposition of temporal elements, for example, a loma built upon a natural levee with a modern house constructed upon the loma.

Forest islands have likewise been formed by various processes during each of these periods. Many islands are likely the result of a series of processes from all three periods.

Chapter 5. Overview of Vegetation Units and Island Types at La Chacra

Local Landscape Units

The landscape of La Chacra (Map 3) is composed of three principal topographic units:

1. The most extensive unit is the *bajío*, which is a low-lying seasonal wetland completely without trees, except on elevated islands.
2. Along the senesced river known as the Cañada de los Lagartos (channel width is ca. 60-70 m), we find the highest ground, largely corresponding to old levee deposits and covered by gallery forest. This unit is known locally as *altura*.
3. Between the alturas and the bajío is what the German ecologists (e.g. Beck 1983) have named *semialtura*. This unit comprises the intermediate ground, where we find what might represent true savanna, that is, a mixed formation of scattered trees and a continuous herbaceous understory. The semialtura is a most interesting zone, as it is here that the balance between woody and herbaceous vegetation is most sensitive to changes in fire, grazing, and soil moisture regimes.

The two basic vegetation units recognized throughout the region are *monte* (forest) and *pampa* (savanna, grassland, or herbaceous wetland). Tall "hylaean" forest is referred to as *monte grande*, which does not occur in the immediate vicinity of La Chacra.

Four basic vegetation types occur at La Chacra.:

1. Aquatic herbaceous formations are the most widespread, occupying the flat, seasonally inundated plains (*bajío*) as well as the bed of the old river channel (*cañada*).
2. Savannas (scattered trees and shrubs in an herbaceous matrix) are found where the flood/drought cycle is less extreme such as on low relief features such as old ant or termite mounds and on the long backslopes of the levees (*semialtura*).
3. Woodlands (visual horizon is closed by trees) are found as well on the levee backslopes.
4. Closed-canopy gallery forests cover the levees proper (*alturas*); however, these are occasionally interrupted by short stretches of savanna or wet herbaceous formations.

Island and Mound Types in the Vicinity of La Chacra

The local classification schemes outlined above are useful; however, they do not discriminate between finer differences which are of interest to biogeographic and landscape development studies. I have identified twelve distinct "forest island" and "vegetated earthmound" types (Table 1) at La Chacra and its immediate vicinity (i.e., within a radius of 15 km or so). These classifications are entirely subjective, i.e., they are the product of a human mind and were not generated by a computer. The categories are based on my field observations, informant data, and airphoto interpretation. Both botanical and geomorphological criteria were used to define the island types. All forests in the region of La Chacra, exclusive of the Mamoré/Ibare gallery forests, can be considered to be insular to varying degrees and of varying magnitudes of area. The gallery forests are largely discontinuous and the larger units of forest are all surrounded by savanna or wetland matrices.

Table 1. Island and vegetated earthmound types identified at or near La Chacra.

Island or mound type	Characteristic plants	Substrate characteristics
Islands of woody vegetation		
Attalea-bearing islands in the bajío	*Attalea phalerata, Ficus trigona,* primarily animal-dispersed taxa.	Deeper, sandier soils, often with calcareous nodules.
Semialtura woodland islands in the bajío	*Copernicia alba,* semialtura-type trees	Eroded A-horizon, clayey, compacted surfaces.
Copernicia-palm groves	*C. alba*	Low islands, clayey, salt accumulations
Semialtura islands	*C. alba, Ficus, Guazuma*	Similar to the above, but somewhat higher, often with sands over clays.
Semialtura woodland islands	*C. alba, Cordia glabrata, Acrocomia, Acacia polyphylla, Pithecellobium scalare*	Silty, light-colored soils, numerous termite and ant mounds
Attalea-palm groves in the semialturas	*A. phalerata, Sterculia apetala, Randia*	Termite mound soils
Termite mound islets ("murundus")	*Tabebuia* spp., *C. alba, Astronium fraxinifolium, G. americana, Cordia, Cereus, Geoffroea, Sorocea, Machaerium*	Termite mound soils
Gallery forest fragments along cañadas or active streams	Diverse: *A. phalerata, Triplaris americana, Ficus, Calycophyllum, Hura, A. polyphylla, Albizia niopiodes, Anadenanthera colubrina, Syagrus sancona*	Variable, depending on landscape position and prehistoric human influences. Rarely as sandy as the islands of the bajío.
Artificial mounds		
Recent mounds	*Acacia albicorticata, G. ulmifolia, Cecropia* sp., *Copernicia*	Earth accumulated for construction of excavated ponds, roadways, etc. Mostly clayey materials.
Prehistoric mounds	Animal-dispersed taxa, similar to the altura-type islands of the bajío.	Earth excavated from the surrounding bajío or semialturas. Rich in ceramic sherds, snail shells, and

other cultural debris.

Table 1. (continued)

Mounds within forests		
Termite and ant mounds	*Cordia* aff. *nodosa*, *Acacia polyphylla*, *Triplaris americana*. Little herbaceous or suffrutescent groundcover.	Earth moved from the subsoil by the burrowing insects. Low organic content.
Prehistoric house mounds	Usually well covered by low-growing herbaceous and suffrutescent plants. Often with older trees than the insect mounds.	Organic and ceramic-rich mounds upon the larger artificial platforms
Artificial platforms and large mounds (*lomas*)	Diverse assemblage of trees and shrubs that reflect the improved drainage conditions and enhanced likely enhanced fertility on the platforms. Lomas support species with most drought tolerance and/or least tolerance to poor drainage.	Organic and ceramic-rich cultural horizons on platforms reworked by soil fauna overlies yellowish clayey material excavated from subsoil. Lomas clayey throughout.
Causeway-like features	Rows of *Attalea phalerata*	Associated with canals and cañada.

Islands of woody vegetation

These include all units of woody vegetation at La Chacra, where there is no "continental" or "mainland" forest or woodland, only numerous fragments and islands.

Attalea***-bearing forest islands in the bajío***

These are the classic islas of the Moxos pampas, 30-100 m diameter, circular to reniform patches of forest, which dot the horizon (Plates 1-3). Probably largely of fluvial depositional origin with subsequent human and biological modifications. Mostly sandy at surface, sometimes with (biogenic) carbonate accumulations. These forest islands usually contain *Attalea phalerata* and *Ficus* spp., possibly with *Sterculia apetala*, *Vitex cymosa*, *Genipa americana*, *Rheedia achachairu*, *Salacia elliptica*, *Coccoloba* sp., *Inga* sp., *Ceiba* sp., *Acrocomia aculeata*, *Guarea* sp., and others. These islands bear little evidence of mound-building termites or ants. The islands are usually surrounded by dense *Cyperus giganteus* stands (*yomomo*) and depressions dominated by *Pontederia subovata* and *Eichhornia azurea*.

These islands do not possess fire-resistant edges, as suggested elsewhere in the literature. Rather, the island edge species are the trees most tolerant of prolonged inundation. In fact, most fires die out before they reach these islands. The 5-10 m break between the *Cyperus giganteus* stands and the trees is dominated by low-growing aquatic vegetation that does not carry fires. The islands are likely to burn only under conditions of extreme wind and drought. These are the islands most isolated from the “mainland” forests, i.e. the gallery forests along the cañada, at distances of 3-5 km. These islands are easily identified on dry-season air photos due to their largely evergreen composition.

Semialtura woodland islands in the bajío

These islands have only scattered trees, which may or may not be relics of a once closed forest. Common trees include *Copernicia alba, Acrocomia aculeata, Vitex cymosa, Pithecellobium scalare, Samanea tubulosa, Cecropia* sp., and *Genipa americana*. The deciduous nature of these islands contrasts greatly with the *Attalea*-dominated semideciduous islands of the bajío. The tree species composition is similar to that of many semialtura surfaces elsewhere. The soils are very heavily trampled and manured, non-calcareous, and clayey at shallow depth. These islands may be covered or surrounded by *Ipomoea carnea* or other weeds such as *Ambrosia* or *Heliotropium*. On air photos, these islands appear as light patches in the pampas.

Copernicia *groves (palmares)*

These are groups of closely-spaced, tall, smooth trunked palms that occur on slightly elevated surfaces in the bajío. The palms sometimes have exposed roots at the base of the trunks which may represent the elevation of a former surface lost to erosion. These islands are completely inundated for long periods; however, the upper portions of the palm root masses are exposed to the air at all times.

Artificial mounds in the bajío

As suggested by Denevan (1966), many of the islas of the Moxos pampas are indeed artificial earthmounds constructed in pre-Hispanic times. There is only a single example of this type of isla at La Chacra. It is found halfway between the north gallery forest and the first *Attalea*-type isla in the bajío. This island is characterized by deciduous semialtura-type trees. The mound itself is flat and low and constructed from the adjacent pampa subsoil.

Islands in the semialtura (not including smaller termite mound islands).

Islands at the semialtura/bajío ecotone. These low islands are dominated by *Copernicia alba, Ficus* spp., and *Guazuma ulmifolia* and measure 15-20 m in diameter. Soils are fine sands at surface, underlain by mottled clays rich in crystals of sulfate salts. These islands may be completely inundated for short periods.

Semideciduous woodland islands. Abundant *Copernicia* and *Acrocomia* palms replace *Attalea* in a matrix of mixed deciduous and evergreen hardwoods such as *Acacia polyphylla, Cordia glabrata, C. alliodora, Enterolobium contortisiliquum, Pithecellobium scalare, Piptadenia robusta, Sterculia apetala* and *Triplaris americana.* Inundation is only very brief and shallow; however, most of the trees occur on low mounds 2-5 m in diameter. At La Chacra, there is only a single, albeit prominent, example of this type of island, which measures roughly 700 by 300 m.

Micro-groves of *Attalea* on old termite mound surfaces in the gallery forest/palmar transition. These groves form upon old mounds which are not inundated. These small palm groves are adventitious, not relictual, as evidenced by the young age of the palms.

Termite mound "murundus[20]" of semialturas

There are actually several variations of this feature. One is the small mounds associated with *Copernicia*, shrubs, and sometimes *Cereus* cacti. Another is the tajibal mound with *Tabebuia heptaphylla* and *Astronium fraxinifolium*. The larger, flattened mounds are often closely spaced and create a type of woodland where the woody plants are largely restricted to the mounds and the intermounds are vegetated by grasses and sedges (Plate 6). The principal trees upon the mounds are deciduous and include *Tabebuia heptaphylla, Tabebuia aurea, Genipa americana, Vitex cymosa, Cordia glabrata, Machaerium* cf. *hirtum, Pithecellobium scalare,* and *Sorocea saxicola* var. *saxicola*. Shrubs are also abundant, especially species of *Celtis, Cupania, Casearia, Randia,* and *Xylosma*.

Gallery forest fragments along the cañada

The gallery forest of La Chacra is really an archipelago of closely-spaced forest fragments (See Map 3). Some of these fragments are clearly of recent anthropogenic origin, however most others are not. In spite of their fragmentation and human disturbance, these forests are rich in mammals (including monkeys) and large birds. Principal trees include *Attalea phalerata, Acacia polyphylla, Ampelocera ruizii, Inga* spp., *Spondias mombin, Triplaris americana, Cordia nodosa, Cordia alliodora, Maclura tinctoria, Sapium glandulosum, Ficus* spp., *Albizia niopoides, Hura crepitans,* and *Calycophyllum spruceanum.*

The gallery forest is extremely heterogeneous, largely in response to drainage characteristics and pre-historic modification. Along the cañada edge, there are complex zones of flood forest characterized by *Hura crepitans* and *Calycophyllum spruceanum*. At the other extreme, the very well-drained sites are characterized by upland deciduous elements such as *Anadenanthera colubrina*. The major zone of pre-historic earthworks is dominated by *Attalea, Ampelocera, Spondias,* and an understory of *Bactris* sp. (See Plate 7).

Mounds within forests

Termite and ant mounds in the gallery forest

Active or recently abandoned termite and ant mounds in the forest are abundant, most frequently along the forest edge. These large flattish mounds often contain numerous trees, shrubs, and saplings; however, an herbaceous groundcover is lacking.

Prehistoric individual house mounds in the gallery forest

These raised surfaces are usually between 5 to 8 m in diameter and generally not more than 1 m high. They contain abundant ceramics, however they are frequently inhabited by mound building ants and termites as well, which contribute to the preservation of these mounds by adding earth materials on the mound surfaces. These are likely individual house mounds from the pre-Hispanic period. These mounds are restricted to the “Ceramic Forest” platforms.

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[20] *Murundu* is a Brazilian term which is widely used in the international literature; however, it is not used in Moxos.

*Artificial platforms and large mounds (***lomas***) within the gallery forest*

These mounds reach at least 2.5 m in height above the adjacent surfaces. The vegetation of these mounds is rather sparse in comparison the surrounding forest, probably due to their construction of compacted clays. Both of the loma-type mounds examined at La Chacra have yielded ceramics on or near their surfaces. Soils are compact, clayey, and yellowish brown.

Causeway-like features of the cañada and its gallery forest

These are low, linear features 50-200 m long which extend into or border seasonally inundated channels or canals. Some of these elongate dikes have been fragmented into discrete units. Like the artificial mounds, these earthworks are composed of rather clayey and compacted soil materials. These features are usually dominated by *Attalea phalerata*, with thick root mats.

Artificial hill/mound complexes : Monovi, Perro Muerto, Perotó, Ibiato, etc.

These are unquestionably prehistoric artificial earthmounds of great relief and extent, usually associated with causeways/dikes and other features. These features are "lomas," never confused with "islas" by the local inhabitants. These features strike the terrestrial observer as true hills, not just low mounds; for example, the Ibibate mound (Map 2), measured by archaeologist Clark Erickson in the nearby Sirionó territory, rises 18 meters above the level of the forest (C. Erickson, pers. comm., 1995). Some of these macro-mounds are in otherwise completely open pampas, several kilometers from the nearest high ground, representing completely artificial forest islands of considerable scale. While none of these macro-complexes lie within La Chacra, they are surround it on all sides (Map 2).

Other mound types

Sandy mounds with low graminoids and forbs

These small mounds (some only 3 m or less in diameter) are sometimes extensions of forested island surfaces and other times are independent of extant forest islands. The vegetation is low-growing and sparse, with abundant sedges and forbs. The surface soils are fine sandy and compact. These low mounds are completely inundated during the summer rainy season.

Artificial mounds constructed by cattle ranchers

There are numerous low mounds created as the by-product of ranch improvement activities, primarily the excavation of watering holes. Such mounds are extremely hard and clayey, but are often colonized by semialtura or ruderal trees such as *Acacia albicorticata, Pithecellobium scalare,* and *Guazuma ulmifolia*.

Roadside berms

When the Santa Cruz highway was constructed in the early 1980s, large quantities of earth and plant debris were accumulated into long, linear berms parallel to the road and just outside of the highway right-of-way. These are well-drained sites and are now entirely covered by a dense tree cover. A conspicuous element here is *Cecropia*, which is only very rarely encountered elsewhere at La Chacra.

Non-forest vegetation units in the region of La Chacra

Here are included what is generally lumped together as “savanna” by tropical vegetation mappers and plant ecologists. On a coarse degree of resolution, I include here woodlands, savannas, and aquatic vegetation. These units comprise the spatially-dominant non-forest matrix (ca. 80%) of La Chacra, within which the islands occur.

Woodlands

I consider those wooded areas without a contiguous canopy, with a well-developed herbaceous understory, and with a closed visual horizon to be woodlands. These woodlands are not dominated by typical Neotropical savanna elements, but rather by deciduous trees. These woodlands largely fringe the forests on the semialturas. Islands of forest trees occur within these woodlands.

Savannas

I restrict the application of the word savanna to formations containing woody plants scattered in an herbaceous matrix, where the woody plants are found on roughly the same ground surface as the herbaceous plants, i.e., not on distinct, elevated islands. Landscapes composed of ecologically and spatially segregated zones of woody and herbaceous vegetation should considered to be parklands, not savannas. One such parkland landscape would be a mosaic of wetland and woody formations where the woody plants are restricted to elevated island surfaces. This is just the situation found in the inner bajíos of La Chacra. Formations devoid of woody plants are either grasslands or wetland formations (i.e., where aquatic taxa are dominant). The “true” savannas are limited to the semialtura surfaces, generally sandwiched between the woodlands or forests and the bajío wetlands.

Wetlands

The majority of the area of La Chacra and the surrounding region is covered by seasonal wetlands. Here, the dominant vegetation is composed of aquatic taxa. This dominance is expressed both in terms of biomass and length of growing season. Although some areas remain wet throughout most years, most of these wetlands experience desiccation during the low-sun season (i.e., winter) dry season, which lasts between 2 to 5 months, depending on the annual variation in precipitation and topographic position. The wetlands are devoid of woody plants, except for those on the islands and occasional aquatic suffrutescents such as *Aeschynomene* and *Ipomoea fistulosa*

In the next four chapters we will investigate the island and mound types, vegetation formations, and topographic features of La Chacra in detail. We will begin by exploring the landscapes by foot, armed with an automatic level, and ready for adventure…

Chapter 6. Topographic Transects.

With the invaluable aid of my assistants Pachito Carrasco and Armando Ruiz, I measured several topographic transects over a variety of surface types at La Chacra with a Sokkia 32x automatic level, tripod, 4-m folding rod, and plenty of machetes. This work was among the most enjoyable and interesting at La Chacra. We had numerous encounters with anacondas and other native fauna as well as with exotic creatures such as rangy Zebu bulls. The locations of the topographic transects are indicated on Map 4.

Transect 1. Gallery Forests-Ceramic Forest-Cañada

The first transect examines the gallery forests and cañada near the house at La Chacra (Fig. 3). We started measuring in a cleared paddock at a point about 40 m from the edge of the forest. This point became our arbitrary benchmark for various transects (i.e. relative elevation of 100 m. The approximate elevation of this site is 160 m above sea level). We followed the trail through the forest, more or less parallel to the cañada. The ground rose and fell, with only about 35 cm of relief. The trail follows the crest of the low natural levee north of the cañada, crossing largely well-drained terrain, with only a few muddy spots. The principal dominant element is the *Attalea* palm. The trail lies above the flooded forest zones characterized by numerous *Hura crepitans.* These flooded zones occupy depressions some 30 cm deep on the average.

The first feature of note is the Trans-Gallery Canal, which must be traversed in order to follow the trail into the West Ceramic Forest and points to the southeast. At the point where the trail crosses, the canal is about 13.5 m across and 30 cm deep. From the point immediately across the canal, the landscape changes abruptly. Here we can sense for the first time that there is a definite slope and that the trail leads "uphill." The slope rises 1.6 m over a distance of 57 m as we reach the edge of the "top" of the platform. We then rise another 60 cm until we reach the foot of the Loma another 33 m away. If we were to take a shovel and randomly dig anywhere upon this elevated surface, we would soon hear the clinking and crunching of steel against ceramic.

Fig. 3. Transect 1. Gallery Forests-Ceramic Forest-Cañada

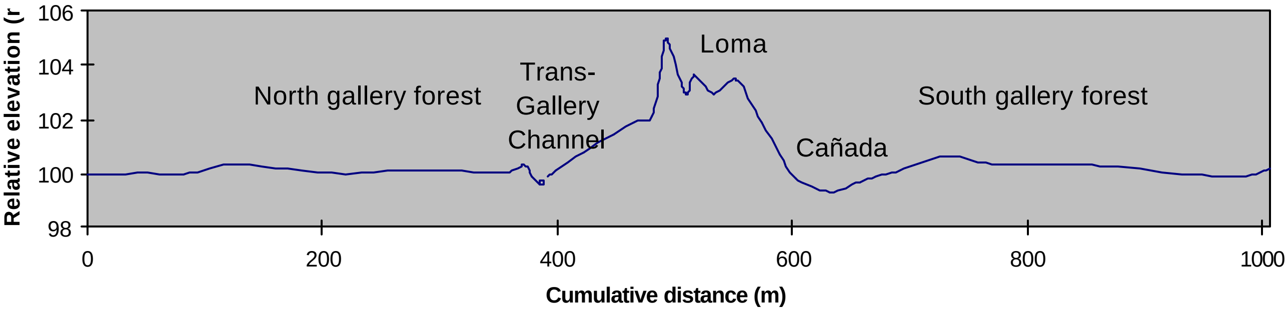


Table 2. Topographic Transect 1 -- Levee forests and Cañada de los Lagartos

Distance (m)	Elevation (m)	Water (cm)	Description
0.0	100.000	0	Near large *Tabebuia heptaphylla* tree by corner of white paddock in cleared altura
10.6	99.916	0	Edge of termite mound with *Copernicia* palm at edge of artificial watering hole
41.9	100.022	0	On trail at gate to gallery forest
82.1	100.003	0	In forest on trail
126.6	100.348	0	In forest on trail
171.3	100.160	0	First bend on forest trail
220.7	99.987	0	In forest on trail
267.6	100.134	0	On trail above area with several *Hura crepitans*
318.6	100.098	0	In forest on trail
355.8	100.028	0	In front of huge Azocaró tree (*Neea* sp.?) in forest.
372.5	100.304	0	High point in forest near bank of Trans-Gallery Canal
378.7	99.905	0	Large tree root at edge of Trans-Gallery Canal
385.2	99.606	0	In Trans-Gallery Canal
391.2	99.876	0	Edge of Trans-Gallery Canal
399.4	100.125	0	Behind Ficus root on trail in forest above canal
422.1	100.760	0	On trail upslope of Ceramic Forest platform
448.2	101.477	0	On trail, before old swidden site with abundant *Urera baccifera*
466.3	101.901	0	Behind Big Cántaro Pit in Pica-Pica clearing
480.8	102.072	0	Near foot of Loma 1, in forest
488.0	103.693	0	On lower slope of loma, in forest
493.1	104.965	0	Top of loma near "Pit 1", in forest
509.0	102.973	0	Down on foot of saddle of loma, in forest
517.0	103.627	0	Crest of loma saddle, in forest
533.2	102.949	0	Trail on loma slope, in forest
552.4	103.461	0	Lower slope of loma near fallen tree (toward cañada) in forest
573.2	101.886	0	Down slope of platform toward cañada, in forest
589.9	100.723	0	Slope down to cañada, in forest
602.1	99.824	0	Edge of cañada
631.7	99.340	51.5	30 m into cañada, in water
656.8	99.686	20	57 m into cañada, in water
672.2	99.866	0	Edge of south gallery forest, 70 m from opposite shore.
690.9	100.122	0	South gallery forest
732.2	100.605	0	Old termite mound in South gallery forest.
777.2	100.296	0	At corner of Chaco fence in forest
848.0	100.323	0	Along fence in forest
975.7	99.847	10	Across cañada in cleared zone near house
1006.7	100.162	0	FS to BM1

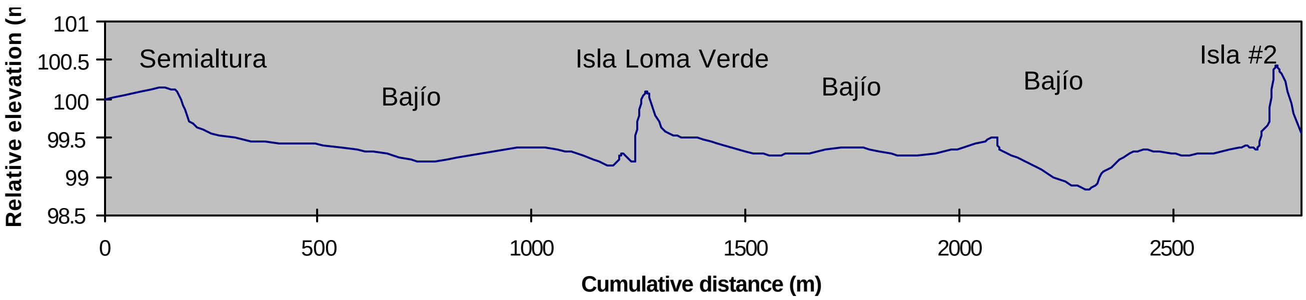
We are in the heart of the “Ceramic Forest.” The elongate loma rises more than 3 m above the platform it sits upon. The slopes of the loma are very steep, often exceeding 45°. We measured a few points on this large mound and then crossed over the lower saddle in its central portion. From there, we descend the platform toward the cañada. The lower slope of the loma descends 3.75 m before reaching the waters of the Cañada de los Lagartos which lies some 50 m away. At this point, the cañada channel is 70 m wide and about 50 cm at its deepest point. The cañada is thus a very broad and flat channel, clogged with dense floating and emergent aquatic vegetation. From the bed of the cañada to the top of Loma 1, there is a rather surprising 5.62 m of relief in an otherwise remarkably flat landscape.

After sloshing across the cañada, we enter the south gallery forests. These are very different from the “Ceramic Forest” we just passed through. Here, the relief is considerably less and the only prominences are those created by the mound-building termites and ants. The greatest elevation we encounter here is on an old termite mound which lies 83 cm above the edge of the cañada. We cross this forest and head back toward our benchmark across the cañada. This transect opened my eyes to the vast amount of earth moved by the prehistoric residents of La Chacra on the north shore of the River of the Alligators.

Transect 2. Semialtura-Isla Loma Verde-Isla 2.

Our next adventure in topography led us across the bajío to Isla Loma Verde and Isla 2 (Fig. 4). We began our expedition in the shade of an *Acrocomia* palm in a very muddy and very urine and manure-laden paddock north of the house on a semialtura surface. This surface is never inundated. We bear toward Isla Loma Verde and proceed out into the pampas of the bajío. At a distance of 340 m we stood in 3 cm of water and a sea of water hyacinths. We descended 54 cm from our starting point. We continued to traverse the gently sloping bajío. All we could see is a flat sheet of water and aquatic vegetation; However, we found that the water continued to deepen gradually. Nearly 1.2 km from the *Acrocomia*, we stood in over 55 cm of warm water. After 1,248 m of wetland, we reached the exposed edge of Loma “Isla Verde.” We staggered on the first firm ground in quite some time and took refuge in the shade of a scraggly *Vitex*. This isla rises 89 cm above the deepest portion of the bajío immediately “offshore.” After enjoying a feast of fried plantain chips (*chipilo*) and fried sun-dried beef (*charque*), we now had enough energy to start off toward our final destination, Isla 2.

Fig. 4. Transect 2. Semialtura-Isla Loma Verde-Isla 2



Further into the bajío, the average water depth increased and the height of the emergent plants increased as well. Eventually we are in the midst of a great swamp of the South American Papyrus, *Cyperus giganteus*. These dense stands of sedges reach over 2.5 m in height and surround most of the islas of the bajío. These swamps are the home of the endangered swamp deer as well as the more reclusive cattle. The microtopography of these sedge stands is hummocky, as the sedges create large clumps which rise above the mucky substrate. It is often easier to use these clumps as steeping stones than to wallow in the organic-rich black mud between the clumps. The accumulation of organic materials raises the *junquillar* some 10 to 30 cm above the surrounding areas.

After passing through the first cordon of junquillos, we encountered a pool with large floating water hyacinths (*Eichhornia crassipes*). This is the deepest point of our transect, with 98 cm of water and a relative elevation of 98.84 m, 1.16 m below the level of our starting point. Standing in this pool, we were now only 415 m from the shore of Isla 2, whose swaying *Attalea* fronds beckoned us on. By this point, I was barefoot. My sandals and socks were lost long ago in the muck. My feet and shins were lacerated by the blades of the sawgrass sedges. But oh, the excitement of topographic data!

As the afternoon sun of early February beat down upon us, only two days before the summer solar peak, we continue towards the enchanted island. After an exhausting 2.72 km of leveling, we reached the shore of Isla 2 at a relative elevation of 99.72 m. The highest point we measured on the island was 100.43 m. Later work would reveal higher points. Between the *Eichhornia* pool and the island, the relief we measured was 1.59 m. This figure is highly significant in an ecological sense, meaning the difference between an aquatic community and a well-drained forest.

Our greatest adventure of the was the trip home. Even in the summer time, the sun sets quickly in the Amazon basin. We arrived in the pitch dark, without flashlights, and I without shoes. Our equipment felt heavier with every step and we began to falter. On a few occasions I considered giving up and sleeping in the swamp. But this was not a good idea given the number of mosquitoes which hummed about my head. The folks at home had become genuinely concerned about us and had sent out a search party. Eventually we saw the light of a flashlight in the distance and we homed in on this welcome beacon. Amazingly enough, my young assistant Pachito did not run off the next morning in search of a better job. In fact, we were so excited by our day's work that we stayed up a few more hours that night number crunching by candlelight.

Transect 3. Loma 1-Palmar

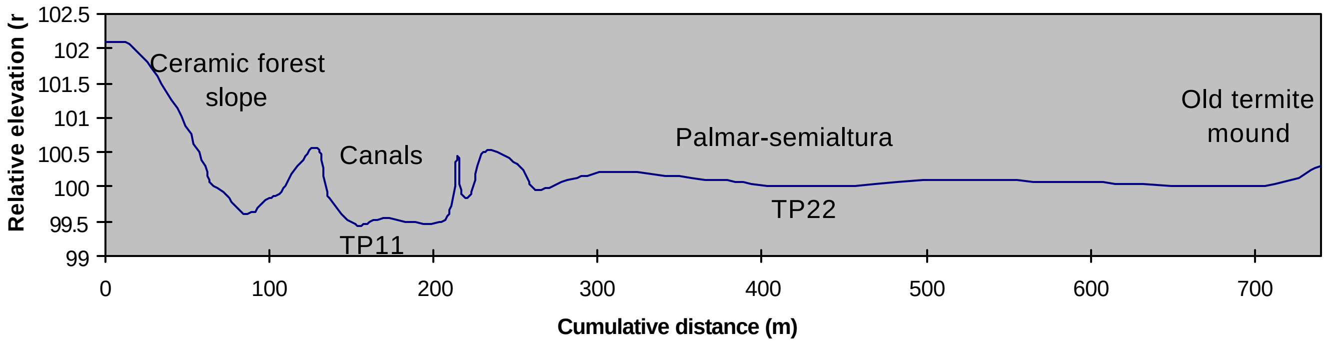
After our trials in the bajío, we decided to stay on more solid ground and out of the sun. Thus, our third transect took us back to the Ceramic Forest and the adjacent palmar to the northeast (Fig, 5). We began at the staked point we established on the first transect on the north foot of Loma 1. We proceeded down the slope towards the semialturas. This slope is very rich in ceramics as well as the extremely spiny *Bactris* understory palms. Over a horizontal distance of less than 70 m, we descended more than 2.4 m in elevation. Most of this elevation is constructed of human refuse and reworked earth (by both humans and insects). At the bottom of the slope, there is a channel with over 30 cm of water. I recovered ceramics from the floor of this channel.

We followed this channel around a bend and then rose up over an earthen ridge overtopped by a massive *Ficus* well over 2 m across the base. The ridge rises about 70 cm above the channel. On the other side of the narrow ridge lies a complex of large canals bordered by many other enormous *Ficus* (Plate 5). These channels create a connection between the cañada and the palmar-semialturas. The channel, or canals, are bordered by narrow ridges or "causeways." The function of these canals cannot be ascertained, but is likely that they were sources for the earth materials used to construct

Table 3. Topographic Transect 2 -- Paddocks - Isla Loma Verde - Isla 2

Distance (m)	Elevation (m)	Water (cm)	Description
0	100	0	By *Acrocomia* in paddock beyond *Guadua* (bamboo) gates to bajío ranges
158.2	100.141	0	On small mound created by poza excavation. *Ipomoea* and *Mimosa pellita*.
207.1	99.676	0	Pampa at foot of artificial mound
341.7	99.462	3	Small tarope (*Eichhornia azurea*), pampa
474.1	99.430	17.5	Pampa, *Scleria*-cortaderas
626.7	99.316	31.2	Pampa, *Scleria*-cortaderas
747.4	99.195	40.8	Pampa, *Eleocharis*
853.9	99.273	33.8	Pampa, *Eleocharis*, *Pontederia*
965.3	99.378	26.8	Pampa, *Eleocharis*, *Pontederia*
1092.1	99.32	36	Cow trail in pampa
1186.5	99.144	55.5	Pampa, *Eleocharis*, *Pontederia*
1212	99.285	41	Pampa, *Eleocharis*, *Pontederia*
1239.4	99.202	55.5	*Eichhornia*, near shore
1247.9	99.667	0	Edge of water at Isla Loma Verde
1268.3	100.090	0	Center of isla
1311	99.594	0	Edge of isla
1402.6	99.487	20	*Eichhornia*, *Ludwigia*, floating grasses
1531.2	99.292	52.0	Tall grass, *Thalia*, *Eichhornia*
1620.6	99.294	52.5	Tall grass, *Thalia*, *Eichhornia*
1759.2	99.376	46.5	At fence toward Isla 2
1869.3	99.269	62.0	Tall grass, *Thalia*, *Eichhornia*
2011.5	99.38	48.5	Edge of *Cyperus giganteus* swamp (junquillar)
2089.2	99.51	33.0	Inside junquillar
2094.5	99.358	42.6	*Eleocharis*/*Cyperus* boundary
2293.5	98.838	98	Big tarope (*Eichhornia crassipes*) pool with open water
2336.8	99.057	71	*E. crassipes* and *Eleocharis* between *Cyperus* stands
2418.6	99.338	41.5	*Cyperus giganteus*
2518.1	99.28	43	*Cyperus giganteus*
2592.9	99.308	43.5	*Cyperus giganteus*
2668.3	99.39	35.5	Edge of *Cyperus giganteus*
2698.3	99.357	41.5	*Eichhornia azurea* in front of Isla 2
2709.1	99.581	19	Flooded isla margin
2722.9	99.718	0	Edge of water on Isla 2
2743.4	100.425	0	Isla slope
2762.5	100.41	0	Isla
2774.3	100.153	0	Near “Snailisol” pit
2785.7	99.743	0	Edge of water
2798.3	99.56	17.5	Flooded “abra”

Fig. 5. Transect 3 - Loma-Canals-Palmar



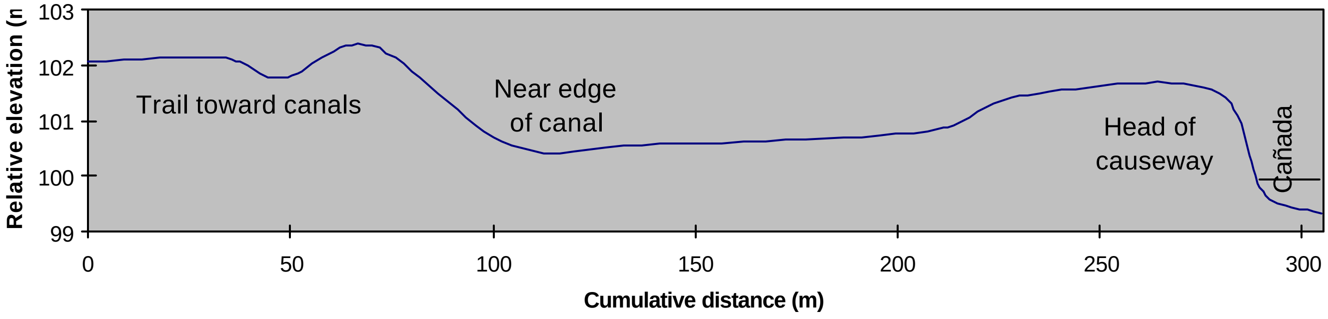
the platform and mounds of the Ceramic Forest. They were also likely to have been used for storage and conveyance of water for domestic use and perhaps for fish cultivation. Even today these canals are teeming with edible fish (mostly bentones (*Hoplias malabaricus*)) during the wet season. The maximum depth of water we recorded in the canals was 45 cm.

We crossed over a series of canals and causeways and followed a trail atop a ridge with the big *Ficus*. This ridge parallels the canals and ends at the forest/savanna boundary. At the edge of the forest, there is a wet zone where water ponds as it runs off the alturas and the semialturas. The semialtura palmares lie at a level above the canals and the lower slopes of the forest. Some of the palmar has ponded water, yet other portions are dry. The microtopography of the palmar appears to be largely a result of long-term termite and ant activity.

Transect 4. More Ceramic Forest Points

We further explored the Ceramic Forest on our next leveling expedition (Fig. 6). East of Loma 1, there is another small mound 1.5 m above the platform level and about 8 m in diameter. There are several such mounds on the platform. These were likely individual house mounds. However, there are also mounds with identical appearance and size but without ceramics. There are mounds created by giant termites and leaf cutter ants. The trail drops down toward a long branch of one of the giant *Ficus* canals.

Fig. 6. Transect 4. Ceramic Forest



This canal runs around the Ceramic Forest platform and eventually connects with the cañada. A long stretch of the canal is bordered by a ridge about 1 m high and 7 m across its base. We followed this ridge towards the cañada and it led us to the point where the "Cañada Causeway" begins. East of the causeway there is a small embayment in the forest. The cañada behind the causeway had water with a depth of 60 cm. From the mound at the head of the causeway down into the cañada there is relief of 2.24 m. The causeway extends into the cañada, but it is fragmented in two places.

Table 4. Transect 3 -- Loma 1 -Palmar

Distance (m)	Elevation (m)	Water (cm)	Description
0.0	102.072	0	Foot of Loma 1
17.2	102.014	0	Edge of big pit in front of loma
41.0	101.262	0	Edge of small pit downslope
60.7	100.301	0	Downslope in *Bactris*
63.8	100.076	0	Exposed ceramics on slope
74.9	99.866	0	Edge of water in forest channel
85.8	99.597	32.5	Center of channel
99.8	99.826	14	Center of channel around bend
106.3	99.914	0	Edge of water/channel
128.4	100.566	0	Crest of ridge along channel, in front of a giant *Ficus*
136.1	99.845	0	Shore of "Bibosi Channel" at head
152.5	99.457	45	Center of channel around bend
169.0	99.544	38	Center of parallel canal to E
184.3	99.622	33	Shot down branching canal
206.8	99.530	42.5	Down the main channel
214.6	99.911	0	Shore of causeway between canals
222.8	100.450	0	Top of causeway
228.2	99.876	16	Center of smaller canal
237.3	100.506	0	On trail above (north of) canal
256.8	100.338	0	Toward the palmar
268.1	99.970	11	In swampy gallery forest/palmar transition
287.0	100.084	0	Edge of main water, beginning of *Paspalum/Mimosa/Copernicia*
316.7	100.222	0	Along trail in semialtura
378.0	100.100	0	Along trail in semialtura
418.4	100.012	0	Behind *Attalea* isla at mouth of the canals from the forest
456.9	99.86	27.5	In mouth of canal
459.3	100.019	10	Back toward the palmar
516.2	100.092	0	Palmar at edge of the "mini-bajío"
589.7	100.066	9	In the "mini-bajío"
708.7	100.025	10	In palmar
742.9	100.303	0	Edge of old termite mound islet.

Table 5. Transect 4 -- Ceramic Forest Points

Distance (m)	Elevation (m)	Water (cm)	Description
0.0	102.072	0	In front of Loma 1
24.9	103.498	0	Top of small mound "E" of loma
32.5	102.141	0	High point of trail eastward
48.1	101.76	0	Low spot at bottom of trail toward canals
70.1	102.356	0	Top of trail on mound
104.3	100.548	0	Down toward branching canal
136.4	100.565	0	On edge of ridge along canal (W)
177.0	100.667	0	On slope of ridge along canal
211.1	100.864	0	Stake
229.9	101.434	0	Top of causeway ridge
261.7	100.275	0	Low near cañada edge
277.7	101.569	0	Near top of mound at head of causeway into the cañada
290.2	99.703	0	Edge of water in cañada
304.8	99.325	59.5	In cañada
328.9	100.38	0	Back toward loma at low spot
381.0	101.282	0	Along cañada (above)
412.2	101.667	0	Toward stake (between cañada and loma)
448.1	101.206	0	Slope between loma and cañada
458.4	101.897	0	FS to T1TP224

Transect 5. Isla 1-Isla 2

We were not to be daunted by our first attempt at pampa surveying. This time we went out on horseback to Isla 1 from which point we would work our way back to Isla 2 (Fig. 7). We began on a deeply inundated portion of the semialtura edge behind Isla 1, where we established our benchmark. At the edge of the isla canopy, there were still over 50 cm of water. Seven meters inward toward the isla center, the water lapped at the shore. The island was not more than 8 cm above the surrounding waters, the highest ground corresponding to a leaf-cutter ant mound built up in the roots of the *Ficus*.

We dropped off the edge of the isla and entered the bajío bearing toward the two *Copernicia* groves which lay between Islas 1 and Isla 2. The average depth of the bajío was around 65 cm, although we passed through a pool 1.15 m deep. Half a kilometer from Isla 1, we reached the first palm grove. Expecting a dry place to rest, we found that the entire surface was covered by more than 20 cm of water. So, we had to sit against the enlarged boles of the palms to eat our *tapeque* (the traditional traveling lunch of fried plantains and dried beef). During this period, I observed that the water was in fact flowing steadily to the northwest. I also observed several fish (ca. 15 cm long) known as *yeyú* swimming about the flooded palm grove. The palms grew upon a low, flat mound 40 cm high and about 30 m in diameter.

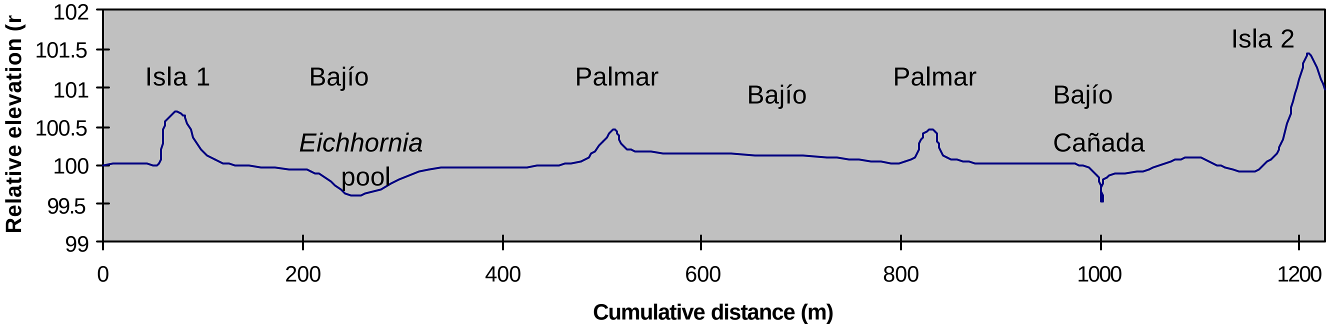
Table 6. Topographic Transect 5 -- Isla 1 to Isla 2

Distance (m)	Elevation (m)	Water (cm)	Description
0	100.000	55.7	Semialtura edge/palmar, *Ipomoea, Eichhornia*
38.7	100.025	52.0	Semialtura edge/palmar, *Ipomoea, Eichhornia*
55.7	100.022	53.0	Edge of Isla 1 canopy
62.1	100.560	0.0	Edge of water
79.7	100.645	0.0	Dry area on *Ficus* roots
110.9	100.057	53.5	Bajío edge, *Eichhornia*
208.0	99.917	69.0	Bajío
254.7	99.602	115.0	Open water in *Eichhornia* pool
327.8	99.945	68.0	*Eichhornia*, Graminae, *Nymphaea*
425.9	99.978	65.5	*Eichhornia*, Graminae, *Nymphaea*
479.1	100.051	60.5	*Eichhornia*, Graminae, *Nymphaea, Rhynchospora*
501.2	100.305	36.5	Edge of palmar
513.8	100.455	21.5	Center of palmar
530.1	100.188	49.0	Edge of *Eichhornia* against palmar shore
630.1	100.142	53.0	Bajío w/widely spaced *Copernicia*
725.4	100.106	77.0	*Eichhornia, Pontederia, Nymphaea*, Grasses
805.2	100.035	65.0	*Eichhornia, Pontederia, Nymphaea*, Grasses, *Eleocharis*
822.9	100.396	28.0	Edge of second *Copernicia* palmar
834.3	100.418	25.5	Center of palmar
846.7	100.100	59.0	Edge of palmar/tarope
898.5	100.012	67.5	*Eleocharis, Rhynchospora, Nymphaea*, some *Eichhornia*
975.	100.010	69.0	*Eleocharis, Rhynchospora, Nymphaea*, some *Eichhornia*
997.2	99.879	82.0	Edge of cañada
1002.5	99.522	118.6	Deepest part of cañada
1006.6	99.847	85.6	Edge of cañada
1048.8	99.946	79.0	*Eleocharis, Rhynchospora, Nymphaea, Eichhornia*
1091.3	100.111	66.0	*Cyperus giganteus* junquillar
1126.0	99.969	70.0	*Cyperus giganteus* junquillar
1153.0	99.919	85.0	*Eichhornia/Cyperus* boundary
1172.2	100.085	70.0	*Eichhornia* in front of isla
1181.8	100.261	44.5	Edge of Isla 2 canopy
1190.3	100.66	0.5	Edge of water
1204.4	101.322	0.0	Edge of Pit 1
1210.5	101.442	0.0	High point behind the big *Sennas*
1225.0	100.986	0.0	Stake for T2TP33

The next palm grove lies 293 m to the northeast and is slightly lower, with 38 cm of relief, lying beneath 25 cm of water. Again, the water between the two palmares averaged about 65 cm deep. However, there are widely scattered *Copernicia* palms here and there. Not far past the second palmar lies the deepest portion we have found in the bajío. This feature is also considered to be a cañada by local folks. Here the water is at least 1.18 m deep and the location of the cañada is marked by a distinct floating vegetation dominated by reddish aquatic ferns (*Azolla* sp.). This cañada is 10 m wide, however its length is indeterminate, as it disappears into dense *Cyperus giganteus* swamps at either end. The exposed segment is about 50 m long. Isla 2 lies beyond the cañada at a distance of 175 m. In this last stretch of bajío, the water averaged some 75 cm in depth and there were abundant *Cyperus giganteus.*

At the edge of the forest island canopy, the water was still 45 cm deep. The outer 8 m of the isla were inundated. The trees of the island edge are those which are most tolerant of inundation and are not found in the island interior. The relief we measured between the higher portion of the isla and the adjacent bajío was 1.53 m.

Fig. 7. Transect 5. Isla 1-Isla 2

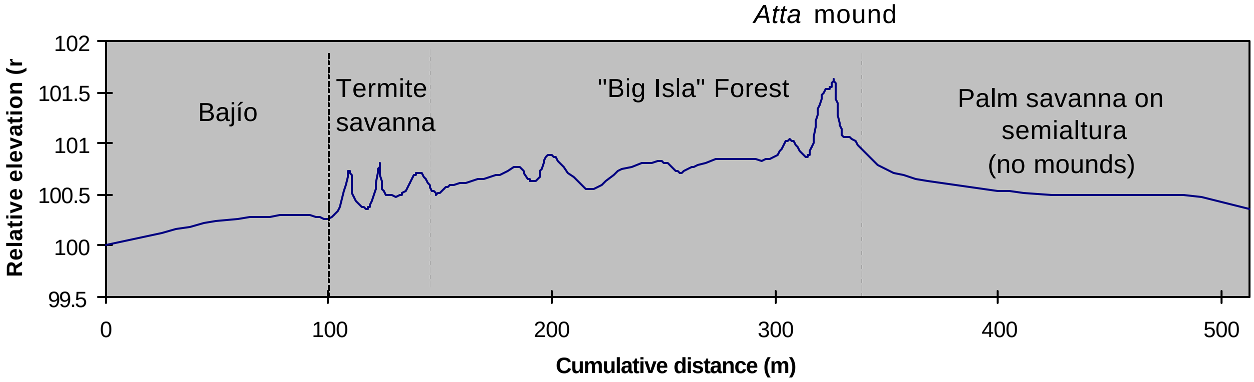


Transect 6. The Big Isla

We examined a large island of woodland and semideciduous forest which I had simply named the "Big Isla." (Fig. 8). We began out transect in the bajío to the north of the island in water 59 cm deep. The semialtura began 86 m inland marked by the occurrence of *Mimosa debilis* in water 29 cm deep. The next zone was marked by the presence of termite mound islets. The islet tops are above the level of the inundations and average about 40 cm in height, not including any active conical mounds that may lie upon the flat mound. At some 55 cm above the level of the bajío, the "Big Isla" begins. The microtopography of the Big Isla is composed of a mosaic of low mounds and intermound swales. The surfaces average between 20 to 30 cm above the level of the inundated semialtura. Large leaf-cutter ant (*Atta* sp.) mounds may rise a meter or so above the general surface.

On the south side of the island, one again enters an inundated semialtura, but without termite mound islets. Likewise, the island is bordered on the east and west by semialturas and bajío. The west side has many termite mound islets and rather abundant *Cereus* cacti.

Fig. 8. Transect 6. "Big Isla"



Transect 7. Semialtura Woodland - Gallery Forest

Near the house, we examined the transition from a *Cordia glabrata-Tabebuia ochracea* semialtura deciduous woodland to *Attalea*-altura gallery forest (Fig. 9). We found only minimal topographic relief on this short transect. The highest point in the forest lay only 18 cm above the lowest semialtura site. The forest/savanna boundary was abrupt and definitive, located on a slight slope down from the forested altura. Here the forest appeared to be advancing into the semialtura. This particular zone of the forest has no trace of indigenous earthmoving or ceramics, the only mounds being those created by ants and termites.

Our transect began on a cleared semialtura surface that appears to have experienced notable erosion, as it lies 10-20 cm below the level of the adjacent uncleared and less heavily grazed/trampled semialtura savanna and woodland across the fence.

Fig. 9. Transect 7. Semialtura woodland - North gallery forest

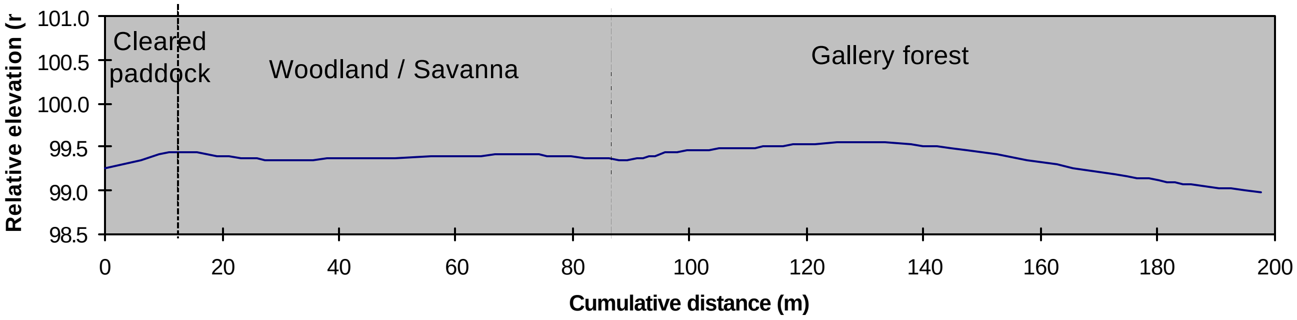


Table 7. Topographic Transect 6 -- “Big Isla”

Distance (m)	Elevation (m)	Water (cm)	Description
0.0	100.000	59.0	Bajío: *Eichhornia, Eleocharis, Scleria, Poaceae*
49.4	100.239	34.5	Bajío
85.9	100.297	29.0	Edge of *Mimosa debilis*
102.5	100.292	29.0	Edge of "murundu"/"gabetillo" boundary
109.4	100.731	0.0	Top of mound: *Copernicia, Pithecellobium, Celtis,* other shrubs
111.3	100.472	11.0	Edge of mound
117.5	100.365	21.5	*M. debilis* between mounds
121.0	100.549	4.0	Edge of next mound: *Copernicia, Ficus, Cordia* (mechero)
123.2	100.797	0.0	High point of mound
124.7	100.529	6.0	Edge of mound
131.8	100.490	12.0	*M. debilis*
136.7	100.606	0.0	Edge of standing water at mound
140.6	100.716	0.0	Center of mound
146.0	100.567	0.0	Edge of water
148.4	100.498	4.8	Center of puddle
151.5	100.553	0.0	Edge of water
154.3	100.590	0.0	Top of mound (in forest)
174.9	100.682	0.0	Forest, dense *Bromelia serra* ground cover.
184.7	100.769	0.0	Forest, low mound
190.7	100.630	3.0	Mud in forest
194.3	100.667	0.0	Edge of large mound
199.9	100.879	0.0	Top of mound
216.5	100.559	3.0	Cow trail, mud
231.9	100.746	0.0	Forest
249.0	100.817	0.0	Scrubbier forest, *B. serra*
257.8	100.719	0.0	Edge of grassy clearing, no mimosas
262.6	100.771	0.0	Middle of clearing
278.4	100.851	0.0	Edge of forest
298.1	100.844	0.0	Forest
306.4	101.037	0.0	Small mound, *Copernicia, Ficus*
313.7	100.871	0.0	Low muddy spot trampled by cattle
316.6	100.965	0.0	Begin *Atta* (leaf-cutter ant) mound
318.1	101.165	0.0	*Atta* mound
320.3	101.383	0.0	*Atta* mound
322.6	101.526	0.0	*Atta* mound
325.1	101.543	0.0	*Atta* mound
326.8	101.621	0.0	Peak of mound
327.7	101.423	0.0	*Atta* mound
329.5	101.145	0.0	*Atta* mound
331.5	101.058	0.0	End of mound
334.7	101.047	0.0	Next to big *Piptadenia* (azotocó).
353.3	100.712	0.0	Edge of forest

Table 7. Topographic Transect 6 -- "Big Isla"

399.5	100.539	20.0	Palmar/gabetillo/grasses

Table 7. (cont'd)

447.5	100.485	25.0	Palmar/delicate *Mimosa* sp./grass
483.6	100.491	24.0	Edge of delicate mimosas
512.7	100.365	37.0	*Mimosa*-free grass, short and intensely green

Table 8. Topographic Transect 7: Semialtura woodland to gallery forest

Distance (m)	Elevation (m)	Water (cm)	Description
0.0	99.244	0	Corner of Big Paddock (cleared semialtura)
12.7	99.436	0	Woodland across fence
28.8	99.352	0	Beginning of VP9 : *Cordia glabrata* (japunaqui) - *Tabebuia ochracea* woodland
71.0	99.410	0	Grassy opening
89.5	99.356	0	Edge of Pit 2 in savanna
97.8	99.449	0	The "World-Famous" Savanna/Forest Boundary
108.4	99.490	0	Edge of Pit 1 in forest
137.8	99.534	0	Forest
176.7	99.150	0	Trail in Forest
197.6	98.977	0	FS to TP3 of Transect 1. Forest.

Transect 8. Bajío-Cañada West

We examined another bajío-semialtura-altura-cañada sequence to the west of the house at La Chacra (Fig. 10). We began in an open bajío with 36 cm of water, at the southwestern boundary of the bajío. Unexpectedly, we soon rose up onto a low ridge that runs parallel to the semialtura "shoreline." The location of this submerged feature is marked by the presence of numerous *Ipomoea carnea*, a giant woody sweet-potato shrub and characteristic weed of wet savannas. Top of the ridge is 21 cm above the level of the bajío where we began. The band of tararaquis is about 35 m wide. We find our first ant mounds in the inundated wetland in water with a depth of 30 cm, on the semialtura-side of the ridge. Tussocks of the coarse semialtura grass *Paspalum virgatum* begin at a depth of 16 cm as we rise. Only at 7 cm of water, or 30 cm above and 114 m "inland" from our starting point, do we find the first termite mounds and *Copernicia* palms. The location of this boundary appears to be very regular along the edge of the semialtura/bajío ecotone.

At a relative elevation of 100.37 m and a distance of 126 m "inland," we encounter the shore of the great expanse of water which extends several kilometers across the bajío (Map 4). We are in the termite-mound savanna of the semialtura. We continued our transect upslope and over a termite mound islet 12 m in diameter with a height of 71 cm (active cone peak is 1.13 m high) above the surrounding surfaces. This mound was dominated by *Copernicia*, *Celtis*, and *Tabernaemontana*.

The tree cover became denser, and at an elevation of 17 cm above the water level we have a semialtura woodland savanna, where the woody plants are no longer restricted to termite islets(relative elevation. 100.54 m, 209 m from start). At meter 272, the gallery forest begins at an elevation of 100.68 m. The forest here is much denser and tangled than the *Attalea*-dominated

Ceramic Forest. We spent much time hacking through the understory with machetes in order to have clear sightings. The crest of the old natural levee formation is at about 100.88 m. The highest points in the forest are upon the termite and ant mounds. Past the crest, the forest slopes toward the Cañada de los Lagartos. The cañada waters start at about 100.55 m in the flooded edge of the forest at a distance of less than 66 m from the levee top. The woody vegetation of the cañada "floodplain" ends at a depth of 26 cm, 12 m from the forest edge. Near the center of the cañada, 58 from the edge, there were 63 cm of water and the bed elevation measured 99.94. Here the cañada lies only 6 cm below the level of the bajío "benchmark."

The relief over the entire transect was only 1.20 m, the highest point being a semialtura termite mound and the lowest the cañada bed. From the levee top to the cañada bed the relief is only 94 cm.

Fig. 10. Transect 8. Bajío-West Gallery Forest-Cañada

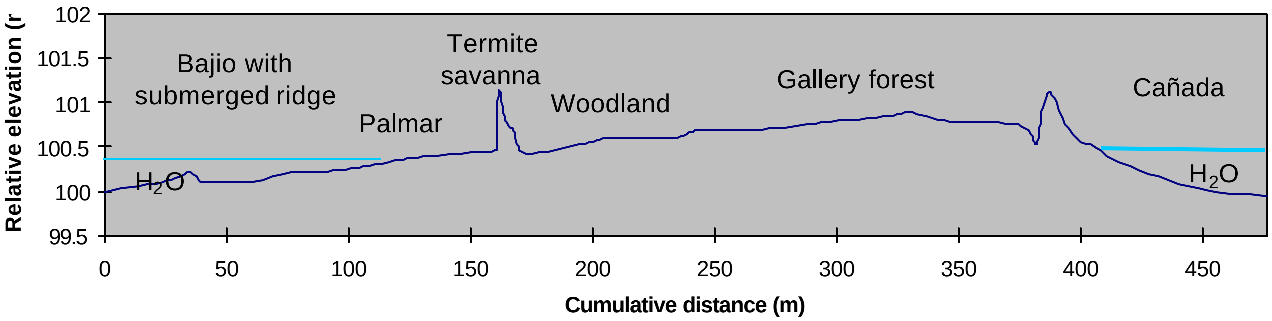


Table 9. Topographic Transect 8: Bajío - West Gallery Forest - Cañada.

Distance (m)	Elevation (m)	Water (cm)	Description
0.0	100.000	36	Open, herbaceous bajío in standing water.
26.0	100.109	24	Upslope on low submerged ridge with woody *Ipomoea fistulosa* (tararaqui).
34.8	100.212	14	Top of ridge which runs parallel to "shoreline.
41.3	100.096	30	Lower area with fewer tararaquis. *Solenopsis* (fire ant) mounds begin.
60.2	100.106	24	End of tararaquis.
76.6	100.206	16	Herbaceous formation with grasses, *Eichhornia, Pontederia, Neptunia.*
85.3	100.208	16	Beginning of *Paspalum virgatum* (paja toruna) bunchgrass tussocks.
102.9	100.259	11	Open water, over cow path?
113.5	100.304	7	Edge of *Copernicia*-palmar, termite mounds begin.
125.8	100.372	0	Edge of standing water, semialtura "shore."
145.5	100.419	0	"Murundu woodland savanna", *Mimosa debilis* (gabetillo).
159.6	100.451	0	Edge of termite islet : *Copernicia, Celtis, Tabernaemontana*

160.4	100.659	0	Mound slope.
161.5	101.142	0	Mound top (non-cone portion, cone is 42 cm higher).
164.3	100.809	0	Mound slope.
167.7	100.678	0	Mound slope.
172.7	100.423	0	Edge of mound.

Table 9. (cont'd)

196.7	100.540	0	Semialtura woodland savanna, gabetillo.
209.5	100.600	0	Semialtura woodland savanna.
234.6	100.601	0	Semialtura woodland savanna.
243.3	100.678	0	Edge of mound/forest.
272.4	100.694	0	Forest.
293.7	100.769	0	Forest.
321.8	100.0	0	Forest
329.6	100.880	0	Turn left around large fallen tree.
346.8	100.786	0	Fence from potreros in forest.
375.9	100.741	0	Forest.
381.7	100.526	0	Edge of mound.
384.2	100.925	0	Slope of mound.
387.6	101.105	0	Top of mound (cone to 1.49 m).
392.6	100.826	0	Slope of mound.
398.6	100.591	0	Base of mound.
406.4	100.485	6	Edge of forest.
417.8	100.300	26	Edge of woody plants in inundated cañada (*Combretum*).
448.3	100.025	58	Edge of sedges.
476.1	99.939	63	Center of cañada, tarope (*Eichhornia*).

Transect 9. **Anadenanthera** *Gallery Forest*

For our last leveling project, we journeyed up the cañada to the far southeast corner of La Chacra, where we encountered some well-developed groves of *Anadenanthera* (Fig. 11). We began our transect on the semialtura in an open woodland (*Cordia glabrata*, *Copernicia*, *Tabebuia* spp., *Jacaranda*, *Astronium*, etc.) without any standing water. The surface rose gently and the trees became denser, grading into a forest composed of *Anadenanthera*, *Astronium*, *Attalea*, *Copernicia*, *Cordia glabrata*, *Enterolobium*, *Guazuma*, *Randia*, Shrub5, *Syagrus*, and *Sterculia*. The forest edge was only 12 cm above the level of the semialtura benchmark some 40 m distant. Much to my surprise, we found that the gallery forest was largely on a long slope down to the cañada and below the level of the semialtura. Only the ant and termite mounds were higher than the semialtura woodlands. The dominance of *Anadenanthera* indicates that the steepness of the slope allows for well drained soils and the establishment of dry forest species not tolerant of inundation.

Fig. 11. Transect 9. *Anadenanthera* -Gallery Forest

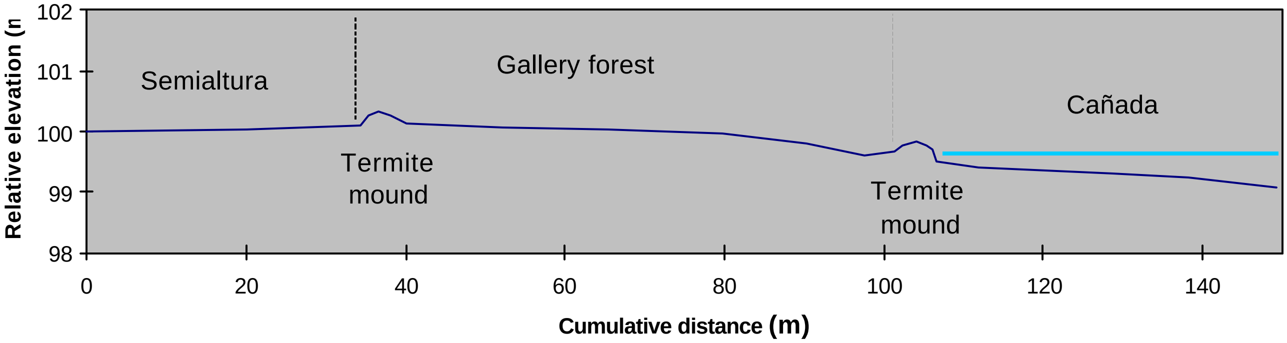


Table 10. Topographic Transect 9: *Anadenanthera* gallery forest.

Distance (m)	Elevation (m)	Water (cm)	Description
0.0	100.000	0	"BM" on semialtura, open woodland
20.2	100.039	0	Semialtura open woodland
34.3	100.099	0	Woodland (shady)
34.3	100.096	0	Edge of termite mound at edge of forest
35.3	100.261	0	Slope of termite mound
36.7	100.326	0	Top of termite mound
38.0	100.249	0	Slope of termite mound
40.0	100.120	0	Edge of termite mound, Forest
52.2	100.054	0	Forest : *Anadenanthera*, *Attalea*, *Enterolobium*, *Randia*, *Copernicia*, *Astronium*, *Guazuma*, Shrub5, *Syagrus*, *Sterculia*, *Cordia glabrata*
65.4	100.035	0	Forest as above
79.7	99.955	0	Forest as above
90.3	99.791	0	Forest as above
97.6	99.591	0	Forest as above
101.3	99.659	0	Base of termite mound along forest edge.
102.4	99.777	0	Termite mound
104.1	99.836	0	Termite mound
105.4	99.771	0	Termite mound
106.1	99.687	0	Termite mound
106.7	99.515	4	Edge of termite mound and cañada water.
112	99.400	23	Cañada
128.7	99.316	23	End of *Paspalum* bunchgrasses
138.3	99.242	31	*Eleocharis*
149.3	99.077	46	Deepest part of cañada

Chapter 7. Forest Islands of the Bajío and Semialtura Savannas

Altura Islands in Seasonal Wetlands

This the “classic” isla type at La Chacra and throughout the Moxos plains. These are true islands of dry land in the midst of wet grasslands and sedge swamps (Plate 1). The most characteristic plant is the motacú palm (*Attalea phalerata*), a highly abundant element in the gallery forests of the Moxos region. Other palms are not nearly as abundant, if present, on these islas at La Chacra. At other localities, Other palms are not nearly as abundant, if present, on these islas at La Chacra. At other localities, *Syagrus sancona* may be found in association with *Attalea*. These islands are recognizable from afar by their canopy structure, often with giant *Ficus* trees. The *Attalea* palms are distinguished by their long fronds. The tree islands appear as dark clumps against the flat, open horizon of the pampas when viewed from a distance of a few kilometers

Isla 2 (Plate 1, right isla; Plate 2). The island of this type most accessible from the house at La Chacra is Isla 2, at a distance of ca. 2.5 km (All numbered and named islands are indicated on Map 3). This island is part of an archipelago of 13 islas Isla 2 is part of an archipelago of 13 islands, all located in the middle of the bajío wetland. It is essentially surrounded by junquillo (*Cyperus giganteus*) and taropes (*Eichhornia azurea*, *Eichhornia crassipes*, *Pontederia subovata*). The elevated surface measures approximately 60 m in diameter and averages well over 1 m in height. Differential leveling revealed relief of 1.07 m between the central portion of the isla and the seasonally inundated bajío 11.5 m to the south of the isla edge. From the high point above Pit 1 to the adjacent wetland below, the relief is 1.53 m.

On Isla 2, there was a nesting pair of jabiru storks, some white-headed hawks, a pair of blue and yellow macaws, and an ibis nest. There was also a large *Hydrodynastes gigas* (“false water cobra”), which later apparently fell victim of the soil pit.

The island is visually dominated by the palm *Attalea phalerata*. The largest canopy trees are *Sterculia apetala*, *Ficus trigona*, and *Vitex cymosa*. These trees reach heights of more than 20 m, much taller than on the semialtura-type islas. There is but a single, thin *Copernicia alba* on Isla 2. The density of trees and canopy cover varies over the surface of the island. Much of the island is shaded, except for a more open zone near the mound summit. The density of the suffrutescent weedy component is directly proportional to the amount of sunlight which reaches the surface. The trees of the outer margin of the island are those most tolerant of inundation: *Genipa americana*, *Vitex cymosa*, *Rheedia* sp., *Trichilia* sp., *Guarea* sp., *Salacia elliptica*, *Sorocea sprucei*, *Inga* sp., and especially *Nectandra* sp. The outer margin has a greater cover of trees than the interior of the island. Table 11 presents the data from the 250 m^2 plot on Isla 2 (see Map 5 for locations of the vegetation plots).

Table 11. Vegetation Plot 5. Isla 2. Altura island of the bajío

Species	**Local name**	**n**[21]	**ba**	**rd**	**rc**	**rd+rc**
Sterculia apetala	Sujo	1	3176.9	0.0147	0.3269	0.3416
Senna occidentalis	Mamuri	21	12.5	0.3088	0.0013	0.3101
Attalea phalerata	Motacú	2	2569.1	0.0294	0.2643	0.2937
Guarea sp.	Trompillo	4	1238.9	0.0588	0.1275	0.1863
Solanum biflorum	s.n.	7	10.3	0.1029	0.0011	0.1040
Salacia elliptica	Guapomó	2	448.9	0.0294	0.0462	0.0756
Malvaceae sp. 4	Malva	5	3.7	0.0735	0.0004	0.0739
Moraceae Tree 21	s.n.	1	530.9	0.0147	0.0546	0.0693
Rhamnidium elaeocarpum	Turere	4	47.2	0.0588	0.0049	0.0637
Genipa americana	Bí	1	437.4	0.0147	0.0450	0.0597
Solanum sessiflorum	Floripondio	1	419.1	0.0147	0.0431	0.0578
Rheedia sp.	Achachairú	2	199.0	0.0294	0.0205	0.0499
Malvaceae sp. 6	Malva	3	2.0	0.0441	0.0002	0.0443
Coccoloba sp. 2	Pororó	2	132.8	0.0294	0.0137	0.0431
Inga sp. 1	Pacay	2	121.4	0.0294	0.0125	0.0419
Trichilia sp. 1	Pitón	2	104.8	0.0294	0.0108	0.0402
Dipteryx sp. ?	Almendrillo	1	203.6	0.0147	0.0209	0.0357
Sorocea aff. *guilleminium*	Sapito	1	54.4	0.0147	0.0056	0.0203
Malvaceae sp. 5	Malva	1	1.8	0.0147	0.0002	0.0149
Ficus cf. *caballina (4)*	Bibosi	1	1.8	0.0147	0.0002	0.0149
Petiviera alliacea	Cutuqui	1	1.1	0.0147	0.0001	0.0148
Malvaceae sp. 2	Malva	1	0.8	0.0147	0.0001	0.0148
Solanum sp. "Shrub 40"	s.n.	1	0.6	0.0147	0.0001	0.0148
Malvaceae sp. 3	Malva	1	0.5	0.0147	0.0001	0.0148
		68	9719.5	1	1	2

Other trees on island: *Zanthoxylum* sp. (saúco), *Ficus* spp. (bibosi), *Vitex cymosa* (tarumá), *Copernicia alba* (palmera), *Nectandra* sp. (negrillo), *Maclura tinctoria* (mora), *Trichilia* sp. (pitón), *Piper* sp. (ambaibillo), *Celtis* cf. *iguanea* (chichapí)

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[21] n= number of trunks or stems in plot; ba = sum of basal areas in cm^2; rd = relative density = n/sum of all species;
rc = ba/sum of all species.

The transition from wooded island to waterlogged herbaceous wetland is very abrupt. During the wet season, many trees along the island edge are in standing water. Water hyacinths push right up to the edge of the tree canopy. Only the central portion of the island is free from inundation. Some altura-type islands, in fact, are completely overtopped for brief periods. Flood-intolerant species, therefore, are not to be found except on the highest zones of the islas.

In the southeast sector of the island, there is a 10-20 cm deep layer of very fine loamy sands (79% sand) at the surface which overlies black and mottled silty clays. We excavated a pit near the center of the island and reached a depth of 125 cm (Table 12). The outstanding characteristics of the soil are 1) the dark brown color and friability down to 110 cm, 2) the lack of significant horizons or sedimentary stratification, and 3) the presence of rock-like concretions and soft, red clayey nodules which seem out-of-place in the friable dark brown matrix. We found three small, intact, flattish snail shells (not *Pomacea*, the lowest at 80 cm) and a piece of bony caiman scute, but nothing we could identify as ceramics. A single fragment of charcoal (wood) was found at 66 cm. Although there were no trees in the immediate vicinity of the pit, roots were present throughout the profile.

Table 12. Isla 2. Pit 1.

0-90 cm	Dark brown (dry) to black (moist) silt loam (30.3 % sand, 60.3% silt, 9.4% clay), no ceramics, but occasional fragments of bone, charcoal, and entire snails (not *Pomacea* type), common soft red to orange “clay balls,” common carbonate concretions.
90-110 cm	Same as above, but more abundant “clay balls” in slightly sandier silt loam (33.5% sand, 56.9% silt, 7.6% clay) matrix,.
110-125+ cm	Slightly clayier silt loam (27.9% sand, 60.0% silt, 12.1% clay), indurated by carbonates, difficult digging.

While in Santa Cruz, I examined a chunk of the rock-like material from the 60-70 cm sample and applied some red wine vinegar to it. To my surprise, the material was violently effervescent! I then placed a few fragments into a dish with vinegar and they bubbled away and the soil particles disaggregated. Simple kitchen-table science had demonstrated that these “rocks” are actually carbonate nodules. I then obtained a bottle of 30% HCl from the British Agricultural Mission soils lab in Santa Cruz. Subsequently, I began testing the soils in the field for carbonates.

The angular concretions are conglomerates of a sort, as they contain a mixture of various types of particles and materials. One has a small piece of charcoal imbedded in the surface, and another contains small bone fragments. Inside they often contain vacuoles with crystals or soft clay balls (oxidized). The concretions are rounded when removed from the soil, as they are covered by calcareous dark brown to black soil particles which rapidly disintegrate in acid or water. This outer soil creates a stronger effervescence than the concretion itself, probably as a result of the much greater surface area available in the loose soil.

There are no natural carbonate rocks anywhere in the region. A possible origin for the carbonates is the long-term addition of shell and bone. Examination of two fallen trees revealed large quantities of snail shells in the soil which remained attached to the exposed roots. A shallow pit adjacent to one of these trees revealed scattered intact, whitened snail shells, below which was a horizon with a large volume of broken and unbleached snail shells in a dark brown soil matrix.

The snail shells are completely dissolved by 30% HCl within minutes. Both fresh and ancient (from 95+ cm) bone react with the acid, but much more slowly than the shells. A second pit (near the smaller of the two fallen trees, closer to the isla edge) revealed shell fragments to at least 85 cm; however, the peak quantities appear to be within 40-65 cm of the surface. From this second pit I recovered several nearly-intact *Pomacea*-type snail shells.

The shell carbonate hypothesis may be correct. It appears that perhaps the shells are preserved under the trees, but are dissolved in the open conditions. (I vaguely recall Werner Hanagarth once mentioning to me that the presence of isolated carbonate accumulations in the pampas may indicate the locations of former trees.) Rodolfo Pinto Parada claims that broken shells were scattered on the surfaces of the mounds by the ancient Moxeños to prevent erosion. Kenneth Lee believed that in many cases the shells are probably refuse left by *caraus* (limpkins).

The soil from the extension of open ground on the north side of the island is extremely rich in organic matter and silts, with not much sand. The organic matter strongly influences the structure and apparent texture of this soil. During the dry season this soil is moist, but not saturated. The organic matter appears to provide a structure which maintains aeration. There are no woody plants on this soil and the boundary with the isla, as well as with the yomomo, is clear. The low and green grass (*Axonopus?*) cover does not seem likely to ever burn, even during exceptionally dry periods

In early January 1994, Isla 2 was completely surrounded by standing water, over 75 cm deep in places. The margins of the wooded island (*Inga*, *Rheedia*, *Genipa*, *Guarea*) were inundated by a few (5-10) cm of water. Many of the weeds along the isla edge had been killed by the standing waters, the plants having turned dry and brown. There were some shrubby *Senna alata* on the flooded isla margin with aerial roots, which appear to be adaptations to seasonal flooding. The center of the isla was dominated in January by a pale-orange flowered, suffrutescent malvaceous weed common on overgrazed alturas, suffrutescent *Senna* as well. In the more shaded zones of the intermediate island slopes there were numerous *Attalea* seedlings, many of which had been recently grazed.

The surface north of the isla was also completely covered by water, now dominated by *Eichhornia* and an aquatic grass. The waters of the isla margins were contaminated by large quantities of capybara feces. There were also considerable amounts of filamentous green algae in the surrounding bajío, as well as a a terrible sawgrass (a sedge of the genus *Rhynchospora*) which completely thrashes bare human skin in a matter of seconds, but which is gladly eaten by horses.

I observed a lone rhea (the South American “ostrich”) resting in the shade of the isla as well as abundant rhea tracks in the mud of the isla edge. It was rather to surprising to find a rhea in the middle of a wetland. When it fled, it had no trouble at all running through the 75-cm deep water and the dense aquatic vegetation.

Isla 3 (Plate 1, left isla)**.** This smaller isla is characterized by many lower-statured trees which are largely a subset of the species from Isla 2, with more abundant *Coccoloba* trees. In mid-May 1994 this isla was completely underwater, except for a small *Atta* ant mound at the base of a *Vitex cymosa*. This island lies about 250 m to the north of Isla 2, connected by a broad, open swath of junquillo-free ground. This surface is an extension of the open “abra” surface discussed above.

Isla 4 (Plate 3, background). This is a larger, elongate isla, some 100 m in length, which contains many very large trees (*Ficus*, *Sterculia*, *Attalea*). This isla was inhabited by some very large and very tame capybaras. There was an extensive grove of bamboo (*Guadua angustifolia*), as well as many tree saplings, and abundant leaf litter. There are two small mounds (“lomitas”) within this isla, however I could not find any ceramics after exhaustive searching. As in some other islas and at

Loma Complex 1, there are abundant soil termites. At first, I did not think that these termites created surface mounds, at least the mounds did not appear like "typical" termite mounds. Later observations revealed that these lomitas are indeed created by a species of giant termite (about an inch in length and with jaws that shear through human flesh like surgical instruments!).

This isla seems to be fairly “intact” in comparison with Islas 2 and 3. Nevertheless, this was for a long time the only isla in which I had actually observed cattle. There is a narrow trail through the center of the isla through which the cattle may travel. The only evidence for human impact (besides the cattle) I encountered on this island was a fruit-bearing lime tree, probably dispersed by a frugivorous bird. This island, as well as all the others in the bajío, is protected by a natural fire break. These islas are bordered by a zone of open ground with very low grass that is likely very resistant to burning, as it is low in biomass and remains green during the dry season.

Isla 4a (Plate 3, foreground). There is a crescent-shaped strip of high, sandy ground with a small forest island, only about 50 m to the southeast of Isla 4. I saw a beautiful trogon perched here. From this point, which is adjacent to the fenceline which divides the ranch into a western and an eastern range, there are several more islas across the fence to the southeast. I briefly examined the closest one and found nothing remarkable, just more bamboo and a nice anaconda (not less than 5 m in length). The majority of these eastern islands proved impossible to reach, as they were surrounded by dense junquillares and treacherously soggy ground throughout the dry season.

Isla 5. This isla has many trees of small stature, abundant leaf litter, lots of sand, and frequent cattle use. There is a large treeless patch of high ground on the east-northeast side of the island. The forested area is approximately 40 x 50 m. There are few palms, only a small patch of five *Attalea* and two *Acrocomia*. The edges of the forest are open, not occupied by vines or shrubs; however, the interior of the grove is rather shady. The soils from the center of the isla demonstrated the presence of carbonates (Table 13). The high ground also contains a small patch of trees denominated “Isla 5a”.

Table 13. Isla 5, Pit 1:

0-6 cm	Loose loamy sand
6-24 cm	Friable dark brown loam
24-40 cm	Clayier silt loam, more compact, dark brown, carbonate concretions, and yellow to orange clay balls
40-45+ cm	Greater abundance of clay balls/mottles in compacted dark brown matrix.

No shell, bone, or ceramics observed in profile.

Isla 6. This island was approximately 20 m in diameter and located about 200 m to the north of Isla 5, connected by a well-trodden trail. This isla is dominated by *Attalea*, many of which have been cut to access honey from bee hives. Soil from 7 cm below surface are effervescent in 30% HCl. I examined a shallow pit in the pampa (*Pontederia*-Grasses-*Cyperus giganteus*), 23 m from the edge of Isla 6 (Table 14). I was rather surprised to find sands on the surface of a bajío soil, as these soils are notoriously heavy. However, it is clear that these sands have been colluvially deposited as they are washed of the slopes of Isla 6. Despite the sandy upper horizon, the vegetation still reflects the poorly drained and seasonally inundated character of the bajío. The sandy clays at 35 cm contrast sharply with the upper two horizons.

Table 14. Pampa soil 23 m from edge of Isla 6.

0-24 cm	Mixed black (organic stained) and white sands
24-35 cm	Gray brown loamy sand
35+ cm	Yellow sandy clay "greda"

In the pampas adjacent to several of these islas, there are small sandy mounds, perhaps averaging 5 m in diameter and 50 cm in height, that are devoid of woody vegetation. They are covered by very low-growing grasses and sedges, sometimes with desiccated *Pontederia*.

Isla 7. I visited this remote island only briefly, after being bucked off my horse, saddle and all. The horse did not wish to become mired in the spongy, waterlogged "ground" which lay between us and the island. This is a very small, open isla located to the northwest of Isla 6. Upon it grew only a few widely spaced trees (four *Attalea phalerata*, one *Coccoloba* sp., one *Genipa americana*) and shrubs and much grass. Beyond this island, there are only a few far-scattered islas in the distance. Further west (ca. 800 m), just beyond the fence with El Sol, lies the westernmost island of the "Chacra Archipelago." There are numerous other *Attalea*-type islands in the bajío of La Chacra. Not all of these were visited, due to problems of access. I made several futile attempts reach these islands by plunging through the 2.5 m high sedge swamps which protect them. On several occasions I and my equipment were completely immersed in the muck and mire after being thrown off the horse, falling off the horse as the saddle slid off, or slipping on the slick silty clays while walking on my own two feet. However, informants told me that all of these islands are rather similar in composition and morphology. None of them were known to contain ceramics.

After all of my excavations, surface combing, and other activities on the *Attalea*-dominated altura-type islas of the bajío of La Chacra, I encountered only one single fragment of pottery. Unless the islas that I observed were constructed by a pre-ceramic snail-eating people, I see little evidence for past human occupation or construction.

Semialtura Islands

Isla 1. This is an isla near the edge of the semialtura and is dominated by *Copernicia alba*. The elevated surface measures 30 m in diameter and 60 cm in height. There are no termite mounds on this isla or in the immediate vicinity. *Genipa americana* grows along the edge of the island. The two larger *Ficus* species are important due to the geomorphological role of the extensive "buttress" root systems. The only tree species present and not encountered in the sample plot (Table 15) was *Pithecellobium scalare*.

Table 15. Vegetation plot 6 -- Isla 1 : Semialtura island.

Species	Local name	n	ba	rd	rc	rd+rc
Copernicia alba	Palmera	12	3829.5	0.4000	0.3548	0.7548
Ficus trigona	Bibosi	1	3599.7	0.0333	0.3335	0.3669
Guazuma ulmifolia	Coquito	5	681.2	0.1667	0.0631	0.2298
Coccoloba sp. 3	Pororó	3	1019.1	0.1000	0.0944	0.1944
Ficus sp. 2	Bibosi	3	769.6	0.1000	0.0713	0.1713
Genipa americana	Bí	1	602.6	0.0333	0.0558	0.0892
Neea sp. 2	s.n.	2	45.0	0.0667	0.0042	0.0708
Sorocea sprucei	Sapito	1	219.0	0.0333	0.0203	0.0536
Celtis cf. *iguanea*	Chichapí	1	23.9	0.0333	0.0022	0.0356
Paullinia cf. *alata*	Bejuco	1	2.5	0.0333	0.0002	0.0336
		30	10792.3	1.0000	1.0000	2.0000

In July 1993, the surface way dry, devoid of herbaceous cover, with fine sandy-silty soil. The soil, however is compact and brilliantly mottled at a shallow depth (21 cm, see Table 16). The winds of the southerly cold front constantly blew the loose fine particles into our eyes when we first visited this island. The roots of the *Ficus* trees spread extensively across the surface of the isla. The bases of some trees had small ant mound accumulations and some had accumulations of bat dung. In the mottled clay loam below 21 cm, we found some 1-2 mm long creamy-colored $MgSO_4$ crystals (identified by J. Barber of the British Agricultural Mission, Santa Cruz, Bolivia).

Table 16. Isla 1, Pit 1. Semialtura island with *Copernicia* palms.

0-5 cm	Grayish brown sandy loam (56.4% sand, 42.4% silt, 1.2% clay).
5-21 cm	Dark brown loam (46.5% sand, 44.7% silt, 8.8% clay).
21-35+ cm	Mottled yellow, red, and black clay loam (25.1% sand, 35.7% silt, 39.1% clay) with clear to opaque MgSO4 crystals.

Further north along the edge of the semialtura, there is another, but less pronounced, *Copernicia* island with a *Genipa*, some small *Ficus*, and a few shrubs. The ground is carpeted by *Cynodon*. The surface soil is a loamy sand to at least 20 cm, being coarser than the sands of Isla 1 or the pampa mounds.

In the adjacent pampa, are several small (ca. 3 m diameter.), rounded, low, flat mounds with sandy to silty surface textures. These mounds stand out clearly due to differences in the vegetation, where the mounds are grassy and the pampa is dominated by a white-flowered forb. The mound soils are very compacted at the surface, but very friable. The fine loamy sands are grayish brown with fine rusty orange mottles along root channels. The first 20 cm, at least, of the palm island is a homogenous loamy sand that is coarser than the corresponding materials from the neighboring mounds and Isla 1. I found absolutely no sign of termite or ant mounds in relation to these "mima-type" mounds. Almost of these "pampa mounds" were submerged in early January 1994. Isla 1 itself was completely surrounded by standing, albeit shallow, water. In May of 1994, only the highest ground under the *Ficus* roots remained above the flood waters.

The "Big Island." Further to the northwest, at the northern extremity of the semialtura *Copernicia* palmar peninsula which separates the bajío of El Sol from that of La Chacra, there is a large island of low forest (denoted at the "Big Island" on Map 3). It is a rather unusual formation, being literally an island of islands (see Chapter 6). The trees are found on countless small, flattened mounds, and there is grass in between the individual patches of trees, creating a strangely park-like landscape. There occasional large leaf-cutter ant mounds over a meter high in the forest. *Bromelia serra* is a common groundcover. There are few larger trees, the largest being *Sterculia*. There are apparently no *Attalea*, although there are some *Acrocomia*. *Cordia glabrata* are common. Strangely, *Cecropia* are also rather common here, being rare elsewhere at La Chacra (except upon the roadside debris berms). This suggests a relatively recent origin for these woody stands. In the lower semialtura to the west of the Big Island, there are many termite mounds and murundus, as well as fairly abundant *Cereus* cacti (on the mounds). The surface soils of this large patch of hardwoods seemed very silty, somewhat like the gallery forest soils. This island appears to be growing vertically as ants and termites continue to bring new materials to the surface. It would seem that eventually conditions favorable for the establishment of *Attalea* will occur and this woodland will someday develop into a more dense and shady forest.

The "Tarumá high ground." This site was first visible as an isolated, leafless tree when viewed from the southwestern portion of the bajío during the dry season. This low mound is located at the edge of a *Cyperus giganteus* stand (*junquillar*). This small patch of high ground is dominated by tararaqui (*Ipomoea carnea*). A shallow pit 3 m to the north of the lone tarumá (*Vitex cymosa*) revealed 6 cm of loose fine loamy sands, followed by a compacted fine sandy loam and a black silty clay with mottles below 22 cm (Table 17). The entire surface was underwater in mid-May of 1994.

Table 17. "Tarumá high ground" site profile.

0-6 cm	Loose fine loamy sands.
6-22 cm	Compact fine sandy loam.
22 + cm	Black silty clay with mottles.

Artificial Islands in the Seasonal Wetland

Isla Loma Verde (Plates 4 and 5). This is the closest island to the ranch house and the gallery forests of La Chacra. I named this isla for its high, green appearance from afar during the dry season. Due to its striking appearance, I was certain that this must be an artificial mound when I first saw it. The apparent height and the greenness during the winter (i.e., the dry season) was caused by an abundance of tall annual weeds (*Ambrosia eliator*). The isla itself is well elevated (0.90 m ove adjacent bajío), but has only what is perhaps a relictual tree cover of deciduous elements. This isla is not surrounded by junquillares, in contrast to the *Attalea*-dominated islas. Dimensions are approximately 40 x 50 m. I found a few small ceramic sherds on the surface, but these were scarce in comparison with those of the Ceramic Forests.

During the wet season, this island was so heavily trampled by the cattle that there was not a single herbaceous plant to be found on the entire island. It was thus an easy matter to completely census the entire population of terrestrial vascular plants on the island (Table 18; 250 m^2 plot in Table 19). In addition to the living trees, there are several toppled trunks of *Vitex cymosa*.. I was later informed that these were knocked down because they were full of bats that were not held in high regard by the human inhabitants of La Chacra.

Table 18. Inventory of all vascular plants on Isla Loma Verde (March 13, 1994):

Species	**n**
Nectandra sp.	13
Vitex cymosa	10
Coccoloba sp. 3	5
Acrocomia aculeata	4
Copernicia alba	3
Genipa americana	2
Pithecellobium scalare	2
Guazuma ulmifolia	1
Samanea tubulosa	1

These trees, with the exception of the *Nectandra*, are all typical of semialturas, although the *Vitex*, *Coccoloba*, and *Genipa* are also found on the alturas and altura-type islas as well. The *Nectandra* is found only along the margins of the islands and the cañada, being a tree fond of seasonal inundations.

Table 19. Vegetation plot 8: Isla Loma Verde.

Species	**Local name**	**n**	**ba**	**rd**	**rc**	**rd+rc**
Vitex cymosa	Tarumá	5	4915.8	0.3846	0.5810	0.9656
Coccoloba sp. 3	Pororó	3	1507.1	0.2308	0.1781	0.4089
Copernicia alba	Palmera	2	770.1	0.1538	0.0910	0.2449
Acrocomia aculeata	Totaí	1	585.3	0.0769	0.0692	0.1461
Genipa americana	Bí	1	390.6	0.0769	0.0462	0.1231

Pithecellobium scalare	Juno	1	292.6	0.0769	0.0346	0.1115
Totals		13	8461.4	1	1	2

The upper 6 cm of the soil is a very fine loam with very little clay (Table 20). This material is full of bone and shell fragments, plant debris, and small bits of ceramics. Beneath this somewhat loose layer is an extremely compact silty clay loam that was very difficult to penetrate with a pickax and shovel during the dry season. This particle size composition of this island is nearly identical to the subsoil of the bajío adjacent to Isla 2. The coarser texture of the upper 6 cm is likely the result of a residual coarsening due to the eluviation of clays.

Table 20. Isla Loma Verde profile.

0-6 cm	Dark gray loam (41.8% sand, 48.6 % silt, 9.6% clay) with abundant fragments of bone, shell, and ceramics.
6 cm +	Black silty clay loam (16.1 % sand, 48.5 % silt, 35.4% clay), abundant red to orange clay balls in matrix.

Isla Loma Verde is the only island in the bajío of La Chacra that has any characteristics that would suggest artificial origins. The first indicator is that the surface is littered with highly abundant bone fragments and occasional ceramic fragments. The concentration of ceramic fragments on this island stands in contrast to the notable rarity of ceramics on the outer islands. The second indication of artificiality is that the soil texture of the mound is nearly identical to that of the pampa subsoil. This match certainly supports the idea that the mound was created from material excavated or scraped out of the surrounding bajío. The location of Isla Loma Verde is also problematic to its incorporation into the levee model applied to the true islas del bajío. Isla Loma Verde is much closer to the semialtura and the Ceramic Forest zone than any other island and is not in the path of the postulated palaeoriver. Unlike the other islands of the bajío, Isla Loma Verde is not surrounded by *Cyperus giganteus* stands, nor does it show any indication of the extensions of lower levee surfaces associated with Islands 2 through 7. This island is certainly very different from the others at La Chacra.

Isla Loma Verde is thus a good candidate for artificiality, even though it is not associated with any other relict earthworks such as raised fields or causeways. It was likely constructed to serve as an outpost in the bajío for hunting expeditions, wetland plant harvests, defense, or other uses.

Chapter 8. Gallery forest segments along the Cañada de los Lagartos

The Cañada de los Lagartos is a seasonally-active senescent river channel that weakly meanders through the southwestern edge of La Chacra. The channel is essentially flat in cross-sectional profile, averaging no more than 50 cm deep and 60-80 m in width. During the dry season, it dries out completely except where water has been ponded by the earthen causeways constructed for the entry roads to the ranches. The cañada is bordered by a diverse range of vegetation types, largely forest or woodland, but occasionally open savanna. These gallery forests are rich in wildlife, including brocket deer, pacas, agoutis, coatimundis, sloths, jaguarundi, five species of monkeys, red squirrels, and a myriad of birds. The number of mammals observed during the day is remarkable if one considers the proximity of the highway (always within earshot) and the ranch houses.

The composition and structure of these forests are highly variable and reflect both natural and human factors. One section of the forest near the house contains large ochoó (*Hura crepitans*), bibosi (*Ficus* spp.), tajibo morado (*Jacaranda cuspidifolia*), and mapajo (*Ceiba pentandra*). Others are dominated by tall deciduous leguminous trees, such as curupaú (*Anadenanthera colubrina*), cari-cari (*Acacia polyphylla*, *A. loretensis*), and gebió (*Albizia niopoides*). Motacú palms (*Attalea phalerata*) is ubiquitous, and in a places forms pure stands. *Copernicia* is locally present as a forest element on lower, clayier surfaces as well as a savanna element. Sumuqué (*Syagrus sancona*) is locally abundant and is fed upon by howler monkeys. Palo diablo (*Triplaris americana*), a painful ant-tree inhabited by red *Pseudomyrmex*, is abundant throughout.

Monocots are abundant in the forests. Epiphytic *Philodendron*, *Anthurium*, and *Monstera* are common. Terrestrial bromeliads (*Bromelia serra*) form thickets in light gaps and along the forest edges; however, epiphytic bromeliads are very rare. *Costus* sp. are also locally abundant. In the wet channels and depressions there are tall *Heliconia*.

The gallery forest is occasionally broken by channels which connect the bajío with the cañada. One of these channels is bordered by a prehistoric causeway, which is fragmented into distinct units. I have found only a single pottery shard on this causeway. It is constructed out of heavy clays, which are brightly mottled red when wet. *Bactris* palms create a spiny understory on the slopes above the channels. Patujú (*Heliconia* spp.), although widespread throughout Moxos, are only locally common at La Chacra, observed only in moist channel bed depressions. These channels are vegetated by an assemblage of species which changes over the seasons. With the first spring rains, large numbers of a purple-flowered *Cleome* emerge and soon dominate the channels. Later, a prickly, aquatic thistle (Compositae) appears. These are followed by various patujuses (*Heliconia* spp., *Thalia geniculata*). Duckweed (*Lemna* sp.) carpets the water surface. Waterlilies (*Nymphaea* sp.) also make their appearance in the summer. These waters are teeming with a air-breathing fish locally known as the *bentón* (*Hoplias malabaricus*). During a rainstorm in January 1994, I observed the water flowing from the direction of the pampas toward the cañada. Between rainfall events, however, no flow was visible.

The Trans-Gallery Channel is the first one east of the house and the largest. It separates the Ceramic Forest from the non-ceramic forest to the west. The canopies of the trees along its banks converge and allow arboreal fauna to pass over the channel. I have frequently observed monkeys crossing in the trees overhead above this channel. For non-swimming terrestrial fauna that are too small to cross by foot (i.e., invertebrates, some lizards), the Trans-Gallery Channel may present a barrier during the wet season. Thus, for some organisms, the Trans-Gallery Channel may effectively create a forest island during at least part of the year. In terms of terrestrial vegetation, the channels are distinct zones of "non-forest" vegetation. In terms of canopy cover, these channels may be insignificant where the forest trees extend over the channel and create a continuos aerial forest cover.

It became apparent in February that in fact the entire core of the West Ceramic Forest is surrounded on three sides by channels of some sort (Plate 6). The canal that branches off the longest of the Bibosi canals (named for the giant *Ficus* trees that are found along these canals) continues all the way to the cañada, albeit through a maze of other branches. This canal enters the cañada just east of the Cañada Causeway structures. I have found ceramics in a few spots east of this system of channels, but the forest rapidly changes to a non-ceramic character (i.e., lower elevation, lighter colored and clayier epipedons, changes in botanical composition). Only the north side of the Ceramic Forest is not dissected by a channel. Rather, the forest surface slopes downward into a lower and more poorly drained forest with abundant terrestrial bromeliads, before grading into a savanna woodland fringe and palmar. The leveling data actually indicate that the some of the palmar surface may actually drain into the lower forest. This is truly an unanticipated finding.

A simple fluvial deposition model predicts that there should be a continually decreasing elevation as one moves away from the bank of the old levee along the cañada, and that the palmar (semialtura) is lower than any portion of the gallery forest. Of course, the field data do not demonstrate such a simple model. There are many points in the semialturas which lie far above many points within the gallery forests. Two important geomorphological agents not accounted for in a simple fluvial landscape model are termites and humans. The highest points in the semialtura palmar are those on surfaces created by old termite mounds, while the lowest points of the gallery forest (including the canals/channels) are ancient excavations made by pre-Hispanic people.

Table 21. Gallery forest pit 1: *Attalea* grove (motacuzal) with some *Triplaris* (palo diablo), ca 30 m from channel, north side, abundant leaf litter of both species. Abundant *Attalea* roots to 27 cm. Fairly dry and hard.

0-3 cm	Grayish silt loam, abundant intermixed organic material
3-12 cm	Yellowish gray clay loam with yellow-orange mottles, dry
12-27 cm	Dark brown clay, few mottles, abundant roots, more moisture
27-35+ cm	Dark brown clay with abundant brick-red mottles, strong angular blocky structure

Table 22. Gallery forest pit 2: 10.6 m from edge of semialtura woodland savanna. Trees: *Attalea, Ficus, Spondias, Cordia, Triplaris, Syagrus, Rollinia, Sterculia*. Pit is in shade. Many roots to 72 cm, few below.

0-4 cm	Very dark gray loam

4-6 cm	Very dark grayish brown sandy loam
6-31 cm	Dark grayish brown sandy loam
31-44 cm	Sandy loam
44-72 cm	Yellowish brown clay with red mottles (40-50%)
72-100+ cm	Same colors as above, but clayier.

No carbonates were found in either profile. On the average, the gallery forest soils are not nearly as sandy as isla soils, although there are local surface concentrations of loose fine sands. The forest soils are generally hard and clayey at shallow depths (30-40 cm). There is apparently little organic matter in the epipedons. In the dry season, they are rather dry and do not demonstrate gleying in the shallow profiles examined.

Flooded Forests

The shallowly flooded forest of the north gallery forest is characterized by *Hura crepitans*. In January 1994 these large (>90 cm dbh) trees were in standing water about 30 cm deep. The standing water is restricted to small basins or depressions, bordered by elevated surfaces and termite mounds. Water from the cañada invades these basins. Overland flow from other forest surfaces also feed into these pools. The aquatic flora is dominated by *Lemna* sp. and waterlilies. Occasionally there are *Bactris* palms in the pools. *Attalea* palms occur only on termite islands or on the elevated margins. The water of these pools, when undisturbed, is clear and reddish-brown (like a tea). There are large amounts of leaves decaying on the bottoms of the pools.

Lomas

I have identified two lomas (large artficial earthmounds) in the northern gallery forest of the Cañada de los Lagartos. The first, baptized as Loma Complex 1, is located very close to the ranch house, a short distance across the Trans-Gallery Channel. This complex consists of an elongate, apparently L-shaped ridge some 2.5 m high and over 60 m long. Shallow excavations and surface combing have yielded numerous broken pottery pieces. The soil of the mound is rather hard, clayey, and yellowish. The vegetation is an open forest with abundant *Triplaris, Syagrus,* shrubs, and vines. On the slopes of a low saddle of the mound, there are fine sands at the surface. The loma is bounded by several trails and apparently was once the site of an old chaco as evidenced by the presence of relict tutumos. Loma Complex 1 is located near the possible artificial channels in the forest which run into the palmar to the north. The relationships of the loma, the channels, the apparent terraplenes, and the islas must be examined further. There is at least 5.61 m of relief between the bed of the cañada and the peaks of the Loma 1. The non-loma platform surfaces of the forest are at least 2.7 m above the channel bed. The more than 5.6 meters of measured relief represents a significant accumulation of earthen and anthropic materials.

A second loma, called Loma 2, is located near the eastern boundary of La Chacra. This loma is less pronounced and has only a single peak. However, Loma 2 is located on a larger surface with a distinct vegetation, dominated by *Anadenanthera colubrina*. This surface appears to be an extensive artificial earthen platform elevated above the natural levee of the cañada. Several small fragments and two large pieces of ceramics were recovered from the surface of Loma 2. Later excavations and surface finds demonstrated the larger extent of this site.

In November 1993, I encountered even more abundant ceramic sites in the north gallery forest. Two sites were located by examining the materials attached to tree roots exposed by tree falls. The first of these sites is located on the edge of a *Heliconia*-filled channel, while the other is in well-drained forest. Obviously, the sites must be older than the trees which grew upon them. One must consider the representativity of tree fall sites. Unless we conclude that trees either preferentially grow upon ceramic sites or that trees upon ceramics are more prone to falling, then these are likely random samples of the forest surfaces. With this in mind, the frequency that ceramics are found in tree fall sites is impressive. Another site was located upon a flattened mound near the intersection of the trans-gallery channel and a lateral tributary near the mouth of the former into the cañada. At this site, ceramics were found in 4 out of 6 very shallow test pits, which were each ca. 30 x 20 cm in area and 10 cm deep. Another low mound near the Loma 1 also yielded ceramics; however, not all such mounds examined have yielded cultural artifacts. A final site was found on a *Bactris*-dominated slope into the channels to the north, where abundant ceramic fragments were found on the surface surrounding an armadillo or rodent burrow. An end section of a cylindrical grinder was found on the forest floor. These findings certainly indicate intensive use of the gallery forest in prehistoric times.

However, during January 1994, I discovered that the entire north gallery forest between the Trans-Gallery Forest Channel and the Cañada Causeway is essentially underlain by ceramics and other cultural materials. It is thus not meaningful to consider individual pits as sites, but rather we should speak of specific earthworks, hearths, middens, or other cultural features. I will henceforth refer to the area described above as the West Ceramic Forest. The area near the boundary of La Providencia which contains Loma 2 discussed above is similarly referred to as East Ceramic Forest. The Cañada Causeway extends into the West Ceramic Forest as a low ridge (ca. 1.15 m high), upon which and along which ceramics are present on the surface. The mound at the head of the causeway on the north bank is 2.24 m above the adjacent channel bed.

These zones are characterized by the presence of both surface and subsurface pre-Hispanic ceramic artifacts, generally deep dark brown to black epipedons, and the abundance of *Bactris* and *Attalea* palms. The lomas, other earthworks, and active termite/ant mounds are lighter colored and clayier than the general background surfaces of the Ceramic Forests. It is apparent that the earthworks and insect mounds were largely constructed with the clayier subsoil. The "non-earthwork" surfaces, however, are not "natural" surfaces. I believe that these are the combination of long-term work by both human and invertebrate activity. The ceramics, bones, shells, and charcoal were deposited in the past by prior human inhabitants of the gallery forest. After the departure of these folk, the earth-moving activity of earthworms, termites, ants, and other soil fauna has covered the anthropogenic materials with a mantle of reworked and organically-enriched soil materials.

A 1.5 m pit (Table 23) in the flat surface immediately north of Loma 1 (surface is 2.95 m lower than the east peak of the loma and at least 2.6 m above the bed of the cañada) revealed that the entire profile is highly influenced by past human activity. The first 15 cm is "sterile" dark brown clay loam, free of ceramics or other visible cultural materials. The zone between 15 and 65 cm is rich in pottery shards, bone, and charcoal, in a dark brown soil matrix. The soil between 65 and 76 cm changes to a yellowish brown, clayier texture, with pottery, much bone, and much charcoal. From 76 to at least 150 cm, the soil is a yellowish clay with some pottery, bone, charcoal, as well as bleached and partially decomposed snail shells. This finding revealed much about the true nature of the "Ceramic Forest." Downslope of this pit, towards the palmar and artificial canals, there are abundant ceramics on eroded surfaces, underground, and even in the subsoil of inundated depressions (indigenous excavations?) at the bottom of the slope (2.42 m below the surface of the 1.5 m pit). I encountered a tremendous variety of grinding boards and grinding cylinders, bowls, platters, jars, clay discs, and other items on this slope where a few old grapefruit trees provided refreshment.

Another pit (Table 24), near the mouth of the Trans-Gallery Channel, revealed highly abundant ceramics between 14 and 31 cm below the surface on a slight mound, perhaps 1.5 m above and 2-3 m horizontally from channels. *Bactris* was the dominant understory plant here. Nearby, I found a large piece of a fluted ceramic grinding plate which was lying on the surface of the forest floor.

Table 23. Pit at foot of north side of Loma 1, West Ceramic Forest.

0-15 cm	Dark brown clay loam, no ceramics.
15-65 cm	Dark brown soil matrix with abundant ceramics, bone, and charcoal.
65-76 cm	Yellowish brown clay, ceramics, much bone, much charcoal.
76-150+ cm	Yellow clay with some ceramics, bone, charcoal, snail shells.

Table 24. Pit near mouth of Trans-Gallery Channel on low mound.

0-14 cm	Very dark brown, friable soil, no cultural materials.
14-31 cm	Same soil as above, but with very abundant ceramics.
31-35 cm	Bone/shell fragment zone, somewhat cemented, in dark soil matrix.
35-55 cm	Brownish gray, clayier, still some bone/shell, charcoal, no ceramics.
55-65+ cm	Yellow clay with brownish gray and orange mottles, no cultural materials.

The yellow clays found in both of the profiles described above are likely the materials the mounds were constructed from. The east shore and the lower west shore (nearest the cañada) of the Trans-Gallery Channel contain abundant ceramic shards in their eroded banks, as first revealed to me by the January rains of 1994.

In the East Ceramic Forest, I encountered an intact tripod vessel embedded in the exposed rootmass of a large fallen tree. A nearby pit revealed scattered pottery shards in dark brown friable soil starting at 25 cm, overlying a clayey horizon with charcoal and shards. Ceramics were encountered at various points on the surface of forest floor. The forest appears to be upon an artificially raised surface, with scattered, low mound tops or "peaks" (including "Loma 2"). As in the West Ceramic Forest, there is a significant raised bank along the Cañada de los Lagartos. Similarly, these banks are dominated by an understory of *Bactris* palms. The forest composition of the general area, however, is very different from that of the West. In the East Ceramic Forest, the tall leguminous tree *Anadenanthera colubrina* co-dominates with *Attalea*. The residents of the nearby house at La Providencia, only a few hundred meters away from the East Ceramic Forest, were unaware of any lomas or ceramics in that ranch or in La Chacra. They also affirmed that were no sites with large forest trees (e.g. giant *Ficus* or *Hura*) in La Providencia. In fact, one person commented that “there really isn't any *real forest* around the area, only pampa-isla.”

There seems to be a negative correlation between soil fauna activity and ceramic yields. This may simply reflect deep burial by bioturbation or zoogenic mounds. Motacú seeds are often found buried at 20-30 cm depth, and these also seem inversely related to ceramics. Occasionally bone and/or shell fragments are encountered with the ceramics. The soil surrounding the ceramics is often black, except on the lomas, which are more clayey. Similarly, the soil of the ceramic-free/insect-rich mounds is generally lighter colored. At one site, abundant ceramics were recovered from gleyed clays below the water table.

Prehistoric ceramics are not unusual items to find in the forests and forest islands of the Llanos de Moxos. Where they occur, they are found in great quantities and are not difficult to find. Therefore, I conclude that the sites where ceramics are not found or where only a few scattered sherds can be found after considerable effort were not sites of permanent or semi-permanent human occupation. The gallery forests of the Cañada de los Lagartos and the Islas del Bajío of La Chacra represent contrasting sites in this respect, the former being locally rich in prehistoric cultural artifacts and the latter being essentially devoid of such materials.

Gallery Forest Vegetation Plots

The first forest plot (VP3, Table 25, Map 5) is on a lower surface without any ceramics. This site is dominated by two palms: *Attalea* as an overstory element and *Bactris* as an understory plant. The *Bactris* palms are extraordinarily spiny and grow in dense clonal clusters. *Picramnia* and *Margaritaria* are common understory shrubs or small trees with simple evergreen leaves. The other trees at this site include the widespread deciduous *Cordia alliodora*, and saplings of *Triplaris* and *Rheedia*, a tree with a very popular edible fruit. This type of palm forest is common throughout the region. It is likely that these palms are favored by livestock which chew on the palm fruits and act as dispersal agents. Cattle commonly enter the forests, especially the bulls. The fruits of both of these palms are fed upon by a number of birds and mammals, including macaws and various monkeys. I have observed owl monkeys feeding on the *Attalea* in this plot.

The forest plot (VP1, Table 26) on the West Ceramic Forest lies between the south edge of Loma Complex 1 and the cañada. This site is well-drained and water never ponds on the surface. The dominant species here is *Ampelocera ruizii*, a very characteristic tree and shrub of the ceramic forests. This tree has high rates of recruitment, as there are large numbers of shrubby juveniles throughout the forest. This species is favored for firewood as well as for ax handles which are cut from the narrow buttresses of mature trees. *Bactris* palms are again abundant understory elements in this site, but *Attalea* was represented only by four juvenile individuals. Another important species present here is *Spondias mombin*, a widespread tree in Neotropical forests and woodlands. Compared to the *Attalea-Bactris* dominated site on the non-ceramic surface to the west, this site has a much greater diversity of species.

Table 25. Vegetation plot 3. Non-ceramic gallery forest.

Species	**Local name**	**n**	**ba**	**rd**	**rc**	**rd+rc**
Attalea phalerata	Motacú	22	10614.2	0.2037	0.8197	1.0234
Bactris major var. *sociabilis*	Marayaú	62	403.2	0.5741	0.0311	0.6052
Cordia alliodora	Picana negra	1	1809.6	0.0093	0.1397	0.1490
Picramnia latifolia	s.n.	4	29.2	0.0370	0.0023	0.0393
Shrub 29	s.n.	4	14.6	0.0370	0.0011	0.0382
Margaritaria nobilis	Cafecillo	4	9.7	0.0370	0.0008	0.0378
Cordia sp. aff. *nodosa* "Suff 2"	Picana	3	2.1	0.0278	0.0002	0.0279
Lianas	Bejucos	2	14.5	0.0185	0.0011	0.0196
Cupania sp.	s.n.	1	38.5	0.0093	0.0030	0.0122
Triplaris americana	Palo diablo	1	9.1	0.0093	0.0007	0.0100
Eugenia aff. *ligustrina*?	Conservillo	1	2.3	0.0093	0.0002	0.0094
Shrub 27	s.n.	1	1.3	0.0093	0.0001	0.0094
Rheedia sp.	Achachairú	1	0.4	0.0093	0.0000	0.0093
Matayba sp.	s.n.	1	0.3	0.0093	0.0000	0.0093
		108	12948.9	1	1	2

Table 26. Vegetation plot 1. Artificial platform with scattered ceramics. Between Loma 1 and north bank of Cañada de los Lagartos.

Species	Local name	n	ba	rd	rc	rd+rc
Ampelocera ruizii	Blanquillo	81	1464.9	0.3568	0.1632	0.5200
Acacia polyphylla	Cari-cari	1	3496.2	0.0044	0.3894	0.3938
Bactris sp.	Marayaú	60	404.2	0.2643	0.0450	0.3093
Lianas	Bejucos	24	333.5	0.1057	0.0371	0.1429
Spondias mombin	Cedrillo	1	1034.9	0.0044	0.1153	0.1197
Cordia alliodora	Picana negra	2	839.8	0.0088	0.0935	0.1023
Neea sp. 1	Azocaró	5	544.2	0.0220	0.0606	0.0826
Randia armata	Espino	9	19.1	0.0396	0.0021	0.0418
Picramnia latifolia	s.n.	8	45.3	0.0352	0.0050	0.0403
Diospyros sp.	s.n.	2	236.8	0.0088	0.0264	0.0352
Attalea phalerata	Motacú	4	91.3	0.0176	0.0102	0.0278
Rhamnidium elaeocarpum	Turere	3	61.8	0.0132	0.0069	0.0201
Eugenia aff. *ligustrina?*	Conservillo	4	4.6	0.0176	0.0005	0.0181
Rubiaceae (Shrub 5)	s.n.	3	31.7	0.0132	0.0035	0.0167
Allophylus cf. *cinnamoneus*	s.n.	2	70.7	0.0088	0.0079	0.0167
Margaritaria nobilis	s.n.	2	34.2	0.0088	0.0038	0.0126
Citrus (orange)	Naranjo	1	77.7	0.0044	0.0087	0.0131
Sterculia apetala	Sujo	1	66.5	0.0044	0.0074	0.0118
Opuntia brasilensis	Cacto	2	16.9	0.0088	0.0019	0.0107
Annonaceae (Tree 1)	s.n.	1	50.1	0.0044	0.0056	0.0100
Urera baccifera	Pica-pica	2	1.8	0.0088	0.0002	0.0090
Salacia sp.	s.n.	2	1.5	0.0088	0.0002	0.0090
Tree 3	s.n.	1	28.3	0.0044	0.0031	0.0076
Swartzia sp.	s.n.	1	15.9	0.0044	0.0018	0.0062
Shrub 17	s.n.	1	3.8	0.0044	0.0004	0.0048
Psychotria sp.	s.n.	1	1.1	0.0044	0.0001	0.0045
Shrub 11	s.n.	1	0.8	0.0044	0.0001	0.0045
Cupania sp.	s.n.	1	0.6	0.0044	0.0001	0.0045
Rourea sp.	s.n.	1	0.2	0.0044	0.0000	0.0044
		227	8978.5	1.0000	1.0000	2.0000

The gallery forest fragment directly south of the house, on the north side of the cañada, has very different soils from those examined anywhere else in the along the cañada (Table 27). These soils are among the sandiest encountered at depth in La Chacra. Even the ant mounds are very soft and sandy (as well as full of wasps!).

Table 27. "House Isla" profile. Vegetation dominated by *Attalea, Triplaris,* and *Acacia polyphylla*

0-10 cm	Dark brown loam
10-22 cm	Lighter, but still rather dark brown
22-50 cm	Yellowish brown sandy loam
50-68 cm	Yellow loamy sand, perched water table
68-85+ cm	Yellow sandy clay with strong orange and black mottles/concretions.

No evidence of ceramics or other anthrofeatures encountered.

The House Isla forest plot (VP4, Table 28) appears to have been subjected to some transient disturbance in the not-too-distant past, as evidenced by the large number of small *Attalea* and *Triplaris* trees. There was also a fairly large *Cecropia*, a tree otherwise uncommon at La Chacra.

Other Gallery Forests at La Chacra

The last isla before La Providencia, north of the cañada, is dominated by *Anadenanthera colubrina* and is notable due to the presence of *Chorisia speciosa* and *Pseudobombax longiflorum*. The dry *A. colubrina* islands and woodlands stand in contrast to the "humid forest" patches with typical "Amazonian" elements such as *Hura, Ficus, Vitex,* and *Calycophyllum spruceanum.*

I have found no evidence of ceramics or other signs of human inhabitation in the southern gallery forests. These forests are generally on low surfaces, with significant flooding by cañada waters and abundant termite and ant mounds. The highest point measured on a transect was on an old termite mound, with a relief of 1.27 m relative to the cañada floor. However, all other points ranged between 0.53-0.98 m above the channel bed. These elevations are much lower than those of the ceramic-rich forest on the opposite bank. I have not identified distinct channels entering these forests. The Cañada Causeway does, however, extend into the south gallery forest. This forest is dominated by trees of much smaller diameter and has a significantly more important woody liana component. There are local *Attalea* groves on the better drained sites. On the driest sites, there are *Anadenanthera* groves as well. The contrasts between the north and south sides of the cañada are rather remarkable, considering their proximity.

The gallery forest is occasionally broken by savanna corridors which extend the semialtura vegetation directly to the edge of the cañada. These savanna intrusions are the "inter-isla" landscape units, or essentially the matrix in which the forest islands occur. One cannot walk continuously under forest cover along the cañada. These savanna segments are not more than 50 to 300 m in width, representing only a small proportion of linear space along the cañada edges.

We have not adequately addressed the fauna of these forest. However, I am pleased to report that the gallery forest islands support at least five confirmed species of monkeys. At La Chacra, I have personally observed and identified capuchins (*Cebus apella*), howlers (*Alouatta caraya*.), night monkeys (*Aotus azarai*), titis (*Callicebus donacophilus*), and silvery marmosets (*Callithrix melanura*). The ranch workers report that squirrel monkeys (*Saimiri boliviensis*) occasionally visit the cañada forests as well.

Table 28. Vegetation plot 4. “House Isla” modern gallery forest fragment.

Species	**Local name**	**n**	**ba**	**rd**	**rc**	**rd+rc**
Attalea phalerata	Motacú	37	15270.3	0.2000	0.7060	0.9060
Triplaris americana	Palo diablo	21	1470.2	0.1135	0.0680	0.1815
Rubiaceae (Shrub 5)	Palo llave	28	217.6	0.1514	0.0101	0.1614
Randia armata	Espino	14	55.1	0.0757	0.0025	0.0782
Shrub 36	s.n.	15	48.7	0.0811	0.0023	0.0833
Acacia polyphylla	Cari-cari	4	1052.8	0.0216	0.0487	0.0703
Cecropia sp. 1	Amabaibo	2	1150.5	0.0108	0.0532	0.0640
Coccoloba sp. 1	Pororó	3	541.3	0.0162	0.0250	0.0412
Annonaceae? Tree 25	s.n.	6	169.3	0.0324	0.0078	0.0403
Sorocea cf. *guilleminium*	Sapito	5	31.3	0.0270	0.0014	0.0285
Tabernaemontana benthamiana	Huevo de perro	3	258.8	0.0162	0.0120	0.0282
Cordia aff. *nodosa* (Tree 11)	Picana	5	21.6	0.0270	0.0010	0.0280
Acrocomia aculeata	Totaí	1	475.3	0.0054	0.0220	0.0274
Urera baccifera	Pica-pica	5	7.1	0.0270	0.0003	0.0274
Albizia niopioides	Gebió	1	463.8	0.0054	0.0214	0.0268
Lianas	Bejucos	4	17.5	0.0216	0.0008	0.0224
Allophylus sp.	s.n.	4	4.4	0.0216	0.0002	0.0218
Cupania sp.	s.n.	4	2.7	0.0216	0.0001	0.0217
Syagrus sancona	Sumuqué	1	298.6	0.0054	0.0138	0.0192
Celtis sp. 1	Chichapí	3	4.8	0.0162	0.0002	0.0164
Shrub 11	s.n.	3	2.1	0.0162	0.0001	0.0163
Casearia aculeata	s.n.	2	11.2	0.0108	0.0005	0.0113
Palicourea sp.	s.n.	2	4.1	0.0108	0.0002	0.0110
Rhamnidium elaeocarpum	Turere	2	1.6	0.0108	0.0001	0.0109
Cordia aff. *nodosa* (Shrub38)	Picana	2	1.4	0.0108	0.0001	0.0109
Malvaceae sp. 1	Malva	2	0.5	0.0108	0.0000	0.0108
Ficus cf. *caballina*	Bibosi	1	33.2	0.0054	0.0015	0.0069
Coccoloba sp. “greenstem"	s.n.	1	6.2	0.0054	0.0003	0.0057
Salacia elliptica	Guapomó	1	2.8	0.0054	0.0001	0.0055
Inga sp. 1	Pacay	1	2.8	0.0054	0.0001	0.0055
Tabebuia heptaphylla	Tajibo rosado	1	1.1	0.0054	0.0001	0.0055
Vitex cymosa	Tarumá	1	1.1	0.0054	0.0001	0.0055
		185	21629.7	1.0000	1.0000	2.0000

Chapter 9. Woodland, savanna, and wetland formations

Cordia-Tabebuia *Semialtura Woodland*

Immediately to the northeast of the house, the gallery forest is bordered by a deciduous woodland on the semialtura backslopes. The trees are small in diameter and there are abundant shrubs as well, the latter often in small clumps. The canopy is open and there is a well developed herbaceous groundcover. Within this woodland, there are small groves of forest species (Plate 8), often shrouded by colorfully-flowered vines.

The deciduous woodland trees present in the vegetation plot are *Cordia glabrata*, *Tabebuia ochracea*, and *Pithecellobium scalare* (VP9, Table 29). Other trees may be found both in forests as well as developing woodlands include *Rollinia herzogii*, *Acacia polyphylla*, *Triplaris americana*, *Inga* sp., and *Vitex cymosa.* Shrubs or treelets are the most numerous element in this formation, the principal ones being *Casearia aculeata*, *C. sylvestris*, *Cupania* sp., *Randia armata*, and *Coccoloba* sp. There is also a considerable suffrutescent understory component in the open gaps. This vegetation is dominated by young trees which have occupied formerly open semialtura pampa (Plate 9).

The small groves of trees are developing forest nuclei (*sensu* Janzen 1988) and contain species such as *Sterculia apetala*, *Attalea phalerata*, *Spondias mombin*, *Guazuma ulmifolia*, and *Genipa americana*, all of which are dispersed by livestock and other vertebrates (see Janzen and Martin 1982).

Semialtura Palmar

This formation is widespread of the Llanos de Moxos, but not where there is permanent soil saturation (where it is replaced by *Mauritia* or *Mauritiella* palms swamps). It is easily identifiable by the abundance of *Copernicia alba* palms which form a true palm savanna.

The *Copernicia* palms occur scattered within an herbaceous matrix of grasses, sedges, and forbs. This formation begins at the bajío/semialtura boundary and continues upslope on to higher portions of the semialtura. As drainage improves, the number of associated woody species increases. That is to say that the outermost portions are almost pure *Copernicia*, while the sites near the altura boundary have a great number of woody species. The shrubs and trees are generally found on termite mounds, but the *Copernicias* are tolerant of considerable inundation. These semialtura surfaces are often infested with spiny suffrutescent *Mimosa debilis* and the woodier *M. pellita.*

The semialtura vegetation plot we sampled (VP2, Table 30) was on the upper portion of the north backlope of the Cañada de los Lagartos, near the edge of the altura forest. Besides the *Copernicias*, there was also a short-trunked *Scheelea.* Trees found adjacent to plot included *Cordia glabrata*, *Tabebuia aurea*, *Tabernaemontana benthamiana*, *Samanea tubulosa*, and *Acrocomia aculeata*.

The soils of the semialturas are among the most clayey in the landscape. The semialtura palmar sample I analyzed in the lab had 73.5% clay at a depth of 30+ cm (Table 31). *Copernicia* palms are indicators of clayey, often salty, soils, in the Orinoco Llanos (J. San José, pers. comm. 1993; Cole 1982). The subsoil of a palmar site at La Chacra contained 73% clay at a depth of just 31 cm. The epipedons are generally light-colored silt loams. During the dry season, these soils are extremely hard and dusty.

Table 29. Vegetation plot 9 -- Semialtura woodland.

Species	**Local name**	**n**	**ba**	**rd**	**rc**	**rc+rd**
Cordia glabrata	Japunaqui	30	3347.1	0.1091	0.6297	0.7388
Tabebuia ochracea	Tajibo amarillo	15	728.4	0.0545	0.1370	0.1916
Vismia sp.	Veneno de víbora	34	37.4	0.1236	0.0070	0.1307
Casearia aculeata	s.n.	30	75.8	0.1091	0.0143	0.1234
Casearia sylvestris	s.n.	21	218.9	0.0764	0.0412	0.1175
Cupania sp.	s.n.	16	98.3	0.0582	0.0185	0.0767
Randia armata	Espino	17	45.2	0.0618	0.0085	0.0703
Coccoloba sp. "Shr44"	s.n.	6	240.1	0.0218	0.0452	0.0670
Rollinia herzogii	Cherimollito	5	242.5	0.0182	0.0456	0.0638
Acacia polyphylla	Cari-cari	16	10.6	0.0582	0.0020	0.0602
Malvaceae sp. 8	Malva	13	5.5	0.0473	0.0010	0.0483
Verbenaceae "Suff3"	s.n.	11	6.5	0.0400	0.0012	0.0412
Hyptis sp.	s.n.	9	4.6	0.0327	0.0009	0.0336
Rubiaceae "Shr5"	Palo llave	6	50.3	0.0218	0.0095	0.0313
Pithecellobium scalare	Juno	1	120.8	0.0036	0.0227	0.0264
Malvaceae sp. 9	Malva	7	3.0	0.0255	0.0006	0.0260
Mimosa debilis	Gabetillo	6	1.5	0.0218	0.0003	0.0221
Triplaris americana	Palo diablo	3	44.9	0.0109	0.0084	0.0194
Inga sp. 1	Pacay	4	4.8	0.0145	0.0009	0.0154
Malvaceae sp. 10	Malva	4	2.0	0.0145	0.0004	0.0149
Solanum riparium	s.n.	3	2.0	0.0109	0.0004	0.0113
Senna sp. 3	Mamuri	3	0.9	0.0109	0.0002	0.0111
Psidium guineense	Guayabillo	2	2.9	0.0073	0.0005	0.0078
Vernonia sp. 3	Paichané	2	0.8	0.0073	0.0001	0.0074
Eupatorium vitalbae	s.n.	2	0.8	0.0073	0.0001	0.0074
Cordia sp. "BLM"	Mechero	1	8.6	0.0036	0.0016	0.0052
Vitex cymosa	Tarumá	1	7.1	0.0036	0.0013	0.0050
Attalea phalerata	Motacú	1	1.5	0.0036	0.0003	0.0039
Cordia sp. "Shr47"	s.n.	1	1.1	0.0036	0.0002	0.0038
Rhamnidium elaeocarpum	s.n.	1	0.8	0.0036	0.0001	0.0038
Shrub 49	s.n.	1	0.5	0.0036	0.0001	0.0037
Bidens sp.	s.n.	1	0.3	0.0036	0.0001	0.0037
Cordia aff. *nodosa*	Picana	1	0.3	0.0036	0.0001	0.0037
Mimosa sp. "3"	Espino	1	0.1	0.0036	0.0000	0.0037
		275	5315.5	1.0000	1.0000	2.0000

Table 30. Vegetation plot 2. *Copernicia* palm savanna near forest boundary on semialtura surface.

Species	Local name	n	ba	rd	rc	rd+rc
Mimosa debilis	Gabetillo	141	0.4	0.5779	0.0001	0.5780
Attalea phalerata	Motacú	1	1590.4	0.0041	0.5001	0.5042
Copernicia alba	Palmera	6	801.2	0.0246	0.2520	0.2765
Platymiscium sp.	Tarara	6	605.7	0.0246	0.1905	0.2151
Vernonia sp. 2	Paichané	37	1.3	0.1516	0.0004	0.1521
Rhamnidium elaeocarpum	Turere	3	146.7	0.0123	0.0461	0.0584
Mimosa pellita	Cerrate puta	10	0.5	0.0410	0.0002	0.0411
Lantana sp. 1	Japutamo	9	0.1	0.0369	0.0000	0.0369
Cordia sp. "BLM"	Mechero	8	11.0	0.0328	0.0035	0.0362
Malvaceae? "Shrub 23"	s.n.	4	4.7	0.0164	0.0015	0.0179
Vernonia sp. 1	Paichané	4	3.4	0.0164	0.0011	0.0175
Eupatorium vitalbae	s.n.	3	5.2	0.0123	0.0016	0.0139
Hyptis sp.	s.n.	3	2.2	0.0123	0.0007	0.0130
Solanum cf. *riparium*	s.n.	3	1.0	0.0123	0.0003	0.0126
Vismia sp.	Veneno de víbora	2	1.5	0.0082	0.0005	0.0087
Vernonia sp. 3	Paichané	2	0.5	0.0082	0.0001	0.0083
Paullinia cf. *alata*?	s.n.	1	2.8	0.0041	0.0009	0.0050
Tournefortia sp.	s.n.	1	1.3	0.0041	0.0004	0.0045
		244	3180.0	1	1	2

Table 31. Semialtura palmar profile. *Copernicia alba* savanna.

0-18 cm	Light greyish brown silt loam (28.2% sand, 55.2% silt, 16.7 % clay).
18-30 cm	Yellowish brown silt loam (24.5% sand, 50.6% silt, 24.9% clay), clayier than above.
30 cm +	Yellowish clay (19.2% sand, 7.4%, 73.5% clay) with occasional red mottles.

To the west of the house at La Chacra, the gallery forest proper is bordered (on both sides) by a type of murundu woodland, where the woody vegetation is largely upon low mounds 2-3 m in diameter (Plate 7). There is a branch of the cañada which apparently drains the semialtura and pampa to the north, not far west from the house. Passing this channel, which was filled with water thistles, sedges, and 35-cm deep water on 18 January 1994, there is a rather scenic termite savanna woodland. One first is impressed by classic termite mound murundus and the abundance of chauchachi trees (*Geoffroea striata*). Further west, there are abundant examples of young (2-3 m tall) tajibos (*Tabebuia ochracea*). There are also small *T. heptaphylla* and *T. aurea* of all sizes. The other abundant trees are *Samanea, Pithecellobium, Cordia glabrata, Copernicia, Guazuma, Tabernaemontana,* and evergreen *Cordia* shrubs. As one approaches the gallery forest edge, *Astronium, Acacia, Acrocomia, Attalea,* and *Piptadenia* are common. The dominant grasses are a tall *Paspalum* and a lower *Panicum*. *Mimosa debilis* is also very abundant. To the north, the semialtura surface rather rapidly grades into the bajío pampas, with only a narrow zone of *Copernicia*-palmar.

South of the cañada, there is a woodland dominated by young *Astronium* and *Tabebuia*, which then grades into an older woodland with large forest-type *Tabebuia, Astronium, Piptadenia, Sterculia,* and *Anadenanthera*. This savanna woodland contains elongate islands of *Attalea*-dominated forest on well-elevated surfaces. However, during the wet season, I did not encounter standing water in the savanna itself. The lower trunks of many of the savanna woodland trees are blackened by fires. To the east (i.e., toward the ranch house), the savanna woodland becomes increasingly less well drained and is soon clogged with spiny mimosas.

Further eastward, the surface becomes inundated and *Eichhornia* is common in the intermound matrix and scandent *Combretum* shrubs are abundant on the mounds. Eventually, tajibos (*T. heptaphylla*) become common on the mounds. The inundated condition of this zone is apparently exacerbated by blockage of downslope drainage by the highway to the south and a series of berms/windrows created by clearing of the woodland toward the entry road. There are numerous dead ("beheaded") *Copernicia* and other dead trees, as well as trees with yellowing leaves. Apparently some of the termite mound murundus were not high enough to prevent waterlogging of the roots of their woody inhabitants.

Curupauzales (groves dominated by *Anadenanthera*) were allegedly much more numerous before many were killed by post-highway inundation regimes. I clearly recall being impressed by the abundance of drowned trees north of the highway between La Chacra and El Sol back in 1986. It appears thus that the cañada may in fact deliver water *to* the semialtura and that this water is retained by the highway. Thus, the zone south of the highway may be somewhat drier than in the past and there *curupauzales* would be favored. (This is evident when traveling on the highway.)

Separating the bajíos of El Sol and La Chacra, the semialtura surface extends northward to the "Big Isla," forming a sort of semialtura peninsula (Map 3). *Copernicia* and *Cordia glabrata* are the primary trees, with *Sterculia* being locally important in the formation of small islas. Erland Suárez, the foreman of La Chacra, noted that in 1983 this area was much more open with only a few scattered islas of woody growth. There had been a significant establishment of shrubs and small trees between 1983 and 1994. Other informants have substantiated this and other similar changes on the semialturas of the Cañada de los Lagartos.

Savannas

I must reiterate that I am rather wary of the use of the word "savanna" in the literature. For many, savanna is simply the equivalent of "non-forest" in the tropical lowlands. I prefer to restrict the use of the word to those formations that are characterized by an herbaceous matrix which contains scattered trees or shrubs. Perhaps one rather surprising result of my study is that savannas in the strictest sense are actually not very important landscape elements in the Chacra region, or even considerable portions of the Llanos de Moxos. Prior to my worka at La Chacra, I had always called the vegetation of the bajíos a savanna like most other ecologists or geographers. However, I, also like most others, had never really examined this vegetation very closely.

On a simply floristic basis, we can see that La Chacra is not a very "typical" Neotropical savanna. One of the most characteristic plants of the Neotropical savannas is *Curatella americana.*

This plant is not to be found anywhere in the vicinity of La Chacra, although it is common in some other areas of the Llanos de Moxos. The only *Curatella*-like plants I could find at La Chacra were the closely related liana *Tetracera* cf. *parviflora* and unrelated sclerophyllous-leafed shrubs of the genus *Coccoloba*. Another very important genus in Neotropical savannas is *Byrsonima,* of which I encountered only a single specimen.

The vegetation which I consider to be savanna occupies only the narrow transition zone between the forests and the herbaceous wetlands of the bajío. These savannas are largely what have been called “termite savannas,” “pimple savannas,” “murundu savannas,” or perhaps even “apêtê” savannas. Here, the woody plants are largely restricted to micro-relief features largely related to insect activity. (One could argue perhaps that these are really parklands on a fine scale, but savanna will suffice for now.)

Common trees on the semialtura termite mounds are *Genipa*, *Copernicia*, *Tabebuia*, *Geoffroea*, *Vitex*, *Astronium*, *Sorocea*, *Guazuma*, *Samanea*, and *Cordia*. Shrubs commonly found on the mounds include *Celtis*, *Cupania*, *Xylosma*, *Cordia*, and *Coccoloba*. Sprawling *Cereus* cacti are important on many mounds. The trees found on these 1-3 m diameter islets are mostly deciduous, but the shrubs are largely evergreen. The plot we sampled was located on the semialtura south of the cañada near the entry road to La Chacra (VP7, Table 32). All of the woody plants except for the *Mimosa*s were restricted to the termite mounds. The ground between the mounds was inundated to a depth of about 25 cm and covered by herbaceous vegetation.

Table 32. Vegetation plot 7 -- Termite mound savanna.

Species	**Local name**	**n**	**ba**	**rd**	**rc**	**rd+rc**
Copernicia alba	Palmera	1	703.1	0.0116	0.3727	0.3843
Eupatorium vitalbae	s.n.	23	33.2	0.2674	0.0176	0.2850
Tabebuia heptaphylla	Tajibo rosado	4	395.5	0.0465	0.2096	0.2562
Mimosa pellita	Cerrate puta	20	26.8	0.2326	0.0142	0.2468
Astronium fraxinifolium	Cuta	1	387.1	0.0116	0.2052	0.2168
Vitex cymosa	Tarumá	1	174.4	0.0116	0.0924	0.1041
Senna sp. 2	Mamuri	8	8.4	0.0930	0.0045	0.0975
Vernonia sp. 3	Paichané	5	2.4	0.0581	0.0013	0.0594
Malvaceae sp. 8	Malva	4	4.8	0.0465	0.0026	0.0491
Psidium guineense	Guayabillo	1	59.9	0.0116	0.0318	0.0434
Samanea tubulosa	Penoco	1	47.8	0.0116	0.0253	0.0370
Cupania sp.	s.n.	3	1.4	0.0349	0.0007	0.0356
Solanum riparium	s.n.	3	1.2	0.0349	0.0006	0.0355
Sapium haematospermum	Leche-leche	1	27.3	0.0116	0.0145	0.0261
Tournefortia sp.	s.n.	2	2.2	0.0233	0.0012	0.0244
Solanum sp. 1	s.n.	2	2.1	0.0233	0.0011	0.0244
Vernonia sp. 4	Paichané	2	1.2	0.0233	0.0007	0.0239
Lantana sp. 2	Japutamo	1	3.5	0.0116	0.0018	0.0135
Hyptis sp.	s.n.	1	3.5	0.0116	0.0018	0.0135

Mimosa debilis	Gabetillo	1	0.6	0.0116	0.0003	0.0120
Lantana sp. 1	Japutamo	1	0.2	0.0116	0.0001	0.0117
		86	1886.5	1.0000	1.0000	2.0000

Wetlands

At least 75% of the "non-forest" surfaces of the Beni corresponds to some sort of herbaceous formation whose composition and function are largely a function of the annual cycle of inundation and desiccation. I prefer to classify these seasonally to permanently inundated vegetation formations which are dominated by grasses, sedges, spike rushes, water hyacinths, water lilies, and other aquatic taxa as seasonal wetlands or simply as wetlands, rather than as savannas. The other 25% of the non-forest vegetation includes the *Copernicia* palm savannas, termite savannas, semialtura woodlands, and the so-called "scrub savanna."

The great shallowly-inundated rainwater flat known as the bajío contains highly productive *arrocillares* characterized by the native aquatic grasses *Leersia hexandra, Luziola peruviana,* and *Hymenachne amplexicaule*. The deeper portions present dense *junquillares,* stands of the giant South American papyrus sedge (*Cyperus giganteus*). The outer edges of the bajío are often dominated by *cortadera* (*Scleria pterota*), a "sawgrass"-type sedge and *paja toruna* (*Paspalum virgatum*), a coarse bunchgrass.

Cyperus giganteus grows in round clonal clumps, which can form extensive marshes many square kilometers in area. The *junquillo* burns readily only during extreme dry years and the tender regrowth is avidly grazed by cattle. There are abundant grasses in the spaces between the clumps of sedges.

The bajío soils are variable. The zones where aquatic grasses and *Eichhornia* are dominant appear to be silty clays which dry and crack in the winter. The soils of the junquillares contain abundant plant material in various stages of decomposition and which retain water well into the driest parts of dry years. These soils are very soft and livestock often become trapped in the squishy mires.

Contrary to what would be expected by the typical fining-outwards sequence in floodplain sediments, I found sands to be locally important even in the bajíos. The sands are at the surface (to about 25-30 cm) and are underlain by deep horizons of silty clays and clays. Near the "Thrashed Roadside Isla" near the gate to Cáceres (Map 3), I found podzol-like profiles, where dark organic-stained sands are underlain by light gray or white sands over mottled clays (some probably contain plinthite). Between Islas 5 and 6, there are sandy soils that are largely black with interspersed pockets of white sands, underlain by gray brown loamy sands over yellow sandy clays or clay loams. The pampa epipedon adjecent to Isla 1 was heavily enriched in sand from the isla (Table 33). The A and A2 horizons cotained 51 and 44% sand respectively. In contrast, the B1t and B2t horizons contained only 17% sand. The B1t contained more clay the B2t, probalbly enriched by illuvial clays from the eroded isla materials.

Table 33. Bajío-pampa wetland profile. *Pontederia, Eichhornia* and other aquatic vegetation.

0-18 cm	Black loam (51.3% sand, 32.4% silt, 16.4% clay).
18-23 cm	Very dark brown loam (44.0% sand, 44.3% silt, 11.7 %clay).

23-32 cm	Gray gleyed clay loam (16.9% sand, 47.7% silt, 35.4% clay).
32-40 cm +	Gray silty clay loam (16.9% sand, 50.9 silt, 32.2% clay) with orange mottles.

All of the bajío soils, however, are imperfectly drained due to the lack of relief and the impermeable, compacted, clayey horizons at shallow depths. These wetlands are maintained by perched water tables during much of the year. Beneath the saturated epipedon, the heavy and compacted sediments remain rather dry.

The surface which extends from the palmar north of Isla 1 to the “Tarumá-Tararaqui high ground” is firm and smooth when dry, a pleasant place to run horses. This contrasts greatly with the dangerously pockmarked and cracked surfaces of the bajío proper. This higher surface is a continuation of the palmar semialtura, but has a longer duration of standing water and thus no woody vegetation.

Termite and ant mounds are absent from the bajío, except the immediate edges. Some islas in the bajío have low mounds, but I did not observe any of the taller conical mounds typical of the semialturas and gallery forest edges.

Seasonal changes in the landscape

The first rains near the end of the dry season (7-10 September 1993) caused appreciable regrowth and germination/emergence in all plant associations. The grasses of the bajío were notably taller and more dense than before. The islas and gallery forests had many more seedlings and herbaceous understory elements. Standing water was present the week of September 20-27 in many places that were dry September 2-9. The shallow junquillar basins of the bajíos filled considerably.

The entire semialtura and bajío surface was covered by standing or flowing water in early November, following intense rains. The cañada had also began to fill. Likewise, the channels of the gallery forest were full of water and, surprisingly, of large numbers of fish. Foot travel in bajío was now very difficult, especially under the nearly perpendicular sun of mid-spring. I traversed water and mud that reached above my knees in the lower sections of the bajío. The water was tea-colored in the pools of the bajío, but more or less colorless in the semialturas. The termite mound "murundus" of the semialtura were now fully functional as islands of dry ground. Likewise, the large islas of the bajío remained high and dry.

By early November the cover of understory plants, seedlings, and saplings was greatly higher in both the gallery forest and the islas, than during the dry season. The semialtura vegetation had completely recovered from the winter fires; the once-scorched trees and shrubs now had verdant new foliage. The early November rains softened the termite mound and alate termites were abundant during this period, after which they were never to be seen again. *Setaria* was common in the wet semialtura “meadows,” where the standing water was not more than 15 cm deep and usually only about 5 cm or so. In the bajío, *Eleocharis* were suddenly abundant in many areas.

There was little precipitation from mid-November until December 10. The water levels of the forest channels had dropped considerably during this period, but they were still mostly filled with standing water. There were significant rains on January 2 and 9, but there it did not rain again until January 19. The bajío still had a considerable volume of water, but it was not much deeper than stirrup-high. The channels and depressions of the north gallery forest were also full. The junquillares had grown tall by January, making travel trough them difficult to impossible. One enters a junquillar at the risk of losing sight of all horizons, lost in a morass of giant sedges, waist-deep water, and slippery floors of mud and muck.

In early February, the bajío was considerably more inundated as the result of a heavy rain in late January. I recorded standing water up to 98 cm deep, but most was between 30-50 cm deep. The lowest point yet measured at La Chacra is 98.734 for a pool of water surrounded by giant *Eichhornia crassipes* tarope, based on an arbitrary benchmark of 100.000 m located northeast of the house. The measured relief in the bajío is not great. Between the center of Isla 2 and the tarope pool, there are 1.59 m of relief. The non-isla relief is on the order of 0.75 m (excluding the pool, ca. 53 cm). Even so, half a meter is still significant. *Cyperus giganteus* stands actually occupy higher surfaces than adjacent non-junquillo vegetation (10.2 cm measured). *Eleocharis-Eichhornia* stands occupy the lowest surfaces, 20-30 cm below the junquillares.

The apparent (i.e., visually dominant) vegetation composition of the bajíos changes significantly with the seasons. In January, various types of water lilies (*Nymphaea* sp.), spike-rushes (*Eleocharis* spp.), sawgrass sedges (*Rhynchospora* sp.) and patujuses (*Canna*, *Heliconia*, and *Thalia*) that were not visible in the dry season, are very prominent. Many of the winter or fall annual “weeds” die with the rising waters, especially on the edges of islas. In the cañada, “water thistles” rise with the waters, but eventually die back and give way to the water hyacinths.

Near the end of the rainy season in mid-May, another big rainfall refilled the bajío, semialturas, and cañada. We crossed the East Range bajío by horse, following the trail to Cáceres. The horses waded through chest-deep, crystal-clear, tea-colored water. The trail had become a canal through the tall, dense *Thalia* and *Cyperus* that had grown over the once nearly-barren pampa.

On summer days when there is no precipitation and the sun is not completely obscured by the clouds, the influence of evapotranspiration is extremely important (The summer solar peak at 15°S is February 9). The exposed soils of the alturas and semialturas dry out rapidly following rains when there is sun, especially on breezy days. The general weather between 5-19 January 1994 was dry, with rather comfortable relative humidities. It was more humid during early November 1993 than early to mid-January 1994. Semialtura isla soils in January were extremely hard and dry. Nevertheless, there was considerably more standing water in the bajíos and channels in January than in November. Late rains in May 1994 again raised bajío and semialtura water levels to near peak levels. The significance of individual storms is great, especially those lasting 12-14 hours or more.

A large percentage of the late winter/early spring plant cover and biomass of the semialtura and bajío is composed of small annual forbs. This period, however, has a very low aboveground plant biomass.

After the first spring rains in September, I observed at least four types of pools or puddles in the bajío. The first type is a sandy/silty-bottomed depression in the semialtura/bajío transition zone, where the coarser sediments are washed down from the higher surface and accumulate in the pools. The second type includes larger ponded zones of open water in the center of a bajío, where there are no *Cyperus giganteus* or *Eichhornia*. This type is found in smaller bajíos with perhaps no outlet, often surrounded by *Copernicia* palmar. A third type is found in the grassy bajío proper and is be filled with *Eichhornia crassipes*. These pools are connected by drainage channels, often created or deepened by the movements of cattle, capibaras, and caimans. When these pools dry, they reveal black, cracked clayey bottoms. The fourth type depression is the yomomo or junquillar, dominated by *Cyperus giganteus*. Here, the soils are highly organic and spongy. These depressions can become dangerous quagmires where cattle may become trapped in the black muck. However, it must be noted again that the junquillo plant clumps themselves are found on low mounds, not always in standing water These mounds are accumulations of plant matter (peats). The trails between the clumps/mounds are where the water collects and flows. After the early part of the wet season, all of these depressions become united under the uniform sheet of water that covers the bajío and, more briefly, the semialtura.

The Llanos de Moxos savannas and wetlands are often referred to as "flood savannas" (e.g., *Überschwemmungssavannen*). The word "flood," however, typically carries the connotation of an event caused by the accumulation of water from overflowing streams or rivers. In reality, we find that the extent of overbank flooding is rather restricted in the Llanos de Moxos. More frequently, the most extensive inundated savannas and wetlands receive their water directly from rainfall and overland flows. Many of the bajíos are local depressions that accumulate rainwater and overland flow from the surrounding higher surface, completely free from modern fluvial influences. "Rainwater flats" is a very appropriate term to describe these non-floodplain bajíos.

The inundations of the rainwater flats are independent of the river floods. In 1994 the floods of the Mamoré and Ibare rivers were late and of low magnitude; however, the bajío of La Chacra was full most of the season. The river floods are related to rainfall in the upper parts of the drainage basin while the bajío inundations are caused by local precipitation events.

Chapter 10. Abiotic and Biogeomorphological Determinants of Forest Island Distribution and Composition at La Chacra

In the next four chapters we will discuss the mechanisms through which the patterns of woody vegetation observed at La Chacra are mediated. First, we will consider relief and drainage as primary determinants of vegetation at La Chacra and in the Llanos de Moxos in general. Next, we will discuss the significance of soil properties as determinants We will then turn to the biological mechanisms which mediate the distribution and abundance of plant species. We then will examine the broader phytogeographical relationships of La Chacra and its surrounding regions. Finally, we examine the role of direct and indirect human manipulation of the vegetation.

Topography and Vegetation Relationships in Neotropical Savannas.

Using the broad definition of savanna, we can identify some savanna landscapes where one could easily dichotomize between areas dominated by tree cover and areas dominated by herbaceous cover. Where human agency is not the primary determinant of the patterns of arboreal cover, we generally find that topographic or edaphic factors are strongly correlated with the distribution of the herbaceous and woody units. The topographic units of the Moxos landscapes generally correspond to distinct vegetation formations: the low bajíos contain wetlands, the higher alturas are forested, and the intermediate positions contain savannas.

Sarmiento (1983) equated the Orinoco *bajos* with hyperseasonal savannas, either entirely herbaceous or with *Copernicia tectorum* as the single woody species. In Moxos, the bajíos are analogous, except the species is *C. alba*. Likewise, Cole (1982) noted that *Copernicia* palm savannas occupy the periphery of herbaceous inundation savanna in a zone of mottled yellowish brown clays in the Apure region of Venezuela (Cole 1982). This is directly analogous to the semialtura palmares in the Chacra region.

Cole (1982) considered many “mosaic distributions of savanna categories” to be “a result of contrasting edaphic conditions caused by the juxtaposition of different combinations of relief and drainage, bedrock and superficial geology variously related to the geomorphological evolution of the landscape and to both long-term and short-term climatic changes.” In other words, different types of savannas are found on different types of substrates. For example, she contrasted between savanna woodlands and savanna grasslands, the latter being favored in “depositional areas where the soil and drainage conditions are inimical to trees.” However, I must add that these “depositional areas” may be presently inactive, receiving primarily rainwater, not fluvial overflows.

We have seen that the vegetation units at La Chacra are largely linked to the topography. When the vegetation changes are not accompanied by topographic or edaphic changes, then human impact is usually important. In Moxos, the mechanisms of topographic determination are largely related to the physiological influences of soil moisture regimes.

Soil Moisture

The role of soil water regimes as a determinant of forest/savanna boundaries has been discussed by numerous authors, perhaps best by Beard (1953). Beard argued that it is the double impact of seasonal waterlogging *in combination* with seasonal drought that often limits the growth of woody plants in tropical American savannas.

Like Beard, Tinley (1982) believes that soil moisture balance is the most significant edaphic feature in determining savanna vegetation patterns, as it overrides all other properties, or influences their effects. Tinley noted that in southern African savannas "the majority of forest patches are related to soil sites with optimal moisture retention and aeration under the present climate and geomorphic dynamics." Forests patches once considered to be relics were demonstrated to in fact be recently developed upon slump scars with ameliorated water balances (Schroder 1976).

Grazing reduces evapotranspiration by the vegetation and may thus contribute to prolonging the period of standing water and saturated soils in the inundated savannas. However, this effect must be balanced against changes in direct evaporation rates influenced by interception of solar energy by the aerial phytomass. Tinley (1982) observed that removal of woody vegetation upon a duplex soil with a pan to have reactivated lateral subsurface flow, which created saturated soil conditions sufficient to kill the margins of forest patches. (See also Denevan 1963; Wilhelmy 1958b)

More recently, Furley (1992) synthesized data from five diverse Neotropical savanna localities and concluded that the soil-water regime seems to be the strongest determinant of the precise location of the forest/savanna boundary.

The soil moisture condition in each topographic position of the landscape responds differentially to a given variation in precipitation. The highest alturas or levee tops are not inundated under even the highest rainfall events, while the lowest bajíos are flooded under almost any quantity of rainfall within the range of inter-annual variations. The intermediate topographic positions are those which are most subject to changing water regimes under rainfall variations.

Relief and Drainage

Drainage conditions are largely a product of two factors: 1) topographic position and 2) soil infiltration rates. The processes which create the topography and influence soil infiltration in the Llanos de Moxos are thus the principal themes of this section. The overriding factors responsible for the existence of the Llanos de Moxos savannas are the regional structural geology and Quaternary process history which created the flat alluvial plains. The general outlines of these phenomena were discussed in Chapter 3. We will now discuss the particular case of the region of La Chacra.

Fluvial History

There is no question that the landscapes of the Llanos de Moxos are largely the products of fluvial deposition and erosion. The only qualifying statement necessary is that the formative processes are largely palaeofluvial, not modern. The alluvial surfaces of the Moxos basin have been reworked repeatedly throughout the Quaternary, leaving a complicated patchwork of landscape features dating from different periods of activity (see Hanagarth 1993: 31-45).

The general topographic sequence of channel-levee-backslope-flood basin is repeated across the Llanos de Moxos. At La Chacra we observe this sequence of features on either side of the Cañada de los Lagartos. In local terminology, this sequence is cañada-altura-semialtura-bajío. These toposequences are of varying ages and may be superimposed upon each other, thus creating the complicated patchwork mentioned above.

La Cañada de los Lagartos

A cañada is a palaeochannel relict or a more recently senesced river. These channels are generally shallow and flat in cross-section profile, not being deeply incised. The relative degree of channel fill from fluvial aggradation and colluvial bank deposition is not known, but both are likely significant. There are no active rivers in the Chacra region, or anywhere I have been in Moxos, with such flat cross-sectional geometries, except for the braided channels near the Subandean Front.

The Cañada de los Lagartos is the most recent of a series of channels to have traversed the “Lagartos basin.” Based on the evidence of localized sandy deposits and relic natural levee features, I conclude that in a prior period there was a channel 2-3 km to the north of the present cañada in the zone of the bajío forest islands.

Levee / Altura formation

The forested altura surfaces along the cañada are natural levee deposits, augmented locally by mound building by prehistoric peoples and millennia of continual ant and termite activity. These are the types of surfaces which ultimately form the ground beneath many of the forest islands in the Llanos de Moxos.

Natural levees are composed of vertical accretion sediments deposited during fluvial flood events. For this to occur, there must be sediments available for entrainment, sufficient moving water to transport these materials to the site of deposition, and overbank floods during which some of these materials are deposited. All of the sediments carried by rivers of the region, between the Mamoré and the San Pablo to the east, are materials stored in the older alluvial deposits through which these low-gradient streams flow. The modern small rivers such as the Mocoví, Matiquipiri, and Cocharcas are not creating levee deposits. These rivers are born in the plains and thus do not have eroding headwater areas to provide the sediment needed to build levees. The minimal energy slopes of these rivers greatly limits their potential to transport coarse particles. Flood events are slow to develop, given the flatness of the basins, and are not associated with especially high-velocity flows.

After rain storms, I have examined freshly deposited sheetflow sediments on the forest floor and these demonstrate clearly sorted strata of sands and finer materials, completely unrelated to any fluvio-depositional events. Sediments that washed into a pit I excavated on a loma demonstrated 2-mm thick layers of pure sand which were separated by thicker layers of mud. We thus see that stratified sand layers do not by any means necessarily indicate fluvial deposition. We must also keep in mind that the texture of a deposit does not necessarily represent the entire range of particle sizes of the source material, only a sorted selection thereof.

The lack (or at least the obscurity) of primary sedimentary structures in the islas, alturas, and other relief features does not negate fluvio-depositional origins for any of these features. It is only the result of intense bioturbation and livestock compaction in the absence of more recent fluvial deposition.

In other words, the low natural levees along the Cañada de los Lagartos are relict features of past fluvial regimes. In the present they are degrading, not developing (except for the contributions of earthmoving insects).

Formation of the semialturas

The semialturas are the very gently sloping backslopes of the levees. Examination of aerial photography reveals that some semialturas of the La Chacra region extend away from the cañada in splay-like “bird’s foot” type patterns (Map 3). The altura-semialtura-bajío sequence is a fining outwards sequence of palaeofluvial deposition, where the occasional semialtura “outbreaks” with sandier materials thus represent splay deposits. The semialturas are finer-textured, flatter, and more poorly-drained than the forested levees.

Fates of Abandoned Fluvial Landscape Features

Erosion and colluvial deposition in the present regime

Given that La Chacra is free from modern fluvial activity, with the exception of the limited flows and overflows of the Cañada de los Lagartos, erosion and colluvial deposition are the primary processes which characterize the present process regime. We will consider the impacts of these processes by examining them in each of the primary landscape units.

Isla erosion and colluvial deposits on the pampas

Movement of surficial materials on islas is highly significant during windy periods in the dry season. Loose sand and smaller particles are whipped about the surface during windstorms. Materials accumulate around the bases of tree trunks or fallen logs. The surficial sand accumulations on the outer slopes of the islas del bajío and on the surface of the adjacent pampa are likely deposited subaqueously during the annual inundations; however, they are not flood deposits. These sands are washed downwards from the higher, unflooded surfaces of the islas. As the sands are carried with the overland flow, they fall out of suspension when the running water hits the standing (more or less) water over the flooded isla margins. This explains the distribution and concentration of loose sands over these outer and lower surfaces of the islas. The distribution of the sand over clay profiles observed in the dry season correspond with the extent of the flooded isla margins in the wet season.

Isla sediments are also washed down into the pampas during rainstorms. Cattle trails serve as conduits for overland flow and much sand is carried down the trails and deposited in micro-fans at the break of slope between isla and pampa surfaces and further outward along the trails.

Altura/cañada levee erosion

In the present regime, the cañada does not contribute significant vertical accretion sediments to the landscape. The alturas along the cañada, however, are subjected to considerable trampling and compaction by heavy and hard-hoofed livestock. Soil mining and surface deposition by soil fauna also provides loose materials subject to transport by overland flow.

Thin residual sand accumulations are locally common in the altura forests; however, the soils along the cañada are only very locally “sandy” in any sense. I observed the formation of residual sand caps on gallery forest surfaces during a rainstorm in January 1994. Finer particles and organic matter are carried away by surface runoff, leaving the light-colored sands behind. Subsequent bioturbation soon buries these sands and creates the layering and micro-sand lenses observed in gallery forest soils. However, the thicker sand sheets observed on the islas del bajío are nowhere found in the gallery forest fragments. This does not suggest refutation of a gallery forest fragmentation model of isla formation, only that the islas del bajío have undergone much more residual coarsening (greater age and more intense livestock trampling) and/or that the original materials were coarser textured.

It is likely that downwasting of the cañada banks and colluvial deposition of levee and mound/platform materials into the cañada have contributed to infilling of the latter. There is no evidence for significant colluvial deposition of altura materials on the semialturas, although it must occur to a limited degree.

Where the vegetation cover is destroyed and the soil is mechanically disturbed, significant erosion can occur over short periods. At El Tajibo (13 km west of La Chacra), surfaces formerly under *Attalea* forest that were cleared for mechanized agriculture eroded at a rate of approximately 10 cm per year and were transformed into waterlogged bajío three years after clearing (E. Sanjinés, pers. comm.). I observed overland sheetflow over palmares and around the margins of islas del bajío during the high waters of March 1994. Laminar erosion rates have not been estimated for the plains of Moxos, but are likely highly significant locally.

In the absence of fluvial deposition, we assume that the forest island surfaces should be losing significant amounts of materials by erosion. This assumes that deposition rates are lower than erosion rates. Maintenance of an elevated surface requires that uplift and/or deposition (accretion) balance subsidence and/or erosion. Assuming that modern fluvial deposition and local tectonic uplift are not acting upon the forest islands, the other possible agents of earthmound maintenance and construction are 1) aeolian deposition and 2) biological activity.

It is unlikely that atmospheric contributions are significant sources of isla sediments in the present. Dust storms are infrequent, even during the dry surazo windstorms of the winter. Locally, significant dust is reworked in zones of intensive human activity that results in bare soil, such as in barnyards, corrals, house compounds, in the city of Trinidad, and most notably along unpaved roads and trails. Within the islands as well there is significant reworking of loose surface sediments by the winds. These sediments are loosened by livestock trampling.

Biological activity, however, is much more strongly implicated as a source of fresh earthmound materials. The activity referred to is the mining of subsurface sediments by burrowing fauna and its subsequent transport and deposition at the surface. The principal agents are ants, termites, worms, and burrowing mammals. I do not imply that these organism are necessarily the creators of all the earthmounds, only that they may maintain or even enlarge existing mounds. We will discuss these and other biological agents in the following chapter.

We can conclude that the forested surfaces of the Chacra are largely experiencing a period of net erosion. The ancient alluvial ridges and their anthromantles receive neither fluvial nor anthropic sediments. Each rainfall washes more material down into the cañada and the pampas and each hoofstep of the livestock loosens surface material. Only the incessant earthmoving by the soil fauna contributes to the maintenance of the elevated surfaces.

Hydrology and Overland Flows at La Chacra

I first observed the water of the cañada flowing downstream (from southeast to northwest) under the narrow bridges at La Chacra and El Sol in January 1994. In March 1994, during a period of high local rainfall, the water was indeed flowing rather violently through the bridge. Thus it clear that the cañada is still a seasonally active channel which carries dissolved and suspended loads, despite its appearance during the dry season. However, its capacity to transport water is greatly limited by the volume of aquatic vegetation that clogs the channel as well as by the restricted flows under the bridges of the ranch entry roads.

In the bajío, during March 1994, I observed the sheet of water flowing to the west over the center of a *Copernicia* palmar island, where there were numerous fish (the yeyú, *Hoplerythrinus unitaeniatus*, 15-20 cm in length). Likewise, water was also flowing to the northwest around Isla 2. The bajíos drain primarily by flowing, not evaporation (hence the absence of salt pans, with the exception of limited areas of semialturas).

In the gallery forest, there is significant overland flow during and after rainstorms. The trail leading from the house to the West Ceramic Forest becomes a small stream with heavy rain. Water runs off the alturas and collects in the depressions and channels (i.e., prehistoric canals). Water from the cañada locally floods the gallery forest where the "banks" are low or non-existent. The ponded water rapidly decants and is very clear except when disturbed. These waters remain throughout the rainy season, but disappear during the dry season.

Water moves quickly off the higher forested surfaces, but accumulates in the semialturas, bajío, and cañada. The bajío drains very slowly by massive sheetflow to the west and northwest where its waters ultimately enter the Mamoré via the Mocoví and Matiquipiri rivers.

Biogeomorphology

The geomorphological consequences of biological activity is what I consider to be the scope of biogeomorphology. We have already been discussing the biological (i.e., “ecological”) consequences of geomorphology. This is a promising subfield of physical geography that deserves more attention (see Viles 1988 for an interesting edited volume on this field).

Woody plants as nuclei of deposition

The presence of a single woody plant in a floodplain significantly alters the local patterns of flow and deposition. Ponce and Cunha (1993) and Oliveira-Filho (1992a) believe that small island mounds in the Brazilian Pantanal and cerrado, respectively, may form by fluvial deposition around isolated plants in floodplains. However, these authors provide no data or detailed conceptual models to support this idea.

Isolated trees also attract fauna which can alter depositional regimes. Birds which rest, nest, or sleep in the trees often contribute materials such shell, bone, feces, and soil particles dislodged from their feet. Ovenbirds (tiluchis or horneros, *Furnarius rufus*) build clay nests repeatedly at the same site. These nests fall or crumble and accumulate on the ground. Ants and termites build nests both around trunk bases and up on the trunks or in the branches. Old nests may fall or crumble and these materials accumulate around the trees. In arid environments, trees and shrubs are effective as traps for aeolian sediments, however, these sediments are of minimal consequence in the Llanos de Moxos.

Roots

Many tropical forest trees are well-known for their massive buttress roots, especially the giant *Ficus* and *Ceiba*. At La Chacra, the *Ficus* are most notable, in both the islas del bajío and the cañada forests. Soil materials accumulate around the bases of the wall-like structures which extend outwards from the massive trunks. Leaf-cutter and other ants often construct large earthen nests against the buttresses. Other large trees such as *Hura crepitans* have extensive root systems that snake across the ground surface, raised perhaps on 5-10 cm above the ground. These also shape the topography of the forest floor.

The dense root mats of *Attalea* palms are effective as preservers of the pre-Hispanic earthworks, preventing erosion of these features. In the West Ceramic Forest of La Chacra, several causeway-type features are marked by straight rows of these palms, each growing upon a pedestal protected by its roots. The intervening segments without palms are largely eroded away.

Livestock impacts

Livestock are highly significant influences on the nature of geomorphic processes across the globe. In the Llanos de Moxos, they are especially important due to the history of cattle ranching as the principal economic activity since the Jesuit period three centuries ago.

Soil compaction

The water stresses in the pampas have likely been exacerbated by soil compaction under livestock hoof action. Compaction of the soil leads to both increased flood stress *and* increased drought stress. Destruction of soil structures decreases porosity and infiltration, leading to slower drainage and increasingly anaerobic conditions. The wetting zone under flooded soils is often very shallow. I have excavated dry clays no more than a centimeter below the upper boundary of the clay pan. In the dry season the massive clay pans yield little available water.

Accelerated erosion

Given that the bajíos are not endorrheic and are indeed drained by massive, albeit slow, sheetflow, there is no doubt that much soil material is lost. The bajío basins may in fact be deepening if transport exceeds deposition over the long term. In livestock free pampas, the water is crystalline; however where cattle graze, the water is opaque and laden with suspended sediments. During the dry season when the dry soils is ground into dust by livestock hooves some materials are certainly lost during windstorms. Thus these great basins may be becoming scoured out under the hooves of cattle. It is also obvious that the impacts on the islands are even more dramatic, given the concentrated activity of animals on these small surfaces

Soil Fauna

The role of soil fauna in the genesis of relief and soils in the tropics has been well documented in the Africa and Australia. In the Neotropics, there have been few specific studies on the geomorphologic and pedogenic significance of soil fauna. Likewise, little is known about the invertebrate fauna of Moxos. However, various invertebrates are highly significant to the development of the soils and geomorphology of the region, as well as to the "general ecology" of forest and savanna systems.

Termites and ants in particular have received special attention by tropical geomorphologists, pedologists, and plant ecologists. The activity of these earth-moving insects is one of the primary determinants of microrelief and soil organization in both tropical forests and tropical savannas.

Termites

Termite mounds are highly important upon archaeological earthworks in the Llanos de Moxos. Raised fields and causeways in the pampas are generally colonized by termite mounds and are often capped by a horizon of reworked termite mound materials, accumulated over the past eight centuries (Erickson 1995). Termites utilize these better drained surfaces and add to them by translocating subsurface soil material to their epigeal mounds. Termite mound fields are evident (especially after burns) on air photos and are useful indicators of possible archaeological sites (See Denevan 1966: 87, his Plate 14-b). The continual upwards transport, erosion, and colluvial deposition of termite mound materials prevents complete obliteration of the prehistoric earthworks.

At La Chacra, termites are highly important geomorphological agents in altura and semialtura environments. However, their presence in the lower bajío is greatly limited by the average height of seasonal inundation. I had previously believed that termites were responsible for the pioneer establishment of elevated platforms in the bajío; however, the present data do not bear this out.

Termite mound distributions at La Chacra are limited by the depth of the annual inundations in the palmar/bajío transitions. During March 1994, maximum water height reached the bases of the conical portions of the mound. The flattened portions were often covered by water for short periods (ants and termites inhabit both the flat and conical portions of the mounds). Termite mounds are common in the edges of the “flood savannas," but are lacking where water depths exceed 50 cm for more than just a few days.

The zone of termite activity is essentially delimited by the occurrence of *Copernicia* palms along the semialtura/bajío front. It also appears that the *Copernicia* palms often precede the ant or termite mounds. I have observed and collected ants and termites from nests constructed around the bases and lower trunk of adult *Copernicia*. Over a period of years, translocated soil materials may then accumulate around the palm, forming a small mound upon which other woody plants later colonize.

In the islas del bajío, the otherwise highly abundant cone-building termites are absent. After extensive searching, I have encountered only the primarily arboreal nasutes and the giant forest mound termites in the islas del bajío. Similarly, Ponce and Cunha documented the “limited presence or even absence of termites” on the larger earthmounds (*capões*) in the Pantanal. These authors used this observation as support for fluvio-depositional origins. The explanation for the rarity of cone-mound building termites on the islas del bajío is likely related to the ability of alates to reach the islands, which in part may be related to dominant wind patterns. Northerly winds dominate during the alate phase in November and these may hinder flight into the bajíos from the semialturas to the south. It is feasible that termites may reach the islas by rafting on materials carried or blown across the floodwaters. Leaf-cutter ants, however, are common in the islas of the bajío. As argued by Hanagarth, these ants are not responsible for the origins of these islas.

The model set forth by Mathews (1977) and later supported by Oliveira-Filho (1992a, 1992b) and Ponce and Cunha (1993) in which there is a sequence of termite species with different tolerances to seasonal flooding which occupy and develop a particular space in a savanna, could not be supported by my observations at La Chacra. Rather, I found that *Solenopsis* (fire ants) and other ants create the pioneer mounds in the lower (i.e., deeper) portions of the savanna at the bajío edge. These ant mounds may later be colonized by cone-building termites when they reach the required elevation threshold.

Ants

Cox *et al.* (1992) report earthmounds up to 1.5 m in height and 20 m in diameter from seasonally waterlogged grasslands in the pampas of Buenos Aires Province, Argentina. They attribute the origins of these mounds to long-term activity of the black fire ant (*Solenopsis richteri*). The individual ant mounds, however, average only 20 cm in height and 60 cm in diameter. These earthmounds, however, are not colonized by woody plants. As reported above, *Solenopsis* mounds are abundant in both inundated and altura savannas and pastures at La Chacra.

Leaf cutter ants (*Atta* spp.) are important throughout the Bolivian lowlands. In the sandy pampas around the city of Santa Cruz de la Sierra, I verified that *Atta vollenweideri* (identified by Pedro J. Salinas) ant mounds do indeed create abundant forest islands in poorly drained interdune swales, as reported by Herzog (1923) and Troll (1936). Hanagarth (1993: 47) reports small *Atta*-mound islas in some savannas of the Beni.

At La Chacra, these ants create large mounds and are present on the islas of the bajío, as well as in the gallery forests and in the semialtura savannas. In the forest, the *Atta* mounds are devoid of herbaceous vegetation, but often have tree saplings and adult trees. On the islas of the bajío, the *Atta* mounds are often constructed around the base of large trees (*Ficus, Vitex*). Nevertheless, I did not encounter islands *created by* Atta at La Chacra.

I am in general agreement with the observations and conclusions of Hanagarth (1993:45-50) concerning the role of soil fauna in the geomorphology of Beni savannas. However, Hanagarth concludes that the ecological importance of *Solenopsis* fire ants is much less than that of the leaf cutter ants. This statement needs to be limited only to the forest islands and gallery forests. In the savanna proper, *Solenopsis* is much more important, especially in the seasonally inundated zones. We both agree that neither ants nor termites are responsible for the creation of the larger evergreen forest islands, rather that they are most important in expanding existing forest areas and creating small wooded mounds (i.e. *murundus* or *apêtê*) in savannas.

The ecological explanation for the differential ability ants and termites to colonize the deeper portions of the inundated savannas is like related to the differential ability to survive outside of the protected environment of the nest. Ants are far more durable creatures than the soft, squishy termites. Ants are capable of removing their entire colony, eggs, larvae, and pupae, and bivouacking out in the open air. Termites are far more sensitive to dry air due to their soft exoskeletons. They are also much slower creatures and appear almost completely helpless outside of their mounds or covered trailways. Ant colonies move out of the subaqueous nest and up into the vegetation growing out or around the flooded nest. These colonies may stay put or simply move off (often by floating *en masse*) to higher ground. Termite queens are also rather immobile beasts in comparison to ant queens.

Wetland vertebrates

Caimans and capybaras are relatively large and abundant native wetland vertebrates. Yacare caimans (*Caiman yacare*) are South American crocodilians somewhat smaller than alligators, but still 1.5-2 m in length. Like alligators, these reptiles create depressions in the wetlands (i.e. “alligator wallows”) which increase the availability of standing water in the dry season. It is widely believed that the local disappearance of the black caimans (*Melanosuchus niger*) due to over hunting for hides has lead to increased flooding in the Llanos de Moxos. These very large crocodylians are said to improve drainage by creating trails which act as drainage ways.

While not being fossorial creatures, the hog-sized capybaras (the world's largest rodents) allegedly perform geomorphic activities. Local folk report that these aquatic herbivores are key in the creation of pools in the bajíos. It is said that the capybaras find the lowest portions of the landscape and wallow there, excavating increasingly larger and deeper pools. Wise ranch owners choose these capybara pools as sites to create artificial ponds, taking advantage of the capybara's geosurveying capabilities.

Conclusions on the role of organisms

While rather interesting, the biogeomorphological processes discussed above do not explain the origins of the typical forest islands (islas) of the Llanos de Moxos. Termite savannas contain small islets, but these have not been shown to expand or coalesce into larger islands. Ant mound islas do occur in the Santa Cruz pampas and are reported from the Llanos de Moxos, but are absent from the region of La Chacra. Rather than creating islands and lomas, ants and termites are, however, highly important in preserving these features through their continual moving of subsoil materials to the surface.

Soils and Pedogenic Processes

General overview of the soils of La Chacra

Table 34 summarizes the general characteristics of the soils of the individual landscape units at La Chacra. Table 35 presents the results of the particle size analyses of 18 representative samples from a sample of the landscape units.

1. Bajío soils. These are the most extensive soils and are inundated for at least five months each year. The epipedon is black when wet, gray when dry, and very silty. When desiccated, the surface is cracked. The epipedon of the *Cyperus giganteus* marshes contains abundant histic material. At a depth of 10 to 30 cm, the clay content abruptly increases with textures ranging from silty clay loams to clays which are largely gleyed or mottled. Beneath the grayish gleyed clays, there is a yellowish to reddish clayey subsoil which extends downward several meters. These deeper horizons were observed in watering hole excavations at La Chacra and El Sol. The rooting zone in these soils is limited due to the impermeable fine-textured horizons. The bajío soils are heavily churned and compacted by livestock. In the epipedon, we occasionally observe anomalous lenses of white sands. These are likely washed down off the islas and incorporated by livestock hoof action, as I discuss later.

2. Semialtura soils. These are apparently much poorer in organic matter than the bajío soils, as they have much lighter colored epipedons. The epipedons of semialtura-type islands are often loamy sands or sandy loams which overlie clay loams or clays. These clays are characterized by bright orange and yellow mottles, not gleys. An exceptional characteristic of the semialtura clays is the presence of macroscopic magnesium sulfate crystals. However, these soils are said to be very poor in sodium salts (Kenneth Lee and Ricardo Bottega, pers. comm.). Recently excavated semialtura clays will become white overnight as capillary action draws these salts to the surface and they crystallize into white crusts. The semialtura soils are subjected to high levels of ant and termite activity and the microtopography is characterized by the flattened mounds of these insects.

3. Altura soils. These are the gallery forest soils. We can easily distinguish three general types of altura soils:

a. Soils of the relatively low, natural, surfaces.

b. Anthropic soils rich in ceramics, bones, shells, and organic matter.

c. Yellowish clays of the lomas, causeways, and other artificial elevations.

The soils of the low natural levees are Alfisols with loamy epipedons and well developed Bt horizons with angular blocky structure. Drainage is variable, but standing water is only of very short duration where present.. They are not notably sandy except in old point bar locations such as the House Isla (Map 3).

The anthropic soils are those of the artificial platforms, middens, and house mounds of the ceramic forests. These soils are much deeper than those of the natural surfaces. They are characterized by an abundance of ceramics, bone, shell, and other debris in the subsoil. Several centuries of ant, termite, earthworm and other biological activity have created a "biomantle" of reworked, organic-rich materials that is generally 30-35 cm deep and overlies the ceramic-rich horizon. These anthropic soils are analogous to the *terra preta* soils described from Brazil. These soils are very favorable for both forest development and swidden cultivation and are used for the latter purpose at many localities. The original *chacras* of La Chacra were cultivated upon these soils.

The large mounds (*lomas*), platfoms, and causeways along the Cañada de los Lagartos were constructed from compacted yellowish clays and are poor in ceramics and other cultural materials. These materials were taken from the natural levee deposits themselves. The borrow pits were likely designed to function as water-retaining canals. These canal probably allowed access to the interior of the forest village by canoes. In the present, these canals hold water well into the dry season. They have likely been filled in considerably by colluvial deposits from the adjacent platforms and and mounds.

4. Isla del bajío soils. These soils are rather unlike the altura/gallery forest soils in several aspects. First, they tend to have mantles of loamy sand on their lower slopes. Second, they are poor to devoid of ceramics. Third, they rarely have mounds of yellowish clays. Fourth, they have a deep organic and carbonate-rich horizon of silt loam, without ceramics. Finally, they generally contain abundant carbonate concretions which I never encountered in the gallery forest soils. These differences, however, do not imply that the islas of the bajío could not be derived from former altura/gallery forest surfaces. Rather, they reflect differences in age, biological activity, livestock use, and human impact. The often sandy surface sediments of the islas of the bajío are the result of a long history of differential translocation and lateral washing of soil particles. The lack of ceramics both at the surface and at depth clearly demonstrates that these islands were only briefly visited by pre-Hispanic peoples and were not the sites of long-term occupations. Likewise, the lack of the compacted yellow clay mounds typical of artificial earthworks demonstrates the natural origins of these relief features. The only light-colored clay mounds encountered in the bajío were two mounds constructed by the giant termites on Isla 4.

The deep dark epipedons, often with bone and shell materials, may at first suggest pre-historic human impact, however the complete absence of ceramics in these horizons makes this unlikely. Rather the organic materials and biological carbonate material (i.e., bone and shell) are an indication of intense biological activity. The source of these materials are the remains of the meals of predatory birds and mammals which have utilized these islas for possibly thousands of years. Early accounts of the Moxos islas note that the islas were the refuges of wildlife during the floods (Eder 1985). Jaguars and pumas were very common until just a few decades ago throughout the Chacra area. The bone fragments and the caiman scute found in Isla 2 were just as likely left behind by feline carnivores as by passing indigenous hunters. Birds of prey continue to nest and roost in the islas as well. The snail shells of the islas of the bajío are of a completely different type of snail than those associated with the anthropic soils of the Ceramic Forest and numerous archaeological sites throughout Moxos. The snails utilized by the indigenous Moxeños were the large apple snails (*Pomacea* or *Pomacea* spp.). The shells incorporated in the soils of the islas del bajío are of a much smaller snail with a flattened ramshorn-type shell. Nevertheless, the apple snails are highly abundant in the bajíos immediately adjacent to the islas. The snail shell accumulations are thus most likely the refuse of various species of snail-eating birds which roost and nest in the isla trees. The decomposition of these shells is also the likely source for the carbonate concretions common in these islands as well.

In addition to the contributions of the native fauna, the centuries of intensive livestock use of the islas has also led to the accumulation of organic matter through the incorporation of manure into the soil. In addition to livestock manure, there is also a considerable deposition of capybara manure on the islas. In the past there were also great numbers of the swamp deer, one of the few animals whose favored habitat is the dense *Cyperus giganteus* swamps of the bajío. There can be no doubt that these animals also utilized the islas as sites for rest and rumination, just as the cattle do today.

The depth of the organic materials and the burial of bone and shell frgaments can be explained by the intense activity of subterranean termites, ants, and earthworms. These invertebrates both incorporate the matter into the soil as well as bury larger fragments, as Darwin (18 observed long ago. The high levels of bioturbation may also account for the uniformity of soil texture observed throughout the upper 110 cm of the pit on Isla 1.

The nature and intensity of bird and mammal usage of the islands was thus very different than that of the gallery forests. One important reason was that the gallery forest was where the prehistoric people lived and worked. As they are today, the islands in the bajío were accessible only by traversing considerable expanses of dense wetlands. Some islas are known as *garceros* (heron or egret rookeries). Isolated tree islands in the center of wetlands are prime nesting sites for wetland birds. The number and diversity of mammalian nest predators (e.g. small cats, coatis, kinkajous, monkeys, etc.) is much reduced in remote islands relative to gallery forest corridors. Old rookery sites certainly have considerable soil inputs not present in non-rookery sites. At present, islas at La Chacra are used as nesting sites by jabiru storks, various ibises, macaws, raptors, and other birds.

The soil of Isla Loma Verde (Map 3, Plate 4) is unlike the soil of any of the others islas in the bajío. The profile demonstrates only two horizons. The shallow epipedon is a loam with a high concentration of bone, shell, and ceramic fragments. The ceramic sherds scattered on the island surface are usually not more than 2 cm in their longest axis. The fragments incorporated in the epipedon are largely the size of medium to coarse sands and granules. At a depth of 6 cm, the texture changes to a high compacted silty clay loam. Unlike the other islas, I interpret Isla Loma Verde to be an example of the artificial islands created by the pre-Hispanic peoples of the Llanos de Moxos. The mound itself is of the same texture as the surrounding bajío subsoil which would indicate that it was built with these materials. The upper horizon is coarsened as the result of differential removal of finer sediments by eluviation. The intense utilization of this island by cattle has led to the high degree of fragmentation of the archaeological artifacts and the compaction of the subsoil.

5. Termite and ant mound soils. These are distinct although spatially limited soil environments; however, over the long run, their impact may be nearly ubiquitous. Probably the all of the altura surfaces have been completely reworked by insects and worms over the past few centuries. In the semialturas, these small islands of elevated soil materials are important as sites for woody vegetation development, since they provide improved drainage conditions.

Table 34. Summary of soil characteristics for landscape units of La Chacra.

Landscape Unit	**Epipedon Characteristics**	**Subsoil Characteristics**	**Presence of Ceramics**	**Inundation**
Bajío	Shallow, black silt loams to loams	Gray clays to silty clay loams with both gleys and red to orange mottles.	None observed	Continual for 6-8 months
Semialtura				
Non-mound	Shallow, light colored silt loam	Yellowish clays with red to orange mottles	None observed	Periodically during wet season.
Termite mound islets	No profile development	Light colored silty clays	None observed	Top of platform just above average water level.
Altura				
Natural surfaces	Shallow, light colored silt loam	Well developed Bt horizons with blocky structure	Occasional on surface, rare at depth.	Only along cañada edge.
Artifcial platforms	Deep, dark, loams to silt loams	Yellowish clays	Abundant at surface and to 1.75 m depth	None.
Lomas	Weak profile development	Yellowish clays	Occasional. at surface and at depth .	None.
Attalea-*islands*	Deep, dark silt loams with shells, bones, $CaCO_3$ concretions. Loamy sands mantles on slopes.	Dark gray silt loams indurated with $CaCO_3$	Rare at surface, none at depth.	Occasional on lower islands and outer slopes
Copernicia-*islands*	Shallow, light-colored sandy loam	Compacted yellowish clays and clay loams with red, black, and orange mottles. Common $MgSO_4$ crystals.	None observed.	Periodically during wet season.
Artificial isla in bajío (Isla Loma Verde)	Dark loam with abundant fragements of bone, shell, and ceramics.	Black compacted silty clay loam identical in texture to surrounding bajío.	Larger fragments on surface, granule to sand-sized fragments abundant in epipedon	None

Table 35. Particle size data for samples from representative sites. See Map 6 for site locations.

Location / Depth (cm)	%Sand	%Silt	%Clay	Texture
Bajío pampa 0-18	51.3	32.4	16.3	Loam
Bajío pampa 18-23	44.0	44.3	11.7	Loam
Bajío pampa 23-32	16.9	47.7	35.4	Clay loam
Bajío pampa 32-40+	16.9	50.9	32.2	Silty clay loam
Semialtura palmar 0-18	28.2	55.2	16.7	Silt loam
Semialtura palmar 18-30	24.5	50.6	24.9	Silt loam
Semialtura palmar 30+	19.2	7.4	73.5	Clay
Isla 1, 0-5	56.4	42.4	1.2	Sandy loam
Isla 1, 5-21	46.5	44.7	8.8	Loam
Isla 1, 21+	25.1	35.7	39.1	Clay loam
Isla 2, 0-10	29.9	60.2	9.9	Silt loam
Isla 2, 30-40	29.7	60.9	9.4	Silt loam
Isla 2, 60-70	31.4	59.9	8.7	Silt loam
Isla 2, 90-100	35.5	56.9	7.6	Silt loam
Isla 2, 110-125	27.9	60.0	12.1	Silt loam
Isla 2 lower slope 0-5	79.0	17.9	3.1	Loamy sand
Isla Loma Verde 0-6	41.8	48.6	9.6	Loam
Isla Loma Verde 6+	16.1	48.5	35.4	Silty clay loam

Origins of surficial sands on the Islas

The overall surface of the Lagartos basin is of Quaternary fluvio-lacustrine origin, the sediments are largely silts and clays, with sands only locally important. In fluvial landscapes, sands are predicted to be most important in point bar and natural levee formations. Presently, the Cañada de los Lagartos is incapable of transporting sands. Modern aeolian deposition of sands has not been observed in the region, as there are no immediate sources of significant volume. Thus, all sands can be considered as deposits from past morphodynamic phases. At the Universidad Técnica del Beni in Trinidad, excavations have revealed a 4-m thick layer of sand with cross-bedding characteristic of dunes, as well as numerous stone ax-heads (Kenneth Lee, pers. comm.). At El Tajibo, a 4-m pit one hectare in area has been excavated for sand for the highway asphalting project between Trinidad and Casarabe. These sands are found underneath an isolated string of *Attalea*-dominated forest amidst a bajío (Map 3).

The observation of thin sand lenses approximately the diameter of a bovine hoof in pampas soils suggests that these may actually form as the result of sorting due to differential settling velocities of soil particles after animal creates a hoof-hole in the clayey subsoil and pulls its foot out. There is a significant churning which would entrain sand-sized particles into the floodwater and then stratification would occur in the hoof-hole. The hoof-hole then fills in over time. During the dry season, such hoof holes are important micro-relief features of the bajíos.

The surficial sand accumulations on the outer slopes of the islas del bajío are likely deposited subaqueously during the annual inundations; however, they are not flood deposits. These sands are washed downwards from the higher, unflooded surfaces of the islas. As the sand are carried with the overland flow, they fall out of suspension when the running water hits the standing (more or less) water over the flooded isla margins. This explains the distribution and concentration of loose sands over these outer and lower surfaces of the islas, as well as in the epipedons of the adjacent pampas.

Soil chemistry

Soil chemistry as a limiting factor

It has long been suggested that soil nutrient status has important consequence on the structure and composition of tropical vegetation. One hypothesis is that tropical forests are limited by soil nutrient availability and Aluminum toxicity. Recent research has demonstrated that the tropical rainforest tree productivity is not limited by soil nutrient availabitly and/or toxicity and they cannot explain the distribution of forests and savannas (Ross 1994, Thompson *et al.* 1992). Ross (1994: 84) concluded that

> "despite debates on edaphic controls on forest and savanna vegetation, these data also indicate the lack of any significant differences in soil chemistry in forest and savanna habitats throughout the [Maracá Island] region, and thus suggest that if there are edaphic controls, they are unlikely to be chemical ones."

Livestock impacts

Highly concentrated livestock use on the islands can have severely deleterious effects on soil properties. The primary impacts are the concentration of urine and fecal materials which can create toxic conditions for plant roots. In addition, such soils are also highly compacted due to the very weight of the animals trampling and resting on the ground. These negative impacts are most noticeable on the islands closest to the ranch corrals (i.e., Isla Loma Verde) or principal trails (i.e., "Thrashed Roadside Isla" near the gate to the Cáceres ranch). None of the other islands at La Chacra are as severely affected as these two.

Undercanopy soil enrichment

As first demonstrated by Kellman (1979), savanna trees enhance the soil properties beneath them. Vieira, Uhl, and Nepstad (1994) demonstrated that pioneer *Cordia* shrubs increased soil fertility and other factors in abandoned Amazonian pastures. While a facilitation model for island formation is certainly plausible in many cases, it does not explain the events which allowed for the initial establishment (i.e., the *origin*) of the trees themselves.

Conclusions

Soils and vegetation both reflect the interactions of climate, parent materials, organisms, time, topography, and drainage conditions. In the case of the low-relief and poorly-drained landscapes of the Llanos de Moxos and similar savanna and wetland landscapes such as the Pantanal, the Llanos of the Orinoco, the Florida Everglades, and the Okavango Delta, soils and vegetation patterns most strongly influenced by topography and drainage. In each of these landscapes, forest islands on elevated surfaces are prominent features.

The processes which determine the topographic features upon which trees grow are in fact the “origins” of seasonally-inundated forest island landscape. However these factors primarily mediate the distribution of the islands, not their botanical composition.

Chapter 11. Processes of Woody Plant Development and Forest Island Ecology

Although there is little literature on forest islands in tropical savannas and wetlands *per se*, there is abundant work on anthropogenic forest fragments in temperate zones (for example Harris 1984) and an experimental Amazonian project near Manaus (see Bierregaard *et al.* 1992). Island biogeography itself is an important subfield of both community and population ecology as well as biogeography. The salient characteristics of ecological islands are due to two primary factors: isolation and limited area. Forest islands as small as 10 or 20 m in diameter and isolated hundreds or thousands of meters from the nearest island are highly sensitive to changes in the diversity, abundance, or behavior of the agents of pollination and dispersal (cf. Aizen and Feinsinger 1994).

Dispersal Modes of the Woody Plants of La Chacra

To understand the distributions of plant species in general, we can not advance far without addressing dispersal, both over short and long distances and short and long time periods There are considerable differences in the abundance of plants of different modes of dispersal among the various woody vegetation types at La Chacra.

Dispersal by water (Hydrochory)

Flotation fibers on seeds: *Ceiba, Ipomoea*
Floating samaras: *Combretum*

We might expect that with so much water there would be a greater predominance of plants with water dispersed propagules. The problem is that the water at La Chacra does not move much. *Ceiba* seeds falling on the waters of the cañada or in the pampas really won't get far before being caught in a tangle of aquatic plants. (In fact, the seed fall of *Ceiba* occurs in the dry season, not the wet season.) The two principal woody plant with hydrochorous seeds, however, are very important invaders of the semialtura savannas: *Ipomoea fistulosa* and *Combretum fruticosum.* The seeds of these plants float across the surface of the inundated pampas.

Dispersal by wind (Anemochory)

Winged seeds: *Calycophyllum, Jacaranda, Tabebuia*.
Persistent calyces: *Astronium*
Persistent corolla: *Cordia alliodora*, *Cordia glabrata*
Persistent perianth: *Triplaris*
Cottony fibers: *Ceiba, Pseudobombax*
Pappus: *Vernonia*
Samaras: *Combretum*

Many of the more important trees at La Chacra are wind-dispersed. These trees are highly efficient colonizers of the semialturas, for example *Cordia glabrata*, *Tabebuia ochracea,* and *Astronium fraxinifolium.* Some of the principal gallery forest trees are also wind-dispersed, such as *Calycophyllum spruceanum, Triplaris americana,* and *Ceiba pentandra.* However, wind-dispersed species are largely absent from the islas, except for *Ceiba* whose seeds also float on water. According to Janzen (1988), wind-dispersed species are generally incapable of long-distance dispersal (not more than 200 m, usual range 0-100 m) and the establishment of widely dispersed forest patches, unlike vertebrate-dispersed species which can be carried wide and far by wandering beasties.

Janzen believes that once established, the wind-dispersed forests will usually remain as such, as they provide few attractants for vertebrate dispersal agents due to the lack of attractive fruits. Secondly, he believes that the colonizing trees discourage future succession by rapidly creating shady canopies. Also, the parent trees are limited to those of the forest edge, as only a few tens of meters of forest are necessary to "thoroughly filter out wind-borne tree seeds." Thus, wind-dispersed forests are inherently less diverse than mixed or purely vertebrate-dispersed forests.

Post-ingestion dispersal by animals (Zooendochory):

Berries (single-seeds): *Nectandra, Nectandra*
Berries (multiple seeds): *Genipa, Rheedia* (arils), *Salacia, Solanum*
Woody capsules: *Guazuma*
Drupaceous berries (larger): *Spondias, Vitex*
Drupaceous berries (smaller): *Verbena*
Drupes: *Ampelocera, Celtis, Sorocea*
Fleshy calyces: *Coccoloba* (achenes)
Fleshy capsules (?): *Guarea, Trichilia*
Fleshy legumes: *Geoffroea, Hymenaea, Inga* (arils), *Samanea*
Fleshy syncarpia: *Rollinia, Cecropia, Maclura*
Woody follicles with edible seeds: *Sterculia*
Syconia: *Ficus*
Explosive schizocarp with heavy seeds: *Hura crepitans*

By far, the most important dispersal mode for the trees of the islas del bajío is that of dispersal by vertebrate agents. We can break these into several subgroups based on seed size, dispersal agent species, etc. The majority of these trees have fruits which are edible by humans as well as other vertebrates. The fruits are ingested and the seed are either spit out our defecated later on. The sizes of the seeds range from minuscule (e.g. *Ficus, Cecropia*) to very large (e.g. *Attalea*). The tiny-seeded fruits are largely dispersed by birds and bats, while the largest ones are dispersed by livestock or carried about by medium-sized rodents (pacas and agoutis). *Psidium, Guazuma,* and *Acrocomia* seeds are ingested and dispersed by livestock; thus these plants have thus increased under intensive grazing in Central America (Budowski n.d., cited by Parsons 1975).

Not all of the common animal-dispersed species, however, are successful in reaching or establishing themselves on the islands of the bajío. For example, *Spondias mombin,* which is well known as a livestock-dispersed tree in Costa Rica (Janzen and Martin 1982), is mysteriously absent from these islands even though it is very important on the semialturas and in the cañada forests. I have not observed *Spondias* fruits or seeds lying about on any islas in bajío and can see no apparent factors which would limit the establishment of this otherwise highly successful tree on these islands. Therefore, I must conclude that the seeds never reach these islands.

The corrals at La Chacra are full of green-stained *Acrocomia* and *Attalea* seeds. The cattle sometimes suffer for their role as a *Attalea* dispersal agents when the abundant and coarse fibers of the endocarp accumulate in a large ball in one of the cow's stomachs, causing gastric disorders (Neco Melgar, pers. comm.). However, at La Chacra, *Acrocomia* is not reproducing very well. It appears that horses continually defoliate the young palms and inhibits their survival. Elsewhere, however, these palms are very abundant.

Vertebrate-dispersed forest islands often form under/around "nuclear trees" (Janzen 1988). Representative nuclear trees in the Costa Rican savannas are *Enterolobium, Samanea, Guazuma,* *Spondias*, and *Ficus*, all of which are important at La Chacra. Under the canopy of these nuclear trees, Janzen found reproducing treelets and shrubs, such as *Piper*, *Psychotria*, and *Casearia*, to be common; however, these are usually lacking in wind-dispersed patches. Nuclear tree island composition is influenced by the age and species of the nuclear tree. Janzen believes that the rate of island expansion "noticeably declines as it becomes more that about 0.5-1 ha in area."

"Hitchhikers"

Mimosa, Desmodium

These are seed or fruits which cling to the fur of passing animals or the clothes of passing people. Some of the more important weedy legumes are dispersed in this manner.

Balance between Wind-Dispersed and Animal Dispersed Species

In abandoned Costa Rican pastures free of cattle and fire, Janzen (1988) found vertebrate-dispersed initial colonizers, such as *Cecropia*, *Piper*, *Trema*, and *Spondias* to be almost entirely absent. More than 90% of the colonizing trees were established from wind-dispersed seeds, such as *Cordia alliodora* and *Tabebuia ochracea*. However, the overall tree and treelet flora in Janzen's area is 25% wind dispersed and 64% vertebrate dispersed.

At La Chacra, we can also distinguish distinct woody plant assemblages dominated by either wind- or vertebrate-dispersed species. The islas del bajío are contain largely vertebrate dispersed species such as *Vitex cymosa, Sterculia apetala, Attalea phalerata, Ficus* spp., and *Guarea* spp. In contrast, the semialtura termite/murundu savanna with *Tabebuia heptaphylla, Astronium fraxinifolium*, and *Cordia glabrata* are dominated by wind-dispersed trees. However, the semialtura woodlands are rather mixed, with wind-dispersed *Tabebuia ochracea, A. fraxinifolium. C. glabrata*, and *C. alliodora*, as well as vertebrate-dispersed species such as *Spondias mombin, Samanea tubulosa, Guazuma ulmifolia, Pithecellobium scalare*, and *Acrocomia aculeata*. The ecological significance of livestock is highly evident here, as the large-seeded trees have an abundance of bovine and equine dispersal agents. Using Janzen's (1988) perspective, we can conclude that the woodlands at La Chacra are rather well represented dry forest formations, without the negative characteristics associated with purely wind-dispersed tree communities.

Regeneration Niches for Germination and Establishment

For plant to successfully increase its range, its propagules must first be dispersed. The next requirement is that the propagule happens to be placed in environmental conditions that are suitable for its germination and establishment. These required conditions vary with individual taxa; thus there is no one ideal condition for all species. Soil and ground surface microenvironments are sensitive to changes in fire, grazing, and annual climatic regimes. Thus, factors which alter these condition will also ultimately alter the composition and structure of the vegetation.

Some examples of the different strategies of Chacra plants include:

1. Gap colonizers: *Triplaris, Cordia nodosa, Acacia polyphylla, Spondias mombin, Cecropia, Jacaranda, Vismia.* These taxa are shade intolerant pioneer trees that regenerate exclusively by seeds (Hartshorn 1989). All of these are found in semialtura woodlands and regenerating forest clearings. Many of these trees have either long-lived seeds in the seed-bank or they produce large quantities of short-lived seeds to maintain high viable seed bank populations.

2. Post-fire colonizers: *Mimosa*. These plants germinate and establish in bare soil after fires.

3. "Thatch babies": *Copernicia* palms are able to avoid herbivory by growing under the cover of spiny thickets. This is likely a facultative strategy which is useful under heavily grazed conditions.

4. Insect mound colonizers: *Genipa, Cordia, Celtis, Tabebuia*. These trees become established upon termite mounds in the seasonally inundated semialturas. The termite mounds are relatively fire free and present open microenvironments.

5. Shade tolerant: *Ampelocera, Attalea, Bactris, Randia, Eugenia, Sterculia.* These are species which germinate and establish themselves under forest cover. These include understory shrubs. Some of these species remain in an immature stage until a gap opens and more light is available for accelerated growth (a sit and wait strategy). This is case for *Attalea* which remains acaulescent and *Ampelocera* which has a shrubby habit until exposed in a gap. *Sterculia* saplings have a very soft wood and little branching with the leaves and apical meristem all well elevated above the ground. These are common in both the forest and the woodlands.

Site modification by plants

Nuclear trees and autogenic forest nuclei

Belsky and Amundson (1992) observe that the trees themselves are often responsible for the environmental discontinuities at forest/savanna boundaries. These boundaries do not necessarily indicate underlying substrate heterogeneity, but rather often occur in rather homogeneous environments. Belsky and Anderson point out that where rainfall is sufficient to support tree growth, the vegetation can fluctuate between grassland, savanna, and woodland. The actual state of the vegetation depends upon the frequency and intensity of disturbances. At La Chacra, this statement holds true only for the semialtura surfaces.

Guevara *et al*. (1992) found undercanopy vegetation beneath isolated relict *Ficus* and *Nectandra* trees to have greater diversity and stem density of woody plants than in adjacent canopy edge or pasture. A combination of a more favorable microenvironment and higher propagule availability (zooendochory) under the canopies is proposed as the mechanism responsible. The effect was not species specific ("nurse tree" species), however, the authors suggest that under deciduous trees such as *Ceiba pentandra,* a different type of community may be found.

Menaut *et al*. (1990) present a simulation model of woody vegetation dynamics where tree/shrub invasion is inevitable except under the most extreme conditions. Clumping of the woody plants (i.e. island or grove formation) is also "an unavoidable process." They propose that competition among woody species may lead to periodic clump reduction, where taller species eventually overtop and shade the clumps leading to reduce growth rates and increase the mortality rates of the understory trees/shrubs. The opening of the understory then leads to invasion of herbaceous plants, leading to the return of fire and further reduction of woody plants in the former clump. The final stage is the occurrence of lone taller trees, which originated in a clump of woody vegetation. I find this cyclical model pleasing. It is obvious that tree/shrub invasions are not irreversible processes, otherwise many savannas would not exist. Likewise, trees just don’t disappear; otherwise there would be no forests either!

The principal elements key to forest expansion in the Chacra region appear to be *Sterculia* and *Attalea*. These trees rapidly create shady undercanopy environments which favor the establishment of other forest species and they are the principal nuclear trees of the semialtura forest nuclei.

Factors Which Influence Plant-Plant Interactions

Competition between woody and herbaceous plants has been suggested as an important process in some savanna systems. Ponce and Cunha (1993) discuss competition between entire plant communities, in their case, woody cerrado vs. herbaceous campo. They believe that the herbaceous campo can competitively exclude the cerrado trees from the surfaces with seasonally-fluctuating water tables. Perennial grasses can inhibit the establishment by preemptive utilization of soil moisture during the dry season (Medina and Silva 1990). Fire, grazing, and climatic variability are all important in altering the outcomes of plant-plant interactions.

Fire effects

Fire is generally considered to be one of the primary determinants of the composition and structure of grasslands and savannas. There is no doubt that fire has been a significant factor in the Llanos de Moxos since at least the arrival of the first humans and especially during the present cattle ranching regime. Nearly all semialturas and bajíos are burned to improve forage conditions for the livestock. We might reasonably assume that the savannas and forests have been greatly influenced by these fires.

In early September, in the late dry season, when pampa fires raged into the night in the parched bajíos, I attempted to create some forest fires in the gallery forest fragments along the cañada. Much to my dismay, I could not get anything to carry much of a flame. Even the driest appearing materials proved rather fire resistant!

I also tried burning the semialturas from time to time during the dry season; again my efforts were foiled, this time by the lack of contiguous fuel to carry the fire. Grazing by livestock was intense enough to create a mosaic of rather open, non-flammable areas with local clumps of fuels, those being clumps of shrubs or weeds or dried *Copernicia* leaves.

Fires in the bajío are difficult to set due to the low biomass left toward the peak of the dry season. Ranchers have begun to burn the *Cyperus* stands which dry out during the drier years. The islands in the bajío not exposed directly to fires, as the dense *Cyperus* stands are always (at least in all cases I saw) separated from the islas by natural fire breaks of very low growing, moist aquatic vegetation. Fires, of course, may jump these barriers under windy conditions. Even if fires did lap up against the isla edges, they would encounter few fine fuels to carry themselves.

I observed active burns on the semialtura/gallery forest edge and watched the fires quickly die out at the forest edge. Some *Attalea* were scorched as fires climbed up dry fronds, but this damage is transient. Fires do occasionally penetrate the forests under exceptional conditions. After a period of intense grazing which opened up the forest understory, an exceptionally wet year allowed for an invasion of the forest floor by grasses and other herbaceous plants. This created unusually high fine fuel loads in the gallery forest and the forest exploded in an intense burn during the dry season. In any case, even this rare inferno did not destroy the forest in any sense. It simply opened it up and allowed for a rapid response from the *Attalea* and *Syagrus* palms and numerous hardwood trees, lianas, and terrestrial bromeliads. This burned over forest is difficult to pass through due to the prodigious regrowth.

Regardless of the low flammability of the forests and the bajío wetlands, fire is still an important factor in the balance between woody and herbaceous vegetation on the semialturas. In the long term perspective, we know that fires have been a significant feature of the Moxos dry season since at least the time of human settlement at least 3,000 years ago. The frequency of lightning fires in the Llanos de Moxos has not been estimated scientifically, but pre-human fires were certainly likely, especially during postulated Holocene aridity phases (cf. Servant *et al.* 1981). However, fire was likely to have been a significant vegetation determinant only on the semialtura-type surfaces. The gallery forests were certainly not any more likely to burn in pre-human times than they are today, except after the onset of arid phases. The bajío wetlands were perhaps more flammable before the introduction of livestock if we assume higher standing crops during the dry season. However, burning was not what inhibits the establishment of trees in the wetlands, just as it is not today. The balance between woody and herbaceous vegetation has not likely changed much on the bajío (broad flood plains, interfluvial flood basins, and extensive rainwater flats) and altura (meander belts, natural levees, islands of high ground, and other non-flooded relief features) surfaces. The dynamic fluctuations due to pre-historic and pre-human fires likely occurred primarily on the intermediate ground of the semialturas, as they do today.

Some effects of herbivory

Differential herbivory: Under typical conditions where animals can exhibit selectivity and the sward is not monotypic, different species will experience different intensities of herbivory. Some species will be experience increases in abundance while others may disappear completely. Quite frequently, the increasers are less palatable species which are considered “weeds,” while those that disappear are the most favored by the animals.

Soil moisture effects: Grazed plants have reduce leaf area and reduced transpiration rates. Intense grazing of semialtura grasses should leave more available water for shrubs and trees. Numerous studies in temperate grasslands have demonstrated that grazing can increase plant available soil moisture by reducing transpiration.

Light availability: Grazing opens the herbaceous canopy and increases the light that reaches the ground surface as well as the basal meristems of many graminoids.

Aboveground standing crop: Grazing can significantly decrease the amount of aboveground plant biomass which remains at the “end” of the growing season. This has important implications on the nature of fires. Many of the vegetation changes commonly attributed directly to grazing are in fact due to the reduced intensity of fires associated with heavier levels of grazing, not to the direct effects of herbivory.

Climatic effects

The primary climatic variables of concern are the timing and quantity of precipitation.The Llanos de Moxos vegetation does not appear to be significantly affected by temperature variations, in contrast to more poleward regions of the Neotropics where the incidence of occasional sub-freezing temperatures limits the distribution of frost-sensitive plants. Precipitation patterns have effects on biomass production, the moisture content of standing vegetation, and the length of inundated conditions. The quantity of biomass and its moisture content are important determinants of fire behavior. In years where it does not rain much, biomass production is low and standing crop near the end of the dry season is very low, thus fires are reduced in intensity. In years with great rains, biomass production is high; the fire intensity then depends on the precipitation patterns during the dry season. Forest fires are most significant when there is a wet

wet season that allows excessive growth of understory herbaceous plants which create a high level of fine fuels during a dry dry season which allows the forest to dry out. Again, the impact of fire is most significant on the semialtura surfaces. Germination and establishment of individual species are also influenced by precipitation patterns. Species that are sensitive to prolonged inundation could become established during a period of a few sequential dry years. Likewise, fire sensitive species can become established during a period of low fire intensity or frequency and if they reach a threshold size, they may be able to persist under subsequent higher intensity or frequency burns.

The interactions of fire, grazing, inundation, and drought have infinite variability that results in the diversity of vegetation formations present in the Llanos de Moxos.

Processes of Forest Degradation

Both natural and anthropogenic processes can lead to a reduction in tree cover in the landscape. Changes in climatic and ground water regimes, natural catastrophic events, disease and pest outbreaks, or even natural "succession" can lead to reductions in tree cover and the degradation of forests in the absence of human agency. Many ecologists believe that much of the Amazon basin forest cover was converted to savanna solely by cooler and drier conditions associated with Pleistocene glacial maxima, long before the arrival of humans in the Holocene.

In fact, the human deforestation of the Amazon is still a magnitude of order less in extent than the alleged Pleistocene savannizations. (However, the patterns of deforestation are rather different.)

Deforested surfaces in the region of La Chacra may be covered by open herbaceous formations for indeterminate lengths of time. At El Tajibo, forested palaeolevee surfaces cleared by tractor have become low bajío grassland after losing soil materials through a decade of accelerated sheet erosion and loss of the forest epipedon. It is probable that these sites will not return to forest due to the loss of the relief that provided a better-drained rooting zone for woody plants. At La Chacra, areas of former gallery forest and woodland have been cleared for paddocks and corrals. These areas remain open under continual moderate grazing pressure and frequent burns, although some shrubs (*Cordia* spp., *Senna* spp.) and a few scattered trees (*Samanea*, *Cordia glabrata*, *Tabernaemontana*, *Genipa*) appear here and there. If the cattle and fire were removed from these areas, it is likely that within a decade they would be dominated by young trees and shrubs, as are the adjacent semialturas.

Degraded forests (in contrast to those that have been entirely cleared/deforested) are represented at La Chacra by some of the islas del bajío and portions of the gallery forests where cattle trampling and manuring impacts are concentrated. These "cattled" surfaces do not become "scrub savannas" or "arboledas," but rather they remain as relict forests with little understory vegetation and little or no regeneration. These forest sites may not persist once the exising trees die off. Although all of the gallery forests and forest islands in La Chacra, and probably almost all of the Llanos de Moxos for than matter, have been altered by livestock herbivory, trampling, and manuring, livestock have in no way led toward a widespread degradation of these forests. The presence of both abrupt and transitional forest/non-forest boundaries along the same forest/savanna front seems to indicate something other than forest degradation as the primary process which determines the existence of woodlands and "scrub savannas."

The gallery forests which were severely burned 4-5 years ago at La Chacra have likewise not been converted or deflected to a savanna or woodland. They are simply regenerating as forests, despite the continued presence of livestock and fire.

Processes of Woody Vegetation Development

Clementsian succession models predict that wherever soil conditions are not inimical to tree growth, forests will be the ultimate expression of natural vegetation development. Thus, many ecologists and geographers find it necessary to explain observed absences of trees in humid tropical landscapes as exceptions to some universal law of forest dominance.

We know that the density, cover, and other quantifiable parameters of plant populations vary over time and may exhibit directional change. When the dominance of woody plants increases over some time period, we may conclude that there has been "development" of woody vegetation. If the woody plants are species typical of forests, then we have an instance of "forest development," otherwise we may have a "shrub invasion" or perhaps even "savannization."

In some cases, the woody plants occupy the landscape in a regular or overdispersed pattern. In other cases, the woody plants have clumped distributions. The first instance is where we have the development of a true savanna, woodland, or forest, depending on the density and cover of the trees. The latter case is where we have the formation of "forest nuclei" or "forest islands." The development of clumped distributions occurs primarily where either the availability of favorable sites is irregular (e.g. trees restricted to microtopographic features such as termite mounds or moist depressions) or where the establishment of one woody plant creates facilitates the establishment of other woody plants under its canopy. These are rather common cases in savannas where they may lead to the development of parklands. A parkland is defined as a landscape where herbaceous assemblages and woody assemblages occurs in a mosaic where each occupies a unique environment, more or less independent of the other. Thus a forest island landscape is a parkland. The forest and herbaceous units are ecologically unique. In contrast, a true savanna has woody plants growing within an herbaceous matrix, where the woody and herbaceous elements have ecological interactions. It is thus that we can have forest islands in a savanna. The forest island is obviously not a savanna; it is merely surrounded by one.

Woody Invaders and Arborization of Savannas

Shrub and tree invasions of heavily grazed savannas are recognized from subtropical and tropical savanna regions worldwide. For example, Johannessen (1963) documented extensive transformation of Honduran savannas over centuries of cattle grazing. Spiny *Mimosa* and *Acacia* were prevalent at most sites, as they are on many semialturas in Moxos. Many of the other genera Johannessen identified as savanna colonizers are common at La Chacra: *Acrocomia, Astronium, Casearia, Hymenea, Maclura, Cordia, Enterolobium, Genipa, Guazuma, Psidium, Tabebuia, Xylosma,* and *Xanthoxylum.*

Archer (1990), demonstrated the development of closed-canopy woodlands in formerly open subtropical savanna parklands of the Río Grande valley of southern Texas, largely led by the establishment of *Prosopis* (mesquite) and the subsequent development and expansion of woody clusters (islands). *Prosopis* is a prime invader species due to several attributes: production of abundant long-lived seeds, germination and establishment under broad range of conditions, seedlings can resprout vegetatively after two-weeks of age, and up to 80% survivorship of 2-3 year old plants after severe burns. In the semialturas around La Chacra, related leguminous trees such as *Acacia albicorticata, Pithecellobium scalare,* and *Samanea tubulosa* may share such characteristics and occupy similar niches (*Prosopis* itself is absent from Moxos, yet is very important in the Chaco, Inter-Andean Valleys, and southern South America).

Development of woody thickets on the semialturas

Mimosa debilis is a thin, very spiny suffrutescent legume which often dominates some areas of semialtura. This plant is not visible to the untrained eye during the dry season, but is impossible to bypass in the late summer. *Mimosa pellita* is a woodier species, more tolerant of inundation, and more structurally persistent, even after burns. In combination or alone, both of these species can create impenetrable thickets on the semialturas. Neither of these species is present under the canopies of woodlands or forests, thus are both are likely obligate heliophiles favored by any clearing process, natural or anthropogenic. Together, these mimosas and other suffrutescent to woody plants can form dense thickets on the semialturas.

Once established, these spiny thickets are notoriously difficult to remove by fire and grazing management. Mimosas produce large amounts of seed each year and rapidly resprout after fires. Only the development of a canopy which overshadows them appears to lead to their reduction. Eventually after several years, these thickets may simply choke themselves out and then burn in a roaring blaze when the inevitable fire finally comes. However, this simply restarts the cycle unless other changes happen. If there are woody survivors after the fire, these may then grow rapidly under the now open conditions. These plants in effect may pre-empt new thicket mimosas, vernonias, and others. These woody plants may then become the woodland or forest nuclei in the semialturas.

Grazing pressure is certainly reduced in the *Mimosa* thickets, but competition for light under the shrub canopy is likely severe. Heliophile seedlings can survive only in gaps in the thicket cover. Such thicket-gap plants, however, are protected from herbivory by livestock. Establishment occurs by germination and growth in a gap and attainment of a size large enough to survive a fire by the time the thicket is burned again. On the other hand, shade-tolerant seedlings would do very well from the outset in these spiny thickets. Termite mounds within the thickets may actually represent gap sites, as I have never observed any *Mimosa* upon these mounds. Termite mounds are also effective as firebreaks (cf. Menaut and Cesar 1982), as the fuel load is rather reduced over their largely bare surfaces.

Survivorship of acualescent and immature *Copernicia* palms at La Chacra appears to be enhanced by the protection from browsers afforded by spiny *Mimosa* thickets; otherwise these palms are often heavily defoliated by livestock when they are exposed.

Another type of thicket is that formed by *Combretum fruticosum* and *Psidium guineense*. These multiple-stemmed shrubs form clumps in semialturas, the former species being a climbing liana at times. These species are also considered range problems by local ranchers; however, they also create excellent wildlife habitat in the pampa edges by providing more cover, perches, and food. The fruits (guavas) of *Psidium* are fed upon by a diversity of birds and mammals which are likely additional dispersal agents. Young tortoises of the genus *Geochelone* are reported to be unusually common in the *Combretum* clump habitat (E. Sanjinés, pers. comm.). Haase and Haase (1995) report that *Combretum laxum* is a major invader of seasonally-flooded grassland in the Brazilian Pantanal.

The ultimate fate and role of dense savanna thickets are not yet clear. Evidence from Ghana suggests that thicket tangles “evidently allow no regeneration of forest species directly below them” and that “it would be misleading to state that the vegetation is becoming forest via a thicket stage” (Swaine *et al*. 1992). However, local informants at La Chacra do claim that “monte” (forest) will eventually develop out of “espinales” (spiny thickets). Haase (1989) reported that, in the savannas west of the Rio Beni,

> "this *Mimosa* scrub is considered a successional stage that can develop into low gallery forest. In some areas, *Mimosa pellita* and tree species of the gallery forest invade the pasture and, eventually, are controlled by slashing and burning before the scrub becomes impenetrable for cattle."

The study from Ghana also suggests that although there are some long-lived thicket specialists, "it is clear that some thicket patches are of recent, secondary origin, and are likely to be ephemeral phenomena in the absence of repeated (often anthropogenic) disturbance."

Development of semialtura woodlands, forest nuclei, and the expansion of gallery forest

We have already discussed the prevalence of young woodlands on the higher portions of the semialturas (see Chapter 9). I have argued that these woody formations have developed in response to increased grazing pressure during the early 1980's which led to a reduction in fire intensity as well as reduced soil water us by herbaceous plants. These conditions were more favorable for the establishment of a number of tree species. It has been suggested the light-seeded, wind-dispersed species are typical the pioneers in forest development (Bormann and Likens 1979: 107). The abundance of wind-dispersed species such as *Cordia glabrata, Tabebuia ochracea,* and *Astronium fraxinifolium* in these woodlands bears this out. The cover and perches provided by these young trees then attract birds and mammals which disperse other trees, such as *Genipa, Vitex, Samanea, Pithecellobium, Acacia, Guazuma, Spondias, Sterculia,* and *Attalea.* Some of these latter species then serve as nuclear trees for the development of forest nuclei, which differ from woodland by their shadier understories with no grasses and a predominance of taxa typical of the gallery forest. The forest/non-forest boundary has likely responded as well; however, there are no clear data to demonstrate this. In the absence of intense fires, the forest edge has likely advanced into the semialtura, but only where drainage and other soil conditions permit.

I suggest that some of what has been categorized as degraded forest by others (e.g. scrub savanna) is in reality a woodland or dense savanna which may have developed from a more open type of savanna in response to grazing-induced changes in the semialtura fire regimes and dry-season soil moisture balance.

Tree island formation described elsewhere

Tamayo (1961:126-133) described *islotes* and *matas* from the savannas of Guárico State, Venezuela. These *islotes* are adventitious forest nuclei and are typical of the boundary zone between the open savanna and the forest. Tamayo believed that *Copernicia tectorum* palms were often the initial nuclear plants in these *islotes*, often accompanied by *Cereus* cacti and parasitic *Ficus* strangler figs. In the Moxos savannas we find exactly the same type of woody island with the same three genera. Also as in Moxos, rubiaceous shrubs of the genus *Randia* are common understory elements.

Tamayo described another *islote* formed by a large *Platymiscium* (also at La Chacra), with an *Annona jahnii* (replaced at La Chacra by *Rollinia herzogii*), a *Spondias mombin* (also at La Chacra), and some other shrubs. The outer edge of the woody island was formed by shrubs and suffrutescents of the genera *Hyptis, Mimosa*, *Psidium, Pavonia, Melochia,* and *Sida* (all are common in Moxos). Tamayo observed that these shrubs and suffrutescents were the pioneers which allowed for the expansion of the islands by creating shady understory microenvironments favorable for the establishment of forest trees. These often frequently coalesce into large islands or *matas*.

Tamayo’s *islotes* are completely analogous to many Moxos *islas* in terms of structure, composition, and origin. They are natural features which indicate a development of isolated woody formations in otherwise “savanna”. As Tamayo noted, such forest islands are typical features of many forest/savanna boundaries environments; this is also what Parker (1992) argued for the allegedly artificial *apêtê* in the savannas of the Rio Xingu region of Brazil. They do not indicate deforestation, planting, or any other human activity intended to alter the balance of forest and savanna.

The timing of woody plant establishment in savannas is likely regulated in part by the interplay of dry, fire-prone years and wet, fire-free years (Medina and Silva 1990). Establishment of woody plants is often hindered by dry-season water competition with perennial grasses. Also, woody plants are generally most susceptible to fire mortality when small. Thus, a wet and relatively fire-free period should foster woody plant invasions in savannas where flooding is not a limiting factor. Alternating herbaceous/woody cycles may be initiated by periods of wet years and terminated by periods of dry years. However, in the Argentine Chaco extensive woody invasions of flooded savanna were facilitated to a period of dry years between 1914 and 1937 (Morello 1970). In this case a long period of dry years could lead to reduced biomass production by the flood-adapted herbaceous plants. The reduced biomass means reduced fire intensity which favor woody plants. In any case, the complex interplay of grazing, fire, climatic variability, and other factors make it all the more difficult to identify single causes for shrub and tree invasions.

Chapter 12. Phytogeography of the Flora of La Chacra

Eco-physiographic Regions of Tropical South America and their Relationships to La Chacra

The Amazonian Hylaea

The Llanos de Moxos savannas border, and are penetrated by, the so-called Amazonian Hylaea, the humid tropical forest of the Amazon basin. Amazonian forest elements extend southward along the major river corridors into the the more seasonal zones of Llanos de Moxos and the Precambrian shield regions of Bolivia, as they do in Mato Grosso, for example.

In the *Baixada* wetland region of Maranhão (eastern Brazil), *Attalea speciosa*[22] forests are largely restricted to "topographically elevated islands, which are also the principal sites for shifting cultivation" (Anderson *et al.* 1991, p. 23). These forest islands occur in zones subject to flooding between December and May and subject to burning in the dry season. The vegetation is mostly "a low savanna dominated by sedges and grasses" upon ground water laterites and gleys and grazed by cattle and water buffalo. This seems very similar to a description of the Moxos region, except that *A. speciosa* is replaced by *A. phalerata*. In "primary" and "secondary" forest at Lago Verde, *Spondias mombin* is either the third or second most important tree, respectively, after *A. speciosa*. In primary forest at Lago Verde, other species common to La Chacra include *Casearia sylvestris, Calycophyllum spruceanum,* and *Astronium fraxinifolium.* Secondary forest species include *Cordia sellowiana*, *Casearia sylvestris*, *Enterolobium contortisiliquum,* and *Genipa americana*. It is evident that many of the most common species at La Chacra are widely distributed species elsewhere.

Near Manaus, Junk (1989) found *Calycophyllum spruceanum*, *Ceiba pentandra*, *Genipa americana*, *Rheedia brasiliensis*, and *Spondias lutea* in the "high-level tree community" of a gallery forest with an average of 140 days inundation annually. Junk likened to the "high-level community" to a late-successional forest. I have not found any of the species from lower communities with more prolonged flooding in the region of La Chacra.

Kubitzki (1989) recognized that in the *várzea* (whitewater floodplain forests) one often finds "wide-spread forest species of the Neotropics, such as *Guazuma ulmifolia*, or species of even wider tropical distribution, such as *Spondias lutea*, which in Amazonia have developed flood-resistant ecotypes." He notes that the distinction between várzea and terra firme is blurred in western Amazonia because there is little difference in soil nutrient status, as opposed to the more stark contrast between the richer várzea and the poorer Tertiary terra firme in central Amazonia. He cites the presence of both *Ceiba pentandra* and *Triplaris* spp. on both types of surfaces as examples.

Campbell *et al.* (1986) examined *terra firme* and *várzea* forest along the Rio Xingu (Brazil: Pará, 3°49'S). These forests bear little resemblance to the Chacra forests. "Terra firme" species common to both areas include *Ceiba pentandra*, *Spondias mombin*, *Cordia nodosa*, *Hymenaea courbaril*, *Guarea macrophylla*, and *Guazuma ulmifolia*; however, only *C. pentandra* was important at the Xingu sites. I have not recorded any of the Xingu *várzea* species from the La Chacra area.

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[22] The babassu palm, formerly *Orbignya phalerata.* Known as *cusi* in Bolivia, where it is largely restricted to the Precambrian shield region.

Campbell *et al.* (1992) examined three young (14-50 years old) *várzea* forests on the Rio Juruá (Brazil: Acre; 7°38'S), located. Shared species between the Juruá and forests of La Chacra region include *Ceiba pentandra, Cordia nodosa, Cordia sellowiana, Hura crepitans, Margaritaria nobilis, Guarea guidonia,* and *Maclura tinctoria.* Campbell *et al.* (1986 and 1992) compared their Xingu and Juruá sites and found only one species in common. Between Juruá and Añagu, Ecuador (Balslev *et al.* 1987) there were ten species in common, two of which are also found at La Chacra. They point out that due to the large number of indeterminate species at the sites, there are probably many other shared species. The forests of the La Chacra region and the Llanos de Moxos in general contain only a small subset of the greater flora of the Amazonian Hylaea, largely those species with either broader ecological tolerances or highly successful dispersal histories. On the other hand, the Moxos forests contain many deciduous elements not common to the true "rain forest."

Yungas / Montaña

The eastern Andes are ecologically complex, with deep valleys allowing warm-temperature organisms to penetrate into the cordilleras. The southern and western edges of the Beni and Mamoré basins are abutted by the windward Andean front, a zone of intense orographic precipitation and dense forests where not recently disturbed. Some of the more "inland" Andean valleys are subhumid with seasonality of precipitation. In these valleys, deciduous elements are significant, with representative taxa including *Anadenanthera colubrina, Tabebuia ochracea,* and *Cordia alliodora.* The Andean subtropical forests extend as far south as Tucumán in Argentina.

Cerrados of the Brazilian Precambrian Shield

The Precambrian shield creates a large upland region in central Brazil (i.e., south of the Amazon). This region is characterized by a range of rather scrubby woodland and savanna types collectively known as the Cerrado. The true Cerrado vegetation is highly diverse with numerous endemic elements. East of the Moxos and Chaco plains, the Precambrian shield rocks abruptly rise above the Quaternary alluvium and the environment changes considerably. The steep, shallow, and often lateritic soils of the Precambrian uplands support semideciduous forests and cerrado vegetation. Cerrado elements are typically highly resistant to fire and drought, *Tabebuia aurea* and *Pseudobombax longiflorum* being typical examples that are common in Moxos. Cerrado elements at La Chacra are not particularly evident in the forests proper. The Llanos de Moxos "savannas" have little affinity to the Cerrado overall. The far northern savannas between Riberalta and Guayaramerín, the savannas of the lateritic surfaces, and the Precambrian shield region have greater floristic affinities with the Cerrado than do the central Moxos "savannas." Much of the difference has to do with the soil fertility and inundation characteristics of the regions.

Amazonian Campos

The savannas of Humaitá (Amazonas State, Brazil) north of the Madeira River are the nearest examples of *campos* in the Brazilian Amazon. Janssen (1986) provided detailed phytosociological data on these savannas in her dissertation. The savannas of the Chacra region bear little floristic resemblance to those of Humaitá. For example, the ubiquitous *Cyperus giganteus, Thalia, Eichhornia,* and *Pontederia,* perhaps surprisingly, are absent from the flooded savannas of Humaitá. Certain common and widespread Neotropical trees such as *Ceiba pentandra, Genipa americana,* and *Vitex cymosa* are also absent from the Humaitá savannas, but common at La Chacra. On the other hand, the Neotropical savanna characteristic *Curatella americana* is abundant at Humaitá and missing from

La Chacra. The palm assemblages are entirely different. Floristic commonalties among the woody plants are *Tabebuia ochracea*, *Pseudobombax longiflorum*, *Cordia nodosa*, *Cordia sellowiana*, *Hymenea courbaril, Senna occidentalis, S. sylvestris, Casearia sylvestris*, *Eugenia biflora*, *Calycophyllum spruceanum,* and *Pouteria torta*. Still, this does not indicate great similarity. Janssen (1986:143) described round to elliptical forest islands with trees up to 15 m in height, characterized by *Eugenia biflora*, *Orbignya martiana*, *Oenocarpus bacaba*, *Curatella americana*, *Myrcia paivae*, *Xylopia aromatica*, and *Byrsonima chrysophylla.* These islands are often well elevated in their centers by the earthmoving activities of termites (p. 145). She did not mention the areas of these islands; judging by her map, they appear to average some 200 m in diameter. These islands are largely found within *Curatella* savanna.

The Gran Chaco

Southeast of the Llanos de Moxos plains lies the northernmost region of the Gran Chaco, the "Chaco Boreal." Some authors consider the plains of the Beni and the Chaco to be continuous geologically and biogeographically. These plains are separated by the low and ill-defined watershed divide between the Amazon and La Plata basins. The phytogeographical division, however, is actually rather clear. The Gran Chaco is largely more arid than Moxos; however, the Eastern Chaco is characterized by extensive seasonally flooded environments.

Spichiger and Ramella (1989) note that *Maclura tinctoria* is a very abundant tree in gallery forests of the southeastern Paraguayan Chaco, where continuos flooding can last up to four months. In the northern Paraguayan Chaco, *Geoffroea striata*, *Coccoloba* sp., and *Celtis* sp. are common galley forest elements. Further away from the rivers, *Copernicia alba* is found in temporarily flooded "savanna grasslands." Also in the northern Chaco, there are isolated deciduous forest and savanna shrublands atop large inselbergs where species such as *Anadenanthera colubrina*, *Cordia* sp., *Tabebuia aurea*, and *Jacaranda mimosifolia* are found. However, we must no let these similarities lead us to conclude that the Chaco and Moxos floras are very similar. Rather, these taxa are restricted to exceptional locations (i.e. gallery forests or elevated plateaus) within the more arid thorn forest matrix which is more typical of the Chaco.

Prado *et al* (1992) determined that Chaco vegetation does not intermingle much with the Pantanal/Cerrado mosaic vegetation in southern Mato Grosso do Sul. Likewise, true Chaco elements are not significant in the Beni savannas or woodlands. The few species that are shared between the Beni and the Chaco are wide ranging species from other phytogeographic regions (e.g. *Maclura tinctoria*, *Acrocomia aculeata*, *Copernicia alba*).

The Pantanal of Mato Grosso

The mosaic of seasonal wetland, savanna, cerrados, and forests in the Upper Paraguay River Basin known as the Pantanal shares many similarities with the Llanos de Moxos. The regions are separated by the forests and cerrados of the Precambrian Shield region of Santa Cruz Department of Bolivia. They share many common taxa of both plants and animals, but they are rather different in terms of geology, hydrology, and relief. Moxos is much flatter overall than the Pantanal and its sediments are primarily Andean, not Precambrian.

Wilhelmy (1958b) discussed various wooded formations from the Pantanal. Rain-green dry forest and semi-deciduous moist forest contain taxa such as *Tabebuia aurea*, *Tabebuia "ipe"*, *Tabebuia ochracea*, *Jacaranda mimosifolia*, *Attalea phalerata*, *Anadenanthera colubrina*, *Acrocomia "sclerocarpa"*. Gallery forest (*Dammuferwälder*) elements include *Cecropia*, *Spondias lutea*, *Ficus pertusa*, *Inga*, *Enterolobium*, *Pithecellobium*. The majority of the dominant species are also common in the Beni.

Ferri (1980:93) noted *Attalea phalerata* and *Triplaris formicosa* as typical elements of Pantanal gallery forests with *Genipa americana, Ficus, Inga, Cecropia,* and *Bactris* as common associates. Drier forests of the Pantanal contain *Astronium*, *Pseudobombax*, *Anadenanthera*, and *Tabebuia*, among others. All of these are also common in the forests of La Chacra (*Pseudobombax* is present, but not common).

Dubs (1992) observed forested earthmounds associated with termite nests, or more rarely, a nest of leaf-cutter ants. As in Moxos, the larger islands are dominated by *Attalea phalerata*. An island 22 m in diameter had 29 dicot trees of 10 species and 17 palms, not unlike islas from the Chacra region. The flora of the islands are said to be derived from propagules dispersed from nearby cerrado and semi-deciduous forest stands.

Similarities are numerous, especially the significance of seasonal inundation and topography as determinants of vegetation composition. Also, both regions are low in endemicity and contain elements from diverse source regions. However, the Pantanal flora contains a much greater proportion of true Cerrado species than does Moxos (cf. Prance and Schaller 1982).

Junk and Da Silva (1995) believe that the lower diversity of tree species in the Pantanal relative to the Amazon floodplains is in part related to allegedly extreme Pleistocene aridity which would have supposedly resulted in the elimination of many trees. I find it unnecessary to look back to the Pleistocene for mechanisms which mediate tree diversity in the Pantanal. The present climatic (i.e. seasonal drought) and hydrological regimes (seasonal inundations) likely are strong limitations to the range of species which can survive in the Pantanal. Like the Llanos de Moxos, the Pantanal has low endemicity and the majority of the species are considered immigrants from other source regions. In this respect, both the Pantanal and Moxos can be thought of as relatively “recent” landscapes that have not yet developed endemic floras and that are true “melting pots” for elements from diverse origins.

The Llanos of the Orinoco Basin

As with the Pantanal, the Orinocan Llanos region of Colombia and Venezuela offers valuable comparative perspectives on the occurrence and processes of forest islands. The Llanos de Moxos and the Llanos of the Orinoco are separated by the vast expanse of the Amazonian Hylaea. In terms of their savannas, the Orinoco llanos have a much greater proportion of better-drained, upland savanna types. The islands described earlier by Tamayo demonstrate similar structure, composition, and formative processes for Venezuelan *matas* and the forest groves which develop on the semialturas at La Chacra.

In the drier Colombian llanos, Blydenstein (1967) found *Acrocomia* palms to be primary grove-forming elements which were present in all groves he surveyed. *Acrocomia* (totaí palms) are common in Moxos as well as in the Chacoan regions; however, I have not observed them to be isla-initiating elements in the Chacra region. Blydenstein found *Genipa americana* to be one of the first trees to colonize the developing groves. This observation also holds for the Chacra region. Groves at La Chacra and the Colombian llanos share many common genera, including *Acrocomia, Casearia, Psidium, Eugenia, Rollinia, Cecropia, Genipa, Jacaranda, Nectandra,* and *Vismia*. The groves described by Blydenstein from Colombia did not contain *Curatella, Byrsonima*, or *Bowdichia,* which the principal elements of the *matas* he described from Venezuela (1962). These are also absent at La Chacra. At the generic level, La Chacra and the Venezuelan examples share the following trees and shrubs *Cereus, Platymiscium, Zanthoxylum, Cordia, Casearia, Mimosa, Eugenia, Psidium,* and *Randia*.

Gallery forests described by Zucchi and Denevan (1979:20) near the Apure River in the Venezuelan Llanos are rather similar to those of La Chacra, at least at the generic level. The most important trees along Caño Ventosidad include *Spondias*, *Sterculia*, *Enterolobium*, *Annona*, *Rollinia*, *Genipa*, *Senna*, *Bactris*, *Coccoloba*, and *Casearia*. From other sites in the same area, *Pithecellobium*, *Tabebuia*, *Mimosa*, *Samanea*, *Caesalpinia*, *Inga*, *Guazuma*, and *Cordia* are common. Upon pre-Hispanic earthworks in the savannas, *Cordia*, *Annona*, *Samanea*, *Genipa*, and *Casearia* are important. In the seasonally flooded *sabana-estero*, the important savanna trees *Curatella* and *Bowdichia* are absent, as they are at La Chacra.

The genus *Copernicia* is important in both the Moxos and Orinoco llanos. In the Orinoco, *C. tectorum* is the species. In both regions, these palms are often the only trees in the seasonally inundated savannas where clayey textures dominate and salt accumulations may occur. *Mauritia* is important in the Orinoco, as well as in parts of the Pantanal, yet is nearly absent from Moxos.

Most of the Venezuelan *matas* are typically semi-deciduous and are similar in general structure and appearance to the relict semi-deciduous forests around Santa Cruz de la Sierra (J.J. San José, pers. comm. in the field, 1993). Despite the numerous similarities of the flooded llanos of the Apure basin and the Moxos, relict levee islands have not been suggested in the Orinoco literature.

Extra-Amazonian gallery forests

Oliveira-Filho *et al*. (1990) reported on gallery forests near Cuiabá, Brazil to the northeast of the Pantanal in ravines of a Precambrian shield *chapada* (plateau). These forests do not share a single species with the Chacra region forests, even though they are adjacent to the Moxos-like Pantanal.

Meave and Kellman (1994) reviewed the biogeographical significance of Neotropical gallery forests and conclude that the "combination of rain forest and non-rain forest taxa in the riparian forest does not appear to occur in any modern continuous rain forest." We could certainly apply this statement to the forests of La Chacra. I suggest that the mixture of diverse floristic elements in gallery forests reflects their great environmental heterogeneity (e.g. different topographic positions, soil characteristics, drainage conditions) as well as their role as corridors which connect distant "mainland" forests and traverse non-forest formations, bringing about contact between elements of diverse origins. Prance (1985:161) recognized that "gallery forests and forest islands were most important in the Pleistocene and that not every species was confined to the small pure rainforest refugia." I suggest that indeed the ability of many forest taxa to reproduce in forest islands and gallery forests in savanna landscapes would obviate the need for the so-called rainforest refugia, if indeed there was a widespread savannization of Amazonia in the Pleistocene. I likewise assert that present-day gallery forests and forest island archipelagos are able to maintain highly diverse plant and animal assemblages and are critical habitats in the savanna, cerrado, and wetland environments of tropical America (see also Redford and Fonseca 1986, Kellman *et al.* 1994).

Neotropical dry forests

Tropical dry or seasonal forests were scattered throughout much of Central America and South America wherever local climatic and soil conditions created prolonged deficits of plant available moisture. A considerable percentage of the Chacra trees are characteristic of dry semi-deciduous to deciduous forests and woodlands, not humid evergreen forest. This should not surprise us, given the seasonality of the precipitation and the heaviness of many of the soils. Janzen (1988) considers "dry forest" to be "the most threatened of all the major lowland tropical forest habitats," thus the presence of numerous dry forest elements at La Chacra may be particularly interesting to scholars of biological conservation.

Ratter (1992) describes a very characteristic "calciphilous" semi-deciduous community in the Brazilian Cerrado region where *Astronium, Anadenanthera, Ceiba, Sterculia*, and *Tabebuia* are principal elements, an assemblage typical of some of the better-drained woodlands at La Chacra. Ratter considers these forests to be highly fire resistant; thus he concludes that the transition to more open cerrado vegetation is not linked to fire, but rather entirely to edaphic factors. The forest are found upon the more nutrient-rich soils. Ratter also has observed expansion of gallery forest upslope into cerrado-type savanna. In the absence of fires, cerrado vegetation may close into dense thickets with many fire-susceptible and forest species being established.

Prado and Gibbs (1993) analyzed the distribution patterns of numerous Neotropical seasonal forest trees. Many of the species they examined are actually among the dominants at La Chacra. They identified what they call the "residual Pleistocene seasonal arc" pattern which is exemplified by the range of *Anadenanthera colubrina.* These trees range from the dry interior valleys of the eastern Andes southward into Moxos, the Gran Chaco, then eastward into central and southern Brazil and thence northeastward into the Caatingas[23] regions.

Other Bolivian Forests

Theodor Herzog's travels in Eastern Bolivia provide some of the earliest detailed botanical accounts of the region (Herzog 1909). He observed *Copernicia* woodlands in the eastern Bolivian Chaco, associated with shrubs of the genera *Mimosa, Acacia, Bauhinia, Baillonia,* and *Crateava.* The plains near the Río Paraguay contained seasonal forests with mixture of dry formation elements *Chorisia ventricosa, Pseudobombax marginatum, Calycophyllum multiflorum, Anadenanthera colubrina,* and *Tabebuia heptaphylla.*

Herzog observed that the Chacoan "Monte" formation had a northern limit of approximately 17°S. At this latitude, the "transition forest" was dominant, with a strong palm element comprising *Attalea phalerata, Syagrus sancona,* and *Bactris "infestans,"* with occasional occurrences of *Astrocaryum chonta*. The most characteristic dicot tree is *Calycophyllum spruceanum.* On the Precambrian shield, in the "Velasco hill land," the palm *A. speciosa* assumes absolute dominance, and is associated with brightly flowered deciduous bignoniaceaous trees such as *Tabebuia ochracea, Tabebuia heptaphylla,* and *Jacaranda cuspidifolia*, as well as *Physocalymma scaberrimum* and *Vitex cymosa.* In the seasonally flooded valleys of the Guarayos region, *Mauritia flexuosa* and *Bactris "inundata"* are the dominant palms. Further northward, Herzog visited the forests of the Río Blanco. Characteristic elements include *Triplaris "caracasana", Ficus* spp., various bombacaceae, *Lucuma* spp., *Perebea calophylla, "Copaiba paupera",* and *Swietenia macrophylla.* Other notable elements include *Caesalpinia peltophoroides, Dimorphandra* sp., *Sapium* spp., *Cecropia* spp., *Vitex cymosa, Calycophyllum spruceanum,* and *Jacaratia spinosa.* The Chacra forest flora demonstrates considerable similarity to these eastern forests, although many of the more typical Precambrian shield species are lacking on the alluvial plains of the Chacra region.

Boom's (1986) inventory of *terra firme* forest in the northern Beni (11°45'S) in the Rio Yata drainage contains typical Hylaean humid forest elements not present in the southern zone of the department, such as *Bertholletia, Hevea,* and *Euterpe.* Out of the 94 taxa identified by Boom, only

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[23] *Caatinga*s are a type of semiarid vegetation with abundant cacti and spiny shrubs and trees, characteristic of the drought-prone region of northeastern Brazil.

Attalea phalerata can be confirmed from La Chacra. However, this ubiquitous palm of the Moxos forests was only encountered once in Boom’s 10 x 1000 m transect, while it dominates most forests in the Llanos de Moxos. One major difference between the two sites in terms of *Attalea* biology is the abundance of dispersal agents. At La Chacra, *Attalea* is dispersed by cattle in addition to the abundant native agents such as agoutis, red squirrels, and owl monkeys. Livestock are absent from Boom’s forests and it is highly probable that native mammalian dispersal agents are much less abundant due to the fact that these are staples of the diets of the Chácobo people who live in the forests Boom inventoried.

Other Bolivian Savannas

At La Envidia, near the Río Apere ca. 20 km SW of San Ignacio de Moxos, I observed numerous *Curatella* (chaaco) on pre-Hispanic raised fields. *Vochysia divergens* (aliso) and *Luehea paniculata* (utubo) are common pioneer trees in the savanna. These savannas are not heavily grazed, and thus the more fire-resistant trees *Tabebuia aurea* and *Pseudobombax longiflorum* are more important elements of the landscape due to the greater fire intensity associated with the higher fuel loads. *Copernicia* palms are absent from this area. *Attalea*, however, are dominants of the forest islands (largely the result of afforestation upon archaeological earthworks) and are common in the savanna itself where they form small islets of two or three individuals.

Beck’s (1983) work at Espíritu along the Río Yacuma details various types of woody savanna formations. “*Machaerium hirtum*-bush forests” occur on semialturas and are characterized by *M. hirtum*, *Myrcia* sp. , *Tabebuia heptaphylla*, *Cereus* sp., *Sorocea saxicola*, and *Copernicia alba*. *Curatella americana* was also found in this community. The gallery forests he examined along the savanna streams contained trees such as *Croton*, *Amaioua*, *Nectandra*, *Licania*, *Peritassa*, *Pithecellobium*, *Rheedia*, and *Bactris*. These forests are flooded only 2-3 months annually, but the water is over one meter deep for more than one month. Thus, these formations have little in common with those of La Chacra. Beck only marginally discussed the numerous bajío forest islands which are present at Espíritu. However, it appears that these are largely dominated by *Attalea phalerata*, *Ficus* spp., *Genipa americana*, *Guazuma ulmifolia*, *Syagrus sancona*, *Rheedia* spp., and other taxa common at La Chacra.

Beck (1984) later discussed three categories of islas at Espíritu. The first are those islands occupied by human settlements and corrals. These have few trees, principally *Attalea* and *Ficus*. The second type is apparently the most common at Espíritu and is characterized by ruderal and spiny vegetation such as *Urera baccifera*, *Solanum americanum*, and *Pseuderanthemum bolivianum*. On these degraded islas, the trees exhibit adaptations to xeric conditions with deciduous spiny leaves (e.g. *Sorocea saxicola*) or deciduous hairy leaves (e.g. *Cordia glabrata* var. *eriophylla*). There are also fire resistant species such as *Curatella americana*. The final type of isla is only rarely found at Espíritu, the “little-altered isla with macrophanerophytes” such as the buttress-rooted *Ficus obtusiusicula* or the deciduous *Copaifera reticulata* and *Guazuma ulmifolia*. *Attalea* and *Syagrus* palms are rarely lacking in such islands at Espíritu. Gallery forest trees such as *Genipa americana* and *Rheedia* spp. are also common.

Most of the islas del bajío at La Chacra would qualify as relatively unaltered islands under such as scheme, especially Islas 2 and 4b, with massive *Ficus* and *Sterculia* as well as numerous mesophytic trees. Although *Syagrus* is common along the Cañada de los Lagartos, it is absent from the islas of the bajío. This is in contrast to the abundance of *Syagrus* in islands at Espíritu. Also unlike Espíritu, there are no islas at La Chacra with significant spiny components. The degraded islas of La Chacra are rather characterized by a lack of shrubs and herbaceous understory, just bare soil and a few relict trees.

Haase (1990a) did not encounter "open woodland with scattered trees" (orchard savanna *sensu* Beard) in the savannas west of the Río Beni. However, he describes a *chaparral* dominated by *Curatella, Xylopia aromatica, Nectandra gracilis,* and *Miconia* spp. The driest sites of all were characterized by the presence of *Tabebuia ochracea*. The dominant *chaparral* species of La Chacra (e.g. *Cordia glabrata, Copernicia alba, Acacia albicorticata*) were all absent from Haase's study area.

Breakdown by Distribution Classes for Dominant Woody Taxa

It is rather difficult to find truly representative plants for each region or formation because several species have broad ecological amplitudes. Several species are thus included in more than one category. These classifications have been taken from various authors (e.g. Kubitzki 1989, Prance 1989, Pires and Prance 1985, Prado and Gibbs 1993,

Amazonian Várzea (13): *Vitex cymosa, Calycophyllum spruceanum, Hura crepitans, Cordia tetrandra, Albizia niopioides, Cecropia* spp, *Ceiba pentandra, Guazuma ulmifolia, Triplaris americana. Casearia aculeata, Cordia nodosa, Maclura tinctoria, Rheedia brasiliensis.*

Widespread Neotropical Forests (7): *Ceiba pentandra, Hura crepitans, Spondias mombin, Guazuma ulmifolia, Genipa americana, Maclura tinctoria, Sterculia apetala.*

Widespread Dry Forest (10): *Astronium fraxinifolium, Cordia alliodora, Hymenea courbaril, Tabebuia ochracea, Guazuma ulmifolia, Randia armata, Samanea tubulosa/saman,* C*eiba pentandra, Spondias mombin, Sterculia apetala.*

Residual Pleistocene Seasonal Arc (6): *Anadenanthera colubrina, Enterolobium contortisiliquum, Geoffroea striata, Ipomoea carnea* var. *fistulosa, Tabebuia aurea.*

Southeastern Dry Forests and Cerradão (3): *Cordia glabrata, Anadenanthera colubrina, Astronium fraxinifolium.*

Cerrados (2): *Tabebuia aurea, Pseudobombax longiflorum.*

Gran Chaco (2): *Copernicia alba, Celtis* sp.

This very simple analysis of some of the most common species indicates that indeed the woody vegetation of La Chacra is a hodgepodge of elements from diverse regions or formations. One, however, must question how some trees can be considered typical of both Amazonian várzeas and dry seasonal forests at the same time! This indicates that many of the more successful Neotropical plants might be considered "generalists," or in botanical terms, extremely "plastic."

Soil Nutrient Status and Species Assemblages

We had earlier dismissed soil nutrient status as a determinant of forest/non-forest vegetation boundaries; however, there are still some interesting observations to consider. The dominance of species characteristic of both "várzea" gallery forest trees and "calciphilous" semi-deciduous forest trees and the paucity of "igapó" and "dystrophic savanna" trees would suggest that the soils at La Chacra are near the high end of a relative nutrient gradient in comparison with many other humid tropical lowland sites.

Ratter (1992) describes a very characteristic calciphilous semi-deciduous forest from the Brazilian Cerrado region where *Astronium, Anadenanthera, Ceiba, Sterculia*, and *Tabebuia* are principal elements; this mirrors some of the better drained woodlands at La Chacra. Ratter considers these forests to be highly fire resistant and thus the transition to more open cerrado vegetation is not linked to fire, but rather entirely to edaphic factors. The forests are found upon the most nutrient-rich soils. However, we can not infer unidirectional causal relationships between the forest and higher nutrient-status soils.

Haase (1992) also supports the differentiation of clear-water and white-water gallery forest types by differences in soil nutrient status, driven by the nature of the sediments in the savannas west of the Río Beni. Haase considered *Thalia geniculata* stands to be typical of white-water “floodplains where the surface of the soil becomes dry during the terrestrial phase [i.e., the dry season].” However, this same plant is characteristic of “blackwater” bajíos and gallery forest canals at La Chacra.

Given the dominance of “várzea”, “calciphilous,” and “white water” species, it appears that although the remaining channels in the Chacra region carry essentially “black water” and the bajíos are filled with crystalline rainwater, the vegetation tends to correspond to types described for more nutrient-rich forest, savanna, and wetland systems elsewhere. The absence of *Curatella americana* cannot be linked to flooding alone, as it is abundant on inundated termite “pimple savannas” elsewhere in Bolivia (for example along the upper Iténez/Guaporé at Noel Kempff Mercado National Park). It may well be that certain Cerrado and dystrophic savanna species are competitively excluded in relatively nutrient-rich sites. This would corroborate comments I received from folks in Santa Cruz de la Sierra who indicated that *Curatella* was a “trashy” plant indicative of the poorest soils.

Deciduous vs. Evergreen Woody Plants in Neotropical savannas

Medina and Silva (1990) believe that deciduous trees appear to be more fire sensitive and “are therefore excluded from the set of woody species inhabiting regularly burned savanna.” They also use this as a counter argument to the belief that “predominance of sclerophyllous, evergreen trees [is] a consequence of selection in nutrient poor environments.” The dominance of the deciduous trees *Cordia glabrata*, *Tabebuia ochracea*, *Tabebuia aurea*, *Samanea tubulosa*, and *Astronium fraxinifolium* in savanna woodlands at La Chacra, however, does not support the argument.

Fires during the leafless period should not be a negative factor unless bud meristems are damaged. Huntley (1982) argues that the prevalence of deciduously compound “throw-away branches” in annually burned African Miombo savannas is actually a nutrient-conserving strategy where pre-abscission and pre-fire nutrient translocation protects these deciduous trees from fire-related stresses. Foliage-free trees with corky bark should be especially fire resistant (e.g. *T. aurea*, *S. tubulosa*, and *Pseudobombax longiflorum*). Physiologically "expensive" sclerophyllous leaves are not likely adaptations to fire. Sclerophyllous evergreen leaves, however, are also characteristic of another fire-adapted biome, the "Mediterranean" scrublands. However in the Mediterranean scrubland ecosystems the mean fire recurrence interval is substantially more than one year and the leaves are adaptations to the prolonged summer droughts.

Sarmiento and Monasterio (1983:84) also believed that "truly deciduous trees--that is, those remaining leafless for several months--are far less frequent [in savannas] and they often represent pioneering forest species colonizing certain savannas" (e.g. *Genipa americana*). This may be true, as most of the "savanna" trees at La Chacra are typical of seasonally dry forests elsewhere.

Given these considerations, we may conclude that an invasion of deciduous trees on the semialturas would be facilitated by a reduction in fire intensity or frequency. At other localities in the Beni, I have observed that lightly-grazed semialturas contain only widely scattered and highly fire tolerant (albeit deciduous) hardwoods such as *Tabebuia aurea* and *Pseudobombax longiflorum*, and the palm *Copernicia alba*.

The only savanna shrubs with evergreen sclerophyllous leaves at La Chacra are *Coccoloba* spp., certain *Cordia* spp., *Combretum fruticosum*, and *Psidium guineense*. *Casearia aculeata* and *C. sylvestris* are often considered to be savanna species; however their leaves are not very hardened and they are primarily understory elements of woodlands and islands at La Chacra.

Conclusions

This brief examination of the representative elements of the flora of La Chacra demonstrates how complex the history of plant migrations has been in the southernmost portion of the Amazon basin, where we find species from diverse regions of the Neotropics assembled together in close company on the relict gallery forests, forest islands, semialtura woodlands, and termite savannas of La Chacra. The tight packing of different floristic elements in the limited surfaces favorable for tree growth may shed light on ecological and biogeographical processes of the proposed arid phases for Pleistocene (and portions of Holocene) Amazonia. Bush (1994) states:

> “The glacial-age atmospheric and climatic changes would have almost certainly have resulted in Amazonian forests unlike those of today”…with “the mixing of presently allopatric species to form sympatric associations” and that “plant and animal populations are expected to have undergone radical re-assortment into assemblages without modern analogues.”

However, I believe that in fact such mixes are typical of the forest/savanna/wetland mosaic landscapes of the Orinoco, Moxos, and the Pantanal, as also suggested by Meave and Kellman (1993). The absence of many Hylaean taxa from these forests does, however, suggest that local patterns of species distribution and forest composition may have been radically altered, but does not suggest the formation of completely isolated refugia.

We shall now turn to our final actor in the history of the forest island landscape of La Chacra, *Homo sapiens*.

Chapter 13. Human impacts

Introduction

As indicated in previous chapters, the existence of extensive landscapes in the Amazon basin of northeastern Bolivia without significant woody components can largely be explained by entirely natural processes. However, it is on a finer scale that the impact of human activity is most evident. It is the occurrence of small forest islands, forest strips, patterned ground, linear vegetation patterns, "upland" savannas, local deforestation, and other such phenomena that are of concern here, not regional distributions of forest and savanna.

Surface and subsurface pre-Hispanic ceramics and other archaeological materials, along with anomalous relief and drainage features are the most obvious indicators of past human presence in the forests of La Chacra. We ask what the possible significance of these prehistoric human impacts is for the larger question of forest island origins and regional landscape history.

The human impact is not uniform across the landscapes of La Chacra. If we wish to understand the geomorphology of gallery forests in the region of the Cañada de los Lagartos, we have to acknowledge that prehistoric peoples have highly significant local impacts. When must reach a verdict on the origins of the *Attalea*-covered islas of the bajío, the evidence for a significant human role is lacking. However, the anomalous Isla Loma Verde seems to provide a good case for construction by indigenous folk in the pre-Hispanic past. Of much greater significance for the forest islands, the introduction of livestock to the Llanos de Moxos an their later concentration on fenced ranches has greatly altered the nature of the forest island vegetation and soils.

Archaeology of La Chacra and its Regional Context

Nordenskiöld's (1913) description of Mound Velarde (located near the Ibare River, see Map 2) applies rather well to Loma 1 of La Chacra. The Velarde mound is about 5 m high, 45 m long, and 25 m wide. The mound itself is composed of "hard earth containing only very few potsherds," just as I found at La Chacra. North, east, and west of the mound is a 2-3 m deep cultural horizon. In several places about the mound there are large pits, presumably the source of the mound materials. However, Nordenskiöld did find funeral urns in Mound Velarde. These are likely present at La Chacra, but we just didn't hit any. (I did observe them in similar mounds at La Mónica in 1991.) He also found thin, fragile snail shells as I did at La Chacra. Nordenskiöld hypothesized that the residents lived upon stilted houses, which explains why the shells were not tread upon and broken.

The fact that the larger mound (lomas) are not full of ceramics should not cause doubts about their artificiality; however, one cannot extend this line of reasoning to the ceramic-free islas of the bajío. Many of the large mounds were ceremonial in purpose, often used as burial sites as described above. People did not live *on* these mounds, but the did live all around them.

That islands of woody vegetation do in fact form upon archaeological earthworks in the Llanos de Moxos has in fact been demonstrated by use of repeat air photography:

> "Much of what was open pampa [on 1958 airphotos] is presently occupied by shrubs, thickets, and a number of *islas*, large and small. Much, if not all, of the woody vegetation has established itself upon pre-Hispanic earthworks. Today the ranchers are using tractors to clear this vegetation." (Erickson *et al.* 1994:13)

Erickson *et al.* (1994: 17-19) excavated a forest island (*Isla Rodeo*) at La Envidia near the Río Apere. The island was only raised 40 cm above the level of the surrounding pampa; however they recovered over 200 ceramic fragments from the trench. They concluded that the island was an occupation site that had been enlarged by the accumulation of refuse materials over time. Unlike the any of the islands at La Chacra, this island is surrounded by agricultural earthworks and connected to rectilinear causeways. Also, Erickson *et al.* did not describe any surficial accumulations of sands, in contrast to the bajío islands of La Chacra.

The archaeological sites at La Chacra add to the increasing body of evidence for former high population densities and previously undocumented prehistoric human impact in many parts of the Amazon basin. The river levee occupation sites along the Cañada de los Lagartos are thus not exceptional or isolated features, but simply part of an extensive network of pre-contact human settlement and occupation of the Moxos savannas and gallery forests.

The area east of the Río Mamoré and west of the Río San Pablo is devoid of "white-water flood savannas," the type perhaps once favored for raised-bed hydraulic agriculture. This may be a possible explanation for the lack of extensive archaeological savanna agricultural features in the region, unlike the areas west of the Mamoré. Of course, an absence of savanna agricultural earthworks does not bespeak an absence of people. Some amateur students of Moxos prehistory (e.g. Rodolfo Pinto Parada, Kenneth Lee) have suggested that the eastern zone was connected to the west by a system of artificial canals and possibly by earthen causeways. Under this model, the population centers of the eastern zone could have been fed, in part, by crops grown in the west. The eastern region is characterized by large numbers of often enormous earthmounds. These earthmounds are often associated with moats, defensive palisades, earthen "bunkers," canals, and causeways which often connect the mounds

However, the existence of numerous large mounds and other earthworks does not mean that “earthworks agriculture” was involved at all in the moundbuilders’ economy. It is certainly plausible that each settlement was independently supported by local subsistence activities (hunting, fishing, wild plant harvesting, forest cultivation, etc.), as suggested by Roosevelt (1991:20-26, 403-430) for the moundbuilders of Marajó where there is considerable similarity of landscapes and organisms, but an absence of earthworks agriculture.

Historical Human Impacts

At El Tajibo, many hectares of semialtura and altura have been cleared for pasture since 1985. According to the owner, erosion of these cleared surfaces has been significant enough to convert these formerly higher surfaces into bajíos. Woody material is collected into long windrows and burned. Semialtura woodland is chained to remove palo bejuco.

The gallery forest immediately north of the house at La Chacra has been cleared by tractor within the last 20 years, because the cattle would not freely enter the corrals and to create convenient paddocks for horses. There are relict totaí and motacú which mark the former forest. A large chaco was cleared in 1991 and planted with sugar cane. However cattle entered the area and destroyed the crop, leading to abandonment of the chaco (although the women of the ranch still collect crops such as hot peppers). This chaco is presently colonized by a suite of invasive plant species not common at any other site at La Chacra, including various trees and shrubs.

Construction of the Santa Cruz Highway

The highway, by most accounts, is a hydrological nightmare. The local drainage patterns have been disrupted significantly due to the inadequate number of drainage conduits placed under the roadway. Thus, one side of the road has become more inundated, while the opposite side has lost its inputs of overland flow. The road crosses the cañada near its source east of La Chacra and also cut across a tributary or distributary just west of El Tajibo. This latter site was well known as a difficult crossing on the old trail and brecha. Large areas south of the highway west of the Río San Pablo have been converted into vast *patujusales* dominated by *Heliconia* and the skeletons of drowned forest (or woodland) trees.

Of equal significance are the terraplenes constructed to connect the ranches with the highway. I observed in 1986 that the causeway at El Sol was causing prolonged inundation and tree death in the gallery forest upstream. A landowner north of El Tajibo, downstream from La Chacra, constructed an *atajado*[24] in order to create a pond for raising black caimans. This atajado allegedly raised the base level of the cañada only a few centimeters, yet caused extensive flooding all the way to the potreros of La Chacra.

Modern Human Uses of Islas and Gallery Forest

Wood. Occasionally, a tree may be felled to provide wood for construction or the creation of wooden implements.

Firewood. Firewood is collected in the gallery forest (*Ampelocera* and *Vitex* are favored) and in the semialtura woodlands (*Astronium* is favored). On ranchers with semialturas and gallery forest, such use has not led to depletion of wood resource.

Fruits and seeds. These are eaten or collected rather opportunistically. When one is walking through the forest or resting in an isla during a round up, the wild fruits are exquisitely refreshing. Popular fruits include *Rheedia, Salacia, Genipa, Bactris, Acrocomia, Sterculia, Inga, Trichilia, Talisia, Pouteria, Spondias, Vitex*, and *Coccoloba.* Even the *Attalea* fruits are occasionally gnawed on.

Cutting of trees for honey. Old trees with beehives may often be cut down in order to reach the honey. This is a disastrous use of the resource. I have seen a few trees cut down for this purpose in the islas of the bajío.

Hunting. Occasionally, the men or women will go hunt for armadillos or pacas in the gallery forest. However, hunting pressure is very low due to 1) the availability of fresh beef, chicken, and pork and 2) the lack of idle time.

Swidden agriculture. Although not currently practiced at La Chacra, there is an abandoned chaco in the southeast gallery forest across from the house. This field was planted with sugar cane, but abandoned during the first year due to damage by cattle. It is currently full of weeds, tree resprouts, and saplings (from seed). The forest around Loma 1 contains numerous citrus trees, a coffee plant, a tutu, and other signs of past use as a chacra.

Summary of Recent Landscape Change at La Chacra

Given that we have already discussed most of these phenomena at length elsewhere, I shall only briefly review the most salient impacts on the vegetation over the past few decades.

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[24] Earthern dam or levee to pond water.

Loss of *Cyperus giganteus* in the bajío

Junquillares are also believed to be declining in area due to compaction of the soil and exposure of the root masses by cattle, followed by burning. Much of the now wide-open bajío of the East Range was formerly impassable junquillares. The trail to Cáceres once traversed otherwise impenetrable junquillares. According to one informant, you were in big trouble if you fell off the trail. However, during the wet season, the "open" bajío still becomes congested with tall *Thalia geniculata,* and the trail becomes a narrow waterway between the tall plants.

The demise of the *Cyperus giganteus* stands at La Chacra and elsewhere may have stands are important sediment and nutrient traps (cf. Thompson 1976 for *C. papyrus*). considerable negative impacts on the function of the bajío ecosystem. Dense *Cyperus* rhizomes accumulate stored energy and nutrients. Their roots are also highly efficient in capturing nutrients. Thompson proposed that frequent and persistent burning and/or harvesting of papyrus swamps will reduce growth rates by removing nutrients normally recycled through the system and by reducing the nutrient retaining efficiency of the root and rhizome mat. Beck (1983) noted how the Yacuma river is transformed from a white-water to a black-water river as it is filtered by extensive *Cyperus* marshes. Burning the junquillar and allowing cattle to graze the plants and trample the roots and rhizomes can only lead to degradation of this component of the bajío system. Destruction of the junquillares very likely leads to increased losses of sediments and nutrients from the bajío, and hence the productivity of the range is diminished.

Arborization of the semialturas

In the early 1980s the semialtura palmar between La Chacra and El Sol was clear and open. Likewise, the semialtura woodlands on either side of the highway (La Chacra-El Sol) were also wide open pampas. Now, these surfaces contain the dense woodlands and thickets described earlier.

Reduced cover on islas del bajío

Erland Suárez told me that the islas were all much more densely forested in 1983 than in 1994. He attributes the loss of forest cover to trampling by cattle, urine toxicity, and exposure of tree roots. The islas once had understory cover by spiny/thorny shrubs and by terrestrial bromeliads, as well as more numerous trees. A degraded isla in the far bajío near the gate to Cáceres was formerly full of *cosorió* (*Erythrina* sp.); now there are just "four *sapito* trees" (*Sorocea* sp.), according to Erland Suárez.

Mimosa thickets

Several spiny species collectively known as "cerrate-putas" (*Mimosa pellita* and others) and "gabetillo" (*Mimosa debilis*) are major range management problems in the Moxos savannas. Local knowledge says that these plants are actually favored by burning. These subshrubs form dense thickets, sometimes over 2 m high, which may cover many hectares.

Alteration of hydrology by highway and other causeways

The principal physical change brought about by the road has been an alteration in local drainage patterns. On the north side of the road, the effect has primarily been prolonged and deepened inundation of the semialturas. There has been substantial tree death and loss of tree cover in the are northwest of the Chacra entry road. I first noticed this phenomenon in 1986. South of the road, overland flow has likely been reduced, with an apparent increase in woodland tree cover. At first, almost no drainage structures were placed under the road. Subsequent heavy flooding forced the construction of drainage pipeways.

The cañada has likely been severely affected by both the highways and the entry causeways, although I could not elicit any such observations from my local informants. Behind the entry causeways, the cañada is impounded and ponded, retaining water into the dry season. At La Chacra, a diversion channel was created around the impounded cañada channel. Downstream from La Chacra in a farm formerly belonging to El Tajibo, a low causeway/dam was built across the cañada to create a pond for raising caimans. The dam allegedly raised water levels all the way to La Chacra, causing local flooding in normally dry places.

Conclusion

The human imprint on the landscapes of La Chacra is everywhere evident. There is a mix of both the modern and the ancient, the alien and the indigenous. However, neither past nor present human activity is the primary causal factor of the patterns of the forest and non-forest, isla and pampa, at La Chacra. Rather, the human patterns are superimposed upon the natural ones largely determined by palaeofluvial depositional regimes.

Chapter 14. Conclusions and Perspectives

In the introduction to this dissertation, I proposed to explain the origins and determinants of the forest island types encountered at La Chacra ranch in Amazonian Bolivia. To achieve this, I first described the array of forest island types and then evaluated the data and observations which provided clues to the island origins. In this chapter we will see how these data contribute to the development of landscape historical and biogeographical knowledge of the Llanos de Moxos region specifically and Amazonia in general.

Typology of Forest Island and Vegetated Earthmound Types at La Chacra

The results relevant to the first research objective were presented in Chapters 5-10. I have demonstrated that there is considerable diversity of previously undescribed forest island and mound types at La Chacra (Table 36). These add to previous vegetation descriptions from other areas of the Llanos de Moxos (Beck 1983; Haase 1990, 1991). I identified distinct classes of islands of woody vegetation in the savannas and wetlands as well as earthen mounds within the forests. These are very different types of features, but both are germane to my research.

I have focused heavily on the contrasts between the islas del bajío (the forest islands surrounded by seasonal to permanent wetlands) and the much larger gallery forest fragments along the Cañada de los Lagartos. These two island types are rather different in terms of their soils, botanical composition, prehistoric human impacts, and livestock impacts.

The surfaces of the islands of the bajío are generally much sandier than those of the gallery forest. Also, the bajío islands have deep organic-rich soils which react strongly to HCl due to the abundance of carbonates of biological origin. The gallery forest soils have much thinner and lighter colored A-horizons except where there is evidence of prehistoric occupation.

The trees of the islas del bajío are almost entirely species with larger, succulent, and rather tasty fruits (although some are evidently more tasty to non-human animals). The gallery forest tree flora is much more diverse and has a less-skewed array of fruit and dispersal types. However, some of the more attractive gallery forest fruits are curiously absent from the wetland islands, most notably *Spondias* and *Bactris.*

Evidences for prehistoric impacts on the islas del bajío and the forests along the Cañada de los Lagartos are compellingly different. To state it succinctly, the gallery forests contain two disjunct areas which I named the West and East Ceramic Forests, each of which covers several hectares. In these areas broken prehistoric (or at least non-European) ceramic vessels, grinding boards, rollers (for the grinding boards), spindle wheels, and other implements can be found with a minimum of effort. Besides forming locally dense subsurface horizons, these fragments can also be seen scattered on the surface, especially where they have been tossed out by burrowing mammals or where there has been recent erosion. With the exception of Isla Loma Verde, the islas of the bajío yielded only a single fragment of identifiable ceramic, and this only after exhaustive searching.

Table 36. Summary of principal island types and other vegetation units identified at La Chacra.

Vegetation Unit	Indicator species	Soil characteristics	Examples
Forested units			
Natural levee relict islands of the bajío	*Attalea phalerata*	Loamy sands over organic and carbonate-rich silt loam.	Islas 2-7
Artificial islands of the bajío	Deciduous hardwoods and *Copernicia alba*	Bone, shell, and ceramic-rich loam over carbonate-free silty clay loam.	Isla Loma Verde
Semialtura-type islands	*C. alba*	Sandy loam over clay loam with $MgS0_4$ crystals.	Isla 1
Developing forest nuclei on semialturas	*A. phalerata, Sterculia apetala, Guazuma ulmifolia*	Influenced by ant and termite activity.	Numerous
Termite mound islets	*C. alba, Tabebuia* spp., *Astronium fraxinifolium*	Light colored and silty-clayey.	Numerous
Gallery forest fragments	*A. phalerata, Bactris major, Hura crepitans, Spondias mombin, Acacia polyphylla, Triplaris americana, Calycophyllum spruceanum, Anadenanthera colubrina*	Variable, but sand caps rare. Horizons rich in ceramics, bone, and charcoal locally abundant.	Numerous
Non-forest units			
Semialtura woodland	*Cordia glabrata, Tabebuia aurea, A. fraxinifolium, Samanea tubulosa, Piptadenia* sp., *C. alba, Pithecellobium scalare.*	Silty loams over silty clays.	Bordering the gallery forests.
Palm savanna	*C. alba*	Silty loams over mottled clays.	The outer portions of the semialtura, near the bajío.
Bajío wetland	*Cyperus giganteus, Eichhornia, Pontederia, Nymphaea, Eleocharis, Rhynchospora, Hymenachne, Leersia.*	Silty loams over gleyed silty clay loams and clays. Hydromorphic soils with high organic content in A horizon.	The largest unit of La Chacra and the Moxos savannas in general.

In terms of livestock impacts, the islands of the bajío receive much more concentrated livestock use than do the gallery forests. The soils of the islas reflect many years of intense manuring and trampling by large numbers of animals that seek the islands as dry resting spots during the wet season and as shady retreats during the dry season[25]. The intense trampling of Isla Loma Verde likely accounts for the much smaller size of the ceramic fragments than in the gallery forests. The gallery forests are much larger in area and receive fewer animals overall, thus showing much less concentrated use, except in a few *Attalea* groves near the semialtura edges. The flora of the islas del bajío has been shaped by livestock impacts such as manuring, trampling, and browsing, but also by livestock seed dispersal. For example, the large-seeded *Attalea* palms are carried across the wetlands by cattle who chew on the fleshy mesocarp and then either spit out or defecate the seeds on the islands.

In spite of these differences, the origins of the gallery forests and the *Attalea*-dominated islas of the bajío are actually one and the same. I conclude that the islas of the bajío wetlands of La Chacra represent ancient relics of former natural levee gallery forests, as has been suggested other authors (Braun 1961, Denevan 1966, Beck 1983, Hanagarth 1993). We will return to this discussion shortly.

Other types of forest island and vegetated earthmound at La Chacra include the low artificial island midway between the *Attalea*-type islas of the bajío and the Ceramic Forest, *Copernicia*-palm groves, Semialtura-type islands with heavier soils and more xeric-adapted trees, termite islets, nuclei of forest development on the semialturas, artificial forest fragments along the cañada, and large artificial mounds and platforms in the gallery forests themselves.

Origins of the forest islands at La Chacra

We had discussed various possible causal agents for forest island formation in the Llanos de Moxos and elsewhere. While the data from La Chacra cannot be used to reject hypotheses for island origins outside of La Chacra itself, we can safely evaluate the factors presented in Chapter 2 as they apply to the forest islands of La Chacra. Table 37 concisely summarizes the evidence for each class of causal agents or processes for the forest islands at La Chacra.

Termite and ant mounds

Termite and ant mounds are definitely important features of the forest and savanna landscapes of La Chacra and elsewhere in the Llanos de Moxos. Termites create mounds on the semialtura surfaces and these mounds foster the growth of palms, largely deciduous trees, shrubs, and cacti. Rarely, these mounds coalesce creating somewhat larger mounds up to at least 12 m in diameter. These mounds are restricted to the higher portions of the semialturas. The termites that build the conical mounds are absent from the islas of the bajío and there is no evidence for traces of older mounds.

Ants create only very small mounds in the savannas. In the forests, however, leaf-cutter and other species build large mounds over 3-5 m in diameter. The leaf-cutter ant islands described by Troll (1936) from the pampas of Santa Cruz are absent from the region of La Chacra.

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[25] Prehistoric humans may have utilized the islas of the bajío in a similar fashion during hunting or gathering expeditions, but their impacts were more transitory in nature.

Table 37. Summary of conclusions on the role of proposed island-forming models in each of the three principal landscape units of La Chacra.

Type of origin	Bajío	Semialturas	Alturas
Termite and ant mounds	No.	**Yes.** Small islands of the *murundu* type.	No.
Natural levees remnants	**Yes.** Islas 2-7 are all part of a larger archipelago of levee remnants from a past palaeofluvial regime.	No.	**Yes.** The forested alturas themselves are the natural levees of the Cañada de los Lagartos.
Topographic inversion	No.	No.	No.
Tectonic events	No.	No.	No.
Developing forest nuclei	No.	**Yes.** Linked to reduced fire intensities due to high grazing pressure.	No.
Prehistoric human activity	**Yes.** Isla Loma Verde was probably created as a small occupation site to facilitate use of the bajío resources.	No.	No. Mounds and platforms were constructed within the gallery forest, but did not create forest islands. .
Modern human activity	No.	**Yes.** Altered fire and grazing regimes lead to afforestation.	**Yes.** Fragmentation of gallery forest by clearing and burning.

Natural levee remnants

The gallery forests along the Cañada de los Lagartos grow upon low natural levee formations, except where these surfaces have been raised by prehistoric mound and platform building. All the evidence indicates that the Islands 2-7 in the bajío of La Chacra are likewise remnants of ancient natural levee. Such evidence includes:

1. The coarser textures throughout the isla profiles relative to the surrounding bajío soils, except where sands have been deposited colluvially after washing off of isla surfaces;
2. The presence of adjacent palaeochannel features, such as the small cañada described in the Isla 1-Isla 2 transect;
3. The presence of curving non-forested prolongations of the islas surface between islas;
4. The spatial pattern of the islas is consistent with the gallery forest/levee patterns of the Cañada de los Lagartos (Fig. 12); and

5. The absence on these islands of archaeological materials associated with prehistoric occupations sites on such as those of Isla Loma Verde and the gallery forests of the Cañada de los Lagartos.

Island formation (i.e., by gallery forest fragmentation) in the Llanos de Moxos may in some cases have occurred *after* the abandonment of prehistoric occupation sites. That is to say, some artifact-rich islas could have been "gallery forest" settlements similar to those along the Cañada de los Lagartos. Over an 800-year period, significant changes in forest cover are not unexpected. Thus, some present-day islas may not have even been islas when they were occupied. It is difficult to pinpoint island-forming events; perhaps there are none if the process is simply a slow and steady "erosion" of the forest edge. However, if there were longer periods of extreme drought, abandoned gallery forests would be subjected to several years of water deficits which could easily be fatal to many gallery forest species (cf. Adámoli *et al.* 1990, Sennhauser 1991). Trees would then persist only on the deeper soils with the greatest quantity of available water. Tree death and general reduction of vegetative cover on the old levee surfaces would then lead to accelerated erosion when wetter periods again set in.

Topographic inversion of palaeochannels

The presence of palaeochannel depressions adjacent to the islas would not be expected if the islas themselves were inverted channel bed deposits. Also, the spatial distribution of the islas does not correlate with probable geometry of the palaeofluvial system.

Tectonic processes

The data from La Chacra do not suggest tectonic origins for the any forest islands in the area.

Establishment and growth of forest nuclei in savannas

Developing forest nuclei are present in the semialturas. It is entirely likely that these groves will continue to expand and coalesce into larger islands or coalesce with the existing gallery forests. However, the establishment of trees does not occur in the bajío wetlands under any circumstance except for the creation of artificial islands.

Human impacts

Prehistoric impacts

Isla Loma Verde is the only island in the bajío that appears to be the result of woody plant establishment upon a prehistoric earthwork. The presence of numerous small to tiny ceramic fragments in the surface horizon of this islands immediately suggests that this island is different from the *Attalea*-dominated islands further out in the bajío. The raised surface which comprises the island is of the same material found in the adjacent pampa. There are no clear traces of borrow pits, but these would have filled in by the same processes associated with the sedimentation of the basin described in the model of natural island formation.

I conclude that Islas 1-7 are not artificial because:

1. They are not constructed out of the much clayier pampa soil materials;

2. They do not contain deposits ("horizons") of ceramics or other cultural refuse which would indicate more than just infrequent visits;
3. The trees were not planted (the islas are not apêtê forests); and
4. The forested surfaces which once connected the islands were most likely not deforested by humans.

Historic human impacts (1680s-1954)

We know that the region of La Chacra lies in the zone of the earliest European settlements in the Llanos de Moxos. We also know that cattle and other livestock were introduced to this region over three centuries ago. However, there have never been any important settlements in the immediate vicinity of La Chacra. The population density has always been low due to the practice of extensive ranching. The name "La Chacra" does, however, suggest that the site had been important as a fruit or vegetable-producing establishment in the past. In the gallery forest itself we see evidence for this past land use in the form of a few scattered relic grapefruit, lemon, coffee, and calabash (*tutuma*) trees. But the very place where these trees are is presently a well-developed forest, so we have little evidence that the fragmentation of the gallery forest was related to earlier economic activities.

Present-day human impacts (1955-1994)

Here I include the activities of the La Chacra ranch since its official establishment in 1955 by relatives of the present owner. During this period there has been more intensive manipulation of the vegetation designed to improve cattle production, as well as an intensification of the grazing pressure on the ranch. The road to Santa Cruz was also established in the latter part of this period (i.e., 1979-1986).

The area around the present house at La Chacra was formerly forested and has been cleared for the construction of corrals, the house compound, orchards, gardens, artificial pastures, and the entry road off the highway. This area is rather small, however, on the scale of the entire ranch. This clearing did lead to the fragmentation of several portions of the gallery forest on either side of the cañada. These fragmented forests are clearly artificial and bear little resemblance to the islas of the bajío or even the other gallery forest segments.

The most significant impacts have been those of the cattle and horses of the ranch. The increasing wealth of the owner and easier access to the ranch via the highway led to greatly increased herd sizes at La Chacra. I have testified to the destructive impacts of concentrated trampling, defecation, and urination on some of the islas in the bajío. Such abuse of the islas should be avoided. However, I should point out that only two out of the 14 islands in the bajío have suffered severe impacts. Most of the other islands are too remote to receive such heavy use.

High levels of grazing on the semialturas has led to tree and shrub invasions during the past 10 years (i.e., 1983-1993). While this may decrease forage production for the cattle, this arborization has no negative impact on the landscape or its native organisms. The developing woodlands and forest nuclei are well-represented with diverse elements of Neotropical deciduous and semi-deciduous forest formations. Another benign effect of the livestock has been their role as seed-dispersal agents for numerous trees such as *Attalea, Guazuma, Genipa, Spondias,* and *Samanea.* All of these trees are valuable for wildlife species and have increased as the result of livestock activity.

We can conclude that the role of humans in the *creation* of forest islands at La Chacra has thus been rather limited, with the exception of Isla Loma Verde. Their role in *modifying* the composition and structure of pre-existing forests and forest islands, however, has been much more significant.

Toward a landscape history of La Chacra and the Llanos de Moxos: an integrated model of **isla del bajío** *development*

My final objective was to contribute to knowledge on the landscape history of the Llanos de Moxos. Now that I have concluded that palaeofluvial processes at La Chacra are indeed the primary determinant of the configuration of alturas, semialturas, bajíos, and many of the islas in the bajíos, we must develop a plausible developmental scenario to account for the present landscape. Let us begin with a review the palaeoclimatic data.

Palaeoclimate history

Although there are no specific palaeoclimatic data for the Llanos de Moxos themselves, it is not unlikely that there have been periods of both reduced annual precipitation and greater seasonality in precipitation distribution relative to the present climatic regime. It is known that there have been periods of Holocene aridity in the lowlands to the south at Santa Cruz de la Sierra (Servant *et al.* 1981). Other authors such as Hanagarth and Sarmiento (1990) believe that there were indeed periods of Holocene aridity in the Llanos de Moxos proper, using the presence of *salitrales* (evaporite deposits) as evidence.

Gullison *et al.* (in press) found extensive gully formation under mature tall humid forest on terraces above the Río Chirizi in the Chimanes Forest of western Moxos. The formation of these gullies was completed at an unknown time in the past, as no erosion could be detected between 1992 and 1994. However, a pre-Hispanic earthwork is bisected by one gully, indicating that at least some of the erosion has occurred after the time of abandonment of the earthworks (i.e., probably within the last 500 years). It is not clear whether the period of erosion is linked to climatic or land use changes, or the combination of both.

I find the scenario of periodic Holocene aridity rather pleasing, as it explains several phenomena simultaneously. We may recall the theories regarding the origins of the oriented lakes which are unique to Moxos. I stated that Clapperton (1992) was probably *almost* correct. He concluded that the lakes are of aeolian origin, but he believed that they formed during Pleistocene aridity phases. I find the evidence for Holocene aridity much more convincing and a considerably younger age helps to explain their persistence in the landscape. I conclude that shallow, flat-bottomed lakes were initiated during periods of Holocene aridity as deflation pans in the desiccated plains. The present shape and orientation of the pans does not entirely reflect their original configurations. The shorelines and lake beds have been modified by wave action during the humid periods when these pans have been filled with rainwater to become shallow, flat-bottomed lakes with arcuate shorelines and low beach ridge berms. These features are the result of wave action, not aeolian deflation. These lakes may be as young as 1,400-3,000 years (the last arid period from Santa Cruz, Servant *et al.* 1981). So how does this relate to the formation of forest islands?

The occurrence of periodic Holocene arid phases is critical as a triggering factor for island formation. During both humid and arid periods, the elevation of the islas has multiple significance:

1) In the present regime, the relief provides better-drained sites;
2) in both the present regime and in drier regimes, the deeper profiles of somewhat coarser materials provide greater quantities of plant available moisture during the dry season than the adjacent clay-pan seasonal wetland soils;
3) the coarser and deeper soils of the higher sites therefore offered reduced drought stress relative to the shallower and clayier soils of the bajíos and provided the most favorable sites for tree survival during periods of increased aridity; and
4) the persistence of tree cover protected these already higher surfaces from sheet erosion in subsequent humid periods, while the lower surfaces experienced accelerated erosion under reduced vegetative cover.

It could have been possible that the rivers simply dried up during exceptionally arid phases, but during the humid phases avulsions were very common events in the Llanos de Moxos. Increased regional aridity after an avulsion would have profound impacts on the gallery forests, considering that simply cutting off the river water and its sediments leads to gallery forest degradation without regional climate change in the Gran Chaco of Argentina (Adámoli *et al.* 1990, Sennhauser 1991).

The absence of palaeodune features in the Llanos de Moxos is not unexpected, as there is a general lack of loose sand-sized particles away from the immediate vicinity of the largest rivers. We should remember that much of the potential sand load for the Mamoré is deposited far to the south around the city of Santa Cruz de la Sierra by the Grande and Piraí rivers and in braided channel floodplains at the foot of the Andes in the Chapare region.

Morphodynamic phases of the Moxos basin

Hanagarth (1993: 23-27) discusses three classes of fluvial systems: 1) the ancient network, 2) senescent streams, and 3) the modern fluvial network. The ancient streams are those that are essentially inactive and isolated from the modern network, while the senescent streams are those such as the Cañada de los Lagartos. I do not consider these stages to be representative of distinct time periods, nor does Hanagarth appear to imply this. In a given region, it is often possible to identify sequential river courses in distinct stages of senescence.

Postulated sequence of morphodynamic phases and events in the development of the landscape of the Cañada de los Lagartos basin

Phase 1: 10,000-7,000 BP ? In the center of the modern bajío of La Chacra there was a river that deposited the levees and pointbars whose remnants would later become the "Islas del Bajío."

Event 1: 7,000-4,000 BP? The Phase 1 rivers experienced an upstream avulsion that shifted its course southwest to the present location of Cañada de los Lagartos. Water and sediments were cut off and gallery forest degradation began. Holocene aridity would have exacerbated these effects and led to more rapid disintegration of the old forests as well as to the formation of the nearby oriented lakes.

Phase 2: The new river began to deposit the levees (alturas) and long backslopes (semialturas) on either side of itself. The old floodbasin (the present bajío) began its infilling. This could have occurred in the absence of arid phases or after the termination of such a phase. Degradation of gallery forest continued upon relict levees of the Phase 1 channel, with net erosion of old levee surfaces and fragmentation into forest islands.

Event 2: 3,000 BP- 1600s AD? Indigenous peoples settled in the gallery forests along the active river and constructed forest earthworks, canals, and Isla Loma Verde. Deposition continued in the bajío, filling in the ancient channel scars as well as borrow pits for Isla Loma Verde. Stabilization of the islas del bajío under recovered forest cover.

Event 3: 1680s. Jesuit arrived and introduced ungulate livestock into region. Livestock induced soil compaction, especially in the bajío; soil erosion, especially on the alturas and islas del bajío. Colluvial increased deposition on semialturas and in bajío.

Event 4: Early 1900s. Ranching centers were established. Cattle herds became more concentrated. Annual burns by cattlemen.

Event 5: 1940s-50s. Fencing of ranches began, leading to further concentration of cattle and restriction of herd movement and intensification of livestock impacts, cutting of *Copernicia* palms for fence posts. Senescence of Cañada de los Lagartos began to accelerate in 1960s.

Event 6: 1970-80s. Construction of Trinidad-Santa Cruz roadway upon earthen causeway. Construction of entry causeways to ranches north of the cañada. Alteration of drainage of semialturas south of the cañada.

Final Words

The vegetation and landforms I describe and interpret in the present study provide novel data which complement the scant literature on the Bolivian savannas and forest islands (e.g., Beck 1983, Haase 1990 and 1991, Hanagarth 1993). The *Cordia glabrata-Tabebuia ochracea* woodlands, *Anadenanthera* groves, *Sterculia-Attalea* forest nuclei, and the artificial “ceramic forest” and forest canal complexes represent previously undocumented features of the Moxos landscapes. There are no previously published studies which have examined any single portion of the Moxos landscape in such detail. Hanagarth’s (1993) recent work on the geo-ecology of the Beni savannas is an excellent contribution and contains important new data and synthesis, but it lacks more detailed descriptions and analyses of specific vegetation/landscape/history relationships. My research at La Chacra provides a perspective on a Moxos landscape that can only result from a focused examination of a more tangible piece of the whole.

The archaeological materials I encountered at La Chacra represent new sites for Amazonian Bolivia, but I do not find this to be especially noteworthy. These findings only help confirm that the Llanos de Moxos region was densely populated by earthworking peoples in the pre-Hispanic past. My work complements both the broad examination and synthesis of Denevan (1966) and the more detailed archaeological studies of Erickson (1980, 1995). I also hope to continue on in the spirit of Erland Nordenskiöld, one of the first to ponder the strategies of the indigenous inhabitants of the flooded savannas of Moxos (1916).

It should not surprise us that people chose to live in such a beautiful place long ago. It must have been rather pleasant to paddle up and down the river, traveling between the villages built on dry earthen platforms under the shade of the gallery forests. The wetlands of the bajío were likely not any more welcoming than they are today, but the great flocks of waterfowl and the herds of swamp deer certainly would have made for attractive hunting opportunities. The wetland vegetation likely provided numerous resources as well, such as water lily corms and native grains. Isla Loma Verde was likely the home base for the hunters and harvesters of the wetland resources.

When the last indigenous folks abandoned the villages at La Chacra, they certainly did not leave behind a degraded landscape. The great earthworks and literal tons of broken pottery, after-dinner-bones, and cooking-fire ashes they left behind have become the substrates upon which many generations of forest organisms have made their livings. Earlier in this century, an enterprising Bolivian planted oranges, lemons, grapefruit, coffee, calabashes, and other crops upon these most fertile materials and created La Chacra. This old chacra and its old house in the woods are gone now, except for a few old trees overtopped by the native forest species. The human impact had been rather transient, except for the enduring relief features built long ago.

Today, La Chacra is unmistakably a cattle ranch. We cannot know the long-term results of this current regime, but as long as La Chacra does not succumb to encroaching urbanization along the busy highway or some extensive agricultural conversion, we can be sure that the dynamics and activities of the native organisms will still be important. The balance between trees and herbaceous vegetation will continue to be disputed on the semialturas. The islas of the bajío will likely not be destroyed by the cattle unless stocking rates are permanently raised to unsustainable levels. One important consideration I have failed to mention in this study is the love of the land that is part of the Beniano (resident of the Beni or Moxos) psyche. Cattle ranching, hunting, trekking through the forest, and simply enjoying the outdoors is part of what many people consider to be their tradition. Ranches are passed down through family ties. They are not considered expendable properties. The forest islands are recognized as useful and valuable features of the landscape. Ranchers are not likely to allow their pampas, montes, and islas to be squandered. But of course, there are always exceptions.

It is obvious that I have only begun to tap into the potential that such a landscape offers for biogeographical, geomorphological, archaeological, and other avenues of research. I am especially pleased that I stuck with La Chacra as a study site. We should recall that La Chacra is an old cattle ranch along a busy highway only 22 km outside of the largest urban center of northeastern Bolivia. It is a place that no other person I know would have chosen to research Amazonian ecology or biogeography. I was told by several researchers in Bolivia that such a landscape was far too humanized to reveal anything interesting about nature. I am happy to report that nature does not respect fencelines, grazing rights, or even indigenous archaeological sites. The species that inhabit the bits and pieces of forest and the woodlands, savannas, and wetlands between them at La Chacra continue to “do their own thing” and find strategies to survive just as they always have over evolutionary time scales. The monkey families who followed me about and cursed at me in their most vulgar fashion should be glad they can’t read the ecological literature or else they would find out that they should have left La Chacra or gone extinct long ago!

Glossary

Afforestation	Development of forests upon non-forested surfaces.
Agouti	A guinea pig-like forest rodent about the size of a medium rabbit. Not favored as a food item due to its smell and taste like the fruits of the motacú palm. Local name is *jochi carlucha* or *jochi colorao.*
Altura	High ground, natural levees, artificial platforms, and mounds, usually forested.
Anaconda	*Eunectes murinus*, the world's largest snake. An aquatic member of the Boa family. Very common at La Chacra. Known in eastern Bolivia as the *sicurí.*
Apêtê	Term used by the Kayapó people of the Xingu basin for several types of forest islands, many of which are allegedly created by complex cultural practices.
Arboleda	Woodlands or savannas, more open than *chaparral,* many deciduous trees such as *Astronium, Tabebuia, Cordia, Spondias, Sterculia.*
Armadillo	One of several shelled mammals native to the Americas.
Arborization	Establishment of trees in open landscapes.
Arroyo	A more or less permanent stream.
Atajado	An earthen dam or dike to pond water in cañadas
Atta	The genus of the leaf cutter ants, which are important moundbuilders in the American tropics.
Avulsion	A sudden change in the course of river. An important event in low gradient plains where aggradation of river beds is common and a river may spill over or break through a levee and flow into a lower area.
Bajío	Permanent or seasonally-dry wetlands.
El Beni	The first-order political division which corresponds largely with the former *Provincia de Moxos*. Capital is Trinidad, 22 km west of La Chacra.
Bentón	*Hoplias malabaricus,* a common air-breathing fish in the stagnant waters of the Llanos de Moxos. Easily caught on hook and widely eaten.
Bibosi	Strangler figs of the genus *Ficus* (commonly sold as "rubber plants" for houseplant in the United States). Some species become giant canopy trees with trunks over 2 m in diameter at the base and with massive buttress roots. Some species are especially fond of the *Attalea* palms.

Biogeomorphology	A subfield of physical geography and biogeography which examines the relationships between organisms and geomorphology, with the implicit recognition of the reciprocal nature of the relationships.
Cáceres	The ranch directly northeast of La Chacra.
Campos	Brazilian Portuguese term for open savannas or grasslands.
Cañada	Semi-permanent watercourse occupying palaeofluvial scars or more recently senesced or abandoned channels.
Capão	Brazilian Portuguese term for forest islands.
Capibara	The world's largest living rodent (*Hydrochoerus hydrochoeris*), reaching the size of a small hog. Semiaquatic and typical of flooded savannas and wetlands.
Casarabe	First major village to the east of Trinidad and La Chacra. Founded in the 1930s as an "Indian school" for the Sirionó.
Ceramic Forest	The forests which grow upon extensive platforms, mounds, and other earthworks created by the indigenous people along the Cañada de los Lagartos at La Chacra. The surface and soil of this forest contain highly abundant ceramic artifacts.
Cerrado	Brazilian Portuguese term for a vegetation formation characterized by a high diversity of scleromorphic and pyrophytic shrubs and trees. Centered on the Brazilian Precambrian Shield.
Chacra	Quechua term (widely used in Spanish America) for swidden agriculture plots.
Chaco	Guaraní term (widely used in Spanish America) for a hunting ground or swidden agriculture plot.
Chapare	Forested sub-Andean region of Cochabamba department with high precipitation and reputation as the primary source of coca leaves for the production of cocaine. This region lies directly south of the central Llanos de Moxos.
Chaparral	Semideciduous woodland, often with *C. alba, Cordia glabrata, Pithecellobium, Samanea, Acacia.*
Compaction ridge	A relief feature created by the topographic inversion of palaeofluvial channel bed deposits.
Copernicia	A genus of fan palms with four disjunct species in the seasonal tropics of South America and numerous species in the Caribbean islands. The Carnauba wax palm is *C. cerifera*. *C. alba* is the species found in Moxos, the Pantanal, and the Chacoan region.

Cordilheira	Brazilian Portuguese term for a dry forested ridge allegedly formed by levee deposits in the Pantanal.
Curichi	Permanently or seasonally inundated depression with aquatic vegetation, usually associated with palaeofluvial features, but sometimes caused by tectonic depressions or damming by causeways (both prehistoric and modern).
Curupauzal	A grove of the *curupaú*, a deciduous leguminous tree typical of South American dry forests (*Anadenanthera colubrina*, formerly known as *Piptadenia macrocarpa*).
Forest fragment	A discrete unit of forest that was formerly contiguous with a more extensive forested area. The result of fragmentation by any combination of natural and anthropogenic processes.
Forest island	Any discrete unit of forest that can be perceived as disjunct from other units of forest. Can range in size from a few square meters to several square kilometers. Not always synonymous with *isla*, which may refer to clusters of shrubs as well, and does not include larger forest islands that are not readily perceived as discrete units by earth-bound observers.
Forest nucleus	A cluster of young and expanding forest elements which has either recently established from propagules or is recovering after fragmentation or selective clearing.
Gran Chaco	A semiarid to subhumid region of southeastern Bolivia, western Paraguay, and northern Argentina. Characterized by a mosaic of seasonal thorn forests, woodlands, wet savannas, and gallery forest formations.
Ibare	The principal eastern tributary of the Mamoré, lying between the Mamoré and the city of Trinidad. Ibare means “parallel” in Moxo, referring to the fact that the lower reaches of this river flows parallel to the Mamoré.
Isla	Spanish term applied to any isolated stand of woody vegetation (i.e., shrubs and/or trees) in the lowlands of eastern Bolivia. Generally restricted to wooded units that can been perceived as discrete by observation from the ground.
Junquillar	Dense stands of *Cyperus giganteus* sedges (also *yomomo*).
Junquillo	*Cyperus giganteus*, the South American papyrus sedge. This plant is a denizen of the wetter portions of the *bajíos* and portions of the *cañada*, often forming tall, dense stands that may cover many square kilometers
Lagartos	Tropical American crocodilians (*Caiman sclerops*) 2-2.5 m in length. Highly abundant at La Chacra and also in roadside borrow pit ponds and canals. Nests in the secluded canals of the Ceramic forest. These are distinguished from the much larger and rather dangerous *caimán* (*Melanosuchus niger*) which has been eliminated from much of its former range.

Laguna	Shallow (1-2 m) oriented lake typical of the Moxos plains. Deeper lakes (of fluvial origin) are referred to as *lagos*.
Llanos	Spanish term for plains, used to denote savanna regions in Tropical America.
Loma	An artificial mound, often in a forest, but may be in pampa.
Macaws	Large, long-tailed parrots with naked faces. Genus *Ara*.
Mamoré	The main river of the Moxos plains, a tributary of the Madeira.
Marmosets	A group of diminutive Neotropical monkeys, primarily of the genus *Callithrix*.
Mata	Venezuelan term for forest island in the Llanos. In Brazil, refers to forest in general.
Matiquipiri	A small blackwater river born in the pampas of the region of La Chacra. The Cañada de los Lagartos appears to have been the principal tributary of this river.
Matorral	Dense shrub-dominated savanna/woodland, generally with weedy elements such as *Mimosa, Vernonia, Combretum, Psidium, Eupatorium, Hyptis*.
Mesocarp	Portion of a fruit between the outer skin and the material immediately surrounding the seed(s).
Mocoví	A minor blackwater river born in the pampas just to the northwest of La Chacra. Presently is the outlet of the Cañada de los Lagartos.
Monovi	Large mound complex northwest of La Chacra in the pampas of the Mocoví basin.
Moxos	The region of lowland Bolivia corresponding roughly to the Amazonian savanna region. Formerly a Jesuit mission territory and later a Province of the Department of Santa Cruz. Presently mostly within the Department of the Beni. Named for the Moxo people who occupied the southern savanna zones around the Mamoré River. Region is renowned for the expansive areas of prehistoric raised fields and other archaeological earthworks such as causeways, mounds, and canals. Also *Mojos*.
Monte	Forests in general.
Motacú	The most abundant palm of the Moxos forests, *Attalea phalerata*. Somewhat similar to the well-known babassu palm (*A. speciosa*), with which it is largely parapatric.
Murundu	Brazilian term for small earthmounds attributed primarily to termites, differential erosion, or localized subaqueous deposition.
Palmar	Palm savannas or groves dominated by *Copernicia alba*.
Pampa	"Savanna" *sensu latu*, i.e., non-forest landscapes.

Pantanal	An extensive seasonal wetland in the general sense. When used definitively, refers specifically to the Pantanal of the upper Paraguay river basin in the Brazilian states of Mato Grosso and Mato Grosso do Sul.
La Providencia	Ranch immediately southeast of La Chacra.
Salitral	A place where mineral salts are present at the surface and cattle congregate to consume them. Vegetation is often greatly altered by the cattle.
San Pablo	The first major river to the east (ca. 90 km) of La Chacra. Tributary of the Iténez. Forms part of the departmental boundary between the Beni and Santa Cruz. Also known as the San Miguel, San Julian, and Itonamas.
San Pablo Forest	The forested region beginning just east of Casarabe and extending eastward into the Precambrian shield region. Well-known by the local inhabitants for its abundance of enormous causeways and mounds.
Sartenejal	A landscape unit characterized by small hummocks surrounded by a network of deep and narrow swales or channels. Variously attributed to livestock, earthworms, and Vertisols.
Savanna	Tropical vegetation formation with scattered trees and/or shrubs in an herbaceous matrix. Also applied to any humid to semi-arid tropical lowland vegetation without woody plants (i.e., grasslands and wetlands)
Attalea	The *motacú* palm (see above).
Semialtura	Used only by ecologists and geographers, the zone between the *altura* and the *bajío*, generally associated with the *palmar, chaparral,* or *arboleda.*
Sirionó	Formerly nomadic people of the forests east of the Moxos savannas. Presently, their major population is at Ibiato, a one-time evangelical mission.
El Sol	Ranch immediately west of La Chacra on the north side of the highway. A portion of El Sol was traded to La Chacra in 1986.
Sur, surazo	Weather events associated with polar advections during the low-sun season. Generally includes rapidly falling temperatures, strong winds, lightning storms, and precipitation.
Tajibal	Woodlands dominated by colorfully-flowered deciduous trees of the genus *Tabebuia.* The trees are often restricted to old termite mounds.
El Tajibo	The second ranch to the west of La Chacra and the first site of my explorations of Moxos in 1979. Named after the brightly flowered *tajibo* tree (*Tabebuia* spp.), a symbol of the Moxos plains. 13 km E of Trinidad.

Tapeque	Traditional carry-along lunch, usually consisting of *chipilo* (fried green plantains) and *charque* (fried sun-dried salted beef).
Terraplén	An earthen causeway. Constructed for roadways in the modern period and for water control and transportation in the pre-Hispanic period.
Totaí	A spiny-trunked palm, *Acrocomia aculeata*. Widespread in savanna regions of South America. Edible mesocarp highly desired by both humans and livestock.
Tusecal	Groves of the spiny deciduous legume *Machaerium hirtum*, usually with *Copernicia* palms and associated with *salitrales* (salt deposits in endorrheic depressions) on semialturas.
Vertisol	A soil order characterized by epipedons with a predominance of shrink-swell clays that form large cracks in the dry season and often develop a hummocky microtopography.
Yomomo	Wetlands dominated by *Cyperus giganteus*, often with floating mats of vegetation (*colchas*) which sometimes support small trees.
Zebu	A tropical species of cattle (*Bos indicus*). Introduced to South America in the late 1800's. Has largely replaced the naturalized *Criollo* cattle introduced in the 1600's. Highly resistant to heat, humidity, and parasites.

Appendix I. List of plant species identified in the region of La Chacra

Acanthaceae	
Justicia spp.	
Aesclepidiaceae	
RLP0290	
Alismataceae	
Echinodorus sp.	
Sagittaria sp.	
Amaranthaceae	
Gomphrena sp.	
Amaryllidaceae	
Hippeastrum sp.	Jarojorechi
Anacardiaceae	
Astronium fraxinifolium Schott	Cuta
Spondias mombin L.	Cedrillo
Annonaceae	
Annona dioica St. Hil.	Sinini
Rollinia herzogii R.E. Fries	Cherimoyo
Xylopia sp.	Piraquina
Apocynaceae	
Tabernaemontana benthamiana Müll. Arg.	Huevo de perro
Thevetia peruviana (Pers.) Schumann	Leche-leche
Various lianas	Bejucos
Araceae	
Anthurium sp.	Guembé
Philodendron spp.	Guembé
Pistia stratioides L.	Pochi
Bignoniaceae	
Crescentia cujete L.	Tutumo (Cult.)
Jacaranda cuspidifolia C. Martius	Tajibo morado
Tabebuia aurea (A. Silva Manso) Benth, & Hook ex S. Moore	Alcornoque
Tabebuia heptaphylla (Vell.) Toledo	Tajibo rosado
Tabebuia ochracea (Cham.) Standley	Tajibo amarillo
Tabebuia serratifolia (Valh) Nicholson	Tajibo amarillo
Various lianas	Bejucos, Cutuqui
Bixaceae	
Bixa orellana L.	Urucú (Cult.)
Bombacaceae	
Ceiba pentandra (L.) P. Gaertner	Mapajo
Chorisia speciosa A. St. Hil.	Toborochi
Pseudobombax longiflorum (C. Martius & Zucc.) Robyns	Perotó
P. marginatum (A. St. Hil., Adr. Juss. & Cambess.) Robyns	Pequí
Boraginaceae	
Cordia alliodora (Ruiz & Pavón) Oken	Picana
Cordia glabrata (C. Martius) A. DC.	Japunaqui
Cordia cf. *insignis* Cham.	Mechero

Cordia aff. *nodosa*	Picana
Cordia sellowiana Cham.	Mechero
Cordia tetrandra Aublet	Mechero
Cordia sp.	Mechero
Heliotropium indicum L.	
Tournefortia sp.	
Bromeliaceae	
Bromelia serra Grieseb.	Garabatá
Various epiphytic bromeliads	
Capparidaceae	
Cleome serratifolia Jacq.	
Cactaceae	
Cereus braunii Cárdenas	Caracoré
Opuntia brasiliensis (Willd.) Haw.	
Rhipsalis sp.	
Cannaceae	
Canna glauca L.	
Cochlospermaceae	
Cochlospermum vitifolium (Willd.) Sprengel	Retoño
Combretaceae	
Combretum fruticosum (Loefl.) Stuntz	Palo bejuco, Lagaña de perro
Combretum cf. *leprosum* Mart.	
Commelinaceae	
Commelina sp.	
Compositae	
Ambrosia eliator L.	
Bidens sp.	
Dasyphyllum sp.	
Eupatorium vitalbae DC.	
Vernonia sp. 1	Paichané
Vernonia sp. 2	Paichané
Vernonia sp. 3	Paichané
Vernonia sp. 4	Paichané
"Suffrutescent with winged stems"	
"Aster-bluish daisy"	
"Water thistle"	
Connaraceae	
Rourea sp.	
Convolulaceae	
Ipomoea carnea var. *fistulosa* (Mart. ex Choisy) D. Austin	Tararaqui
Various herbaceous spp.	
Cyperaceae	
Bulbostylis sp.	
Cyperus giganteus Vahl	Junquillo
Cyperus spp.	
Eleocharis spp.	Totorilla
Rhynchospora holoschoenoides (L.C. Rich.) Herter	Cortadera
Rhynchospora spp.	

Sceleria pterota Presl.	Cortadera
Dilleniaceae	
Tetracera parviflora (Rusby) Sleumer	Chaaco bejuco
Ebenaceae	
Diospyros cf. *tetrandra* Hiern	
Euphorbiaceae	
Croton cf. *trinitatis* Millsp.	
Dalechampsia scandens L.	
Hura crepitans L.	Ochoó
Margaritaria nobilis L. f.	Cafecillo
Sapium aereum Klotzch ex Muell. Arg.	Peloto
Sapium haematospermum Muell. Arg.	Leche-leche
Flacourtiaceae	
Casearia aculeata Jacq.	
Casearia sylvestris Sw.	
Xylosma cf. *venosum* N.E. Brit.	
Graminae	
Andropogon spp.	
Axonopus spp.	Cola de ciervo
Guadua angustifolia Kunth	Tacuara
Hymenachne amplexicaulis (Rudge) Nees	Cañuela morada
Leersia hexandra Sw.	Arrocillo
Luziola peruviana Gmel.	Cañuela blanca
Olyra sp.	
Panicum spp.	Paja toruna
Paspalum spp.	
Setaria spp.	
Sporobolus sp.	
Guttiferae	
Rheedia sp.	Achachairú
Vismia sp.	Veneno de víbora
Heliconiaceae	
Heliconia sp. 1	Patujú
Heliconia sp. 2	Patujú
Hippocrateaceae	
Salacia elliptica (C. Martius) G. Don	Guapomó
Salacia sp.	Bejuco
Labiatae	
Hyptis sp.	
Lauraceae	
Nectandra cf. *amazonum* Nees	Negrillo
Leguminosae	
Caesalpinoideae	
Bauhinia mollis (Bong.) D. Dietr.	
Bauhinia sp. 1	
Bauhinia sp. 2	
Caesalpinia pluviosa DC.	Momoqui
Copaifera reticulata Ducke	Aceite, copaibo

Hymenea courbaril L.	Paquió
Senna alata (L.) Roxb.	Mamuri
Senna hirsuta (L.) H.S. Irwin & Barneby	Mamuri
Senna occidentalis (L.) Link	Mamuri
Senna silvestris (Vell. Conc.) Irwin & Barneby	
Senna sp. 1	Mamuri
Senna sp. 2	Mamuri
Tamarindus indicus L.	Tamarindo (Cult.)
Mimosoideae	
Acacia albcorticata Burkart	Espino blanco, aromo
Acacia loretensis F. Macbr.	Cari-cari
Acacia polyphylla DC.	Cari-cari colorado
Albizia niopioides (Spruce ex Benth.) Burkart	Gebió
Anadenanthera colubrina (Vell. Conc.) Benth.	Curupaú
Enterolobium contortisiliquum (Vell. Conc.) Morong	Toco
Inga spp.	Pacay
Mimosa debilis Humb. & Bonpl. ex Willd.	Gabetillo
Mimosa pellita Humb. & Bonpl. ex Willd.	Cerrate-puta
Mimosa spp.	Espinos
Neptunia sp.	
Piptadenia robusta Pittier	Azotocó
Pithecellobium scalare Grieseb.	Juno
Pithecellobium sp.	Juno
Samanea tubulosa (Benth.) Barneby & J.W. Grimes	Penoco
Papilionoideae	
Aeschynomene sensitiva Sw.	Corcho
Aeschynomene spp.	Corcho
Desmodium spp.	Pega-pega
Dipteryx alata J. Vogel	Almendrillo
Erythrina sp. 1	Gallito
Erythrina sp. 2	Cosorió
Geoffroea striata (Willd.) Morong	Chauchachi
Lonchocarpus sp.	
Machaerium cf. *hirtum* (Vell. Conc.) Stellfield	Tusequi
Platymiscium sp.	Tarara
Swartzia jorori Harms	Jorori
Lemnaceae	
Lemna sp.	Pochi
Loranthaceae	
Psitticanthus spp.	Consuelta
Malpighiaceae	
Byrsonima sp.	
Malvaceae	
Various suffrutescent genera	Malvas
Marantaceae	
Calathea spp.	Patujú del monte
Thalia geniculata L.	Patujú

Meliaceae	
Guarea spp.	Trompillo
Trichilia spp.	Pitón
Moraceae	
Cecropia sp.	Ambaibo
Ficus cf. *caballina* Standley	Bibosi
Ficus eximia Schott	Bibosi
Ficus pertusa L. f.	Bibosi palomo
Ficus trigona L. f.	Bibosi
Ficus sp.	Bibosi
Maclura tinctoria (L.) D. Don ex Steudel	Mora
Sorocea cf. *guilleminiana* Gaudich.	
Sorocea sprucei (Baillon) J. F. Macbride	Sapito
Sorocea sp.	
Myrtaceae	
Eugenia cf. *biflora* (L.) DC.	Coca
Eugenia cf. *ligustrina*	Conservillo
Psidium guajava L.	Guayabo (Cult.)
Psidium guineense Sw.	Guayabillo
Nyctaginaceae	
Neea sp. 1	Azocaró
Neea sp. 2	
Nymphaceae	
Cabomba sp.	
Nymphaeaceae	
Nymphaea spp.	Sicuana
Onagraceae	
Ludwigia spp.	
Orchidaceae	
"Yellow palm orchid"	
Palmae	
Acrocomia aculeata (Jacq.) Lodd ex C. Martius	Totaí
Attalea phalerata Mart. ex Spreng.	Motacú
Bactris major var. *socialis*	Marayaú
Copernicia alba Morong	Palmera
Syagrus sancona Karsten	Sumuqué
Passifloraceae	
Passiflora sp. 1	Pachío
Passiflora sp. 2	Pachío
Phytolaccaceae	
Gallesia integrifolia (Sprengel) Harms	Ajo
Petiveria alliacea L.	Cutuqui
Piperaceae	
Piper sp. 1 (Isla tree)	Ambaibillo
Piper sp. 2 (Old-field subshrub)	Ambaibillo
Polygonaceae	
Coccoloba sp. 1	Pororó
Coccoloba sp. 2	Pororó

Coccoloba sp. 3	Pororó
Coccoloba sp. 4 (Savanna shrub)	
Coccoloba aff. *meissneriana* (Britton) Schumann	
Polygonum sp.	
Triplaris americana L.	Palo diablo
Pontederiaceae	
Eichhornia azurea (Sw.) Kunth	Tarope
Eichhornia crassipes (Mart.) Solms	Tarope
Pontederia subovata Seub.	Tarope
Rhamnaceae	
Rhamnidium elaeocarpum Reissek	Turere
Ziziphus sp.	Quitachiyú
Rubiaceae	
Borreria latifolia (Aubl.) K. Schum.	
Calycophyllum spruceanum (Benth.) Hook. f. ex Schumann	Guayabochi
Genipa americana L. var. *americana*	Bí
Genipa americana L. var. *caruto* (H.B.K.) Schumann	Bí
Geophila repens (L.) I.M. Johnst.	
Palicourea sp.	Sangre de toro?
Psychotria sp.	
Randia armata (Sw.) DC.	
Simira sp.? ("Shrub 5")	Palo llave?
Rutaceae	
Citrus spp.	Naranja, Toronja, Limón
Dictyloma peruviana Planchon	
Zanthoxylum spp.	Saúco
Sapindaceae	
Allophylus cf. *cinnamoneus* Radlk.	
Allophylus sp.	
Cupania sp.	
Matayba sp.	
Paullinia spp.	Bejucos
Talisia spp.	Pitón
Sapotaceae	
Pouteria torta (C. Martius) Radlk.	Aguaí
Scrophulariaceae	
Scoparia sp.	
Simaroubaceae	
Picramnia latifolia Tul.	
Smilacaceae	
Smilax sp.	
Solanaceae	
Solanum biflorum	
Solanum riparium Pers.	
Solanum cf. *sessiliflorum* Dunal	Floripondio
Solanum spp.	
Sterculiaceae	
Guazuma ulmifolia Lam.	Coco

Helicteres cf. *gardneriana* St. Hilaire & Naudin	
Sterculia cf. *apetala* (Jacq.) Karsten	Sujo
Ulmaceae	
Ampelocera ruizii Klotzsch	Blanquillo
Celtis cf. *iguanea* (Jacq.) Sarg.	Chichapí
Celtis spp.	Chichapí
Trema micrantha (L.) Blume	
Umbelliferae	
Eryngium sp.	
Hydrocotyle ranunculoides L.f.	
Urticaceae	
Urera baccifera (L.) Gaudich	Pica-pica
Verbenaceae	
Aegiphila sp.	
Lantana sp. 1 (red flowers)	Japutamo
Lantana sp. 2 (orange flowers)	Japutamo
Vitex cymosa Bert. ex Sprengel	Tarumá
Vitaceae	
Cissus sp.	
Xyridaceae	
Xyris sp.	
Zingiberaceae	
Costus sp.	Patujú del monte

Appendix II. Plant Codes used in Vegetation Plot Inventories

Aster1 (*Bidens* sp. ; Compositae)
Cherimoyo (*Rollinia herzogii* ; Annonaceae)
Cordia 1 (*Cordia glabrata* ; Boraginaceae)
Mimosa 1 (*Mimosa debilis* ; Leguminoseae, Mimosoideae)
Mimosa 2 (*Mimosa* cf. *pigra*)
Mimosa 3 (*Mimosa* sp. 1)
Shrub 1 (*Picramnia latifolia* Tul. ; Simaroubaceae). Gallery forest understory, common.
Shrub 2 = Shrub 4.
Shrub 3 = Shrub 4.
Shrub 4 (*Ampelocera ruizii* ; Ulmaceae). Shrub and tree in gallery forest. Very abundant in West Ceramic forest.

Shrub 5 (Rubiaceae). Gallery forest, woodland. No one in Santa Cruz can recognize this very abundant plant!!! (=*Simira catappifolia*?, a shrub collected by Michael Nee near the UTB or *Tocoyena*?, shrub or small tree, white hippocrateriform flower)

Shrub 6 (*Salacia* sp. ; Hippocrateaceae). Liana/shrub.
Shrub 7 = Shrub 1.
Shrub 8 (*Randia armata* (Sw.) DC. ; Rubiaceae). Gallery forest, woodland, termite islets.
Shrub 9 (*Neea* sp. ; Nyctaginaceae) = Tree 7.
Shrub 10 = Shrub 9 = Tree 11.
Shrub 11 ??? Not recognized.
Shrub 12 (*Cupania* sp. ; Sapindaceae)
Shrub 13 (*Eugenia* aff. *ligustrina*? ; Rubiaceae). Abundant in forest and islas.
Shrub 14 (Bignoniaceae). Liana.
Shrub 15 (*Psychotria*? ; Rubiaceae)
Shrub 16 (*Rourea* sp. ; Connaraceae)
Shrub 17 ???
Shrub 18 (*Tournefortia* sp. ; Boraginaceae ?)
Shrub 19 (*Rhamnidium*?)
Shrub 20 (*Paullinia* sp. (cf. *alata*?) ; Sapindaceae). Liana.
Shrub 21 (*Solanum* cf. *riparium* ; Solanaceae)
Shrub 22 (*Vismia* sp. ; Guttiferae)
Shrub 23 (Malvaceae or Tiliaceae?)
Shrub 24 = Shrub 22?
Shrub 25 (*Hyptis* sp. ; Labiatae)
Shrub 26 (*Margaritaria nobilis* ; Euphorbiaceae)
Shrub 27 ???
Shrub 28 (*Matayba* sp. ? ; Sapindaceae)
Shrub 29 ???
Shrub 30 (*Sorocea* aff. *guilleminium*? ; Moraceae)
Shrub 31 = Shrub 36.
Shrub 32 (*Allophylus* sp. ; Sapindaceae)
Shrub 33 = Tree 4.
Shrub 34 = Shrub 36.

Shrub 35 = Shrub 5.
Shrub 36 ???
Shrub 37 (*Palicourea* sp. ; Rubiaceae)
Shrub 38 (*Cordia* aff. *nodosa*? ; Borgaginaceae)
Shrub 39 (*Solanum biflorum* ; Solanaceae)
Shrub 40 (*Solanum* sp.?)
Shrub 41 (*Petiveria alliacea* ; Phytolaccaceae). Common understory element of forests.
Shrub 42 (*Tabernaemontana* sp. ; Apocynaceae)
Shrub 43 (*Casearia aculeata* ; Flacourtiaceae)
Shrub 44 (*Coccoloba* sp. ; Polygonaceae)
Shrub 45 = Shrub 5?
Shrub 46 (*Casearia aculeata* ; Flacourtiaceae)
Shrub 47 (*Cordia* sp. ; Borgaginaceae)
Shrub 48 (*Casearia sylvestris* ; Flacourtiaceae)
Shrub 49 ???
Shrub 50 = Shrub 21 (*Solanum riparium* ; Solanaceae)
Suff 1 (*Eupatorium vitalbae* DC. ; Compositae)
Suff 2 (*Cordia* sp. ; Boraginaceae)
Suff 3 (Verbenaceae or Labiatae?)
Sujo (*Sterculia* sp. ; Sterculiaceae)
Tabebuia 1 (*Tabebuia heptaphylla* ; Bignoniaceae)
Tabebuia 2 (*Tabebuia ochracea* ; Bignoniaceae)
Tree 1 (Annonaceae)
Tree 2 (*Diospyros* sp. ; Ebenaceae)
Tree 3 (Annonaceae or Lauraceae?)
Tree 4 (*Rhamnidium* sp. ; Rhamnaceae)
Tree 5 = Sujo.
Tree 6 (*Margaritaria nobilis* L.f. ; Euphorbiaceae)
Tree 7 (*Neea* sp. 1 ; Nyctaginaceae)
Tree 8 (*Swartzia* sp.; Papilionoideae)
Tree 9 (*Acacia loretensis* ; Leguminosae: Mimosoideae)
Tree 10 (*Allophylus* cf. *cinnamoneus*? ; Sapindaceae)
Tree 11 (*Cordia alliodora* ; Boraginaceae)
Tree 12 = Tree 11.
Tree 13 = Tree 4.
Tree 14 (*Platymiscium* sp. ; Leguminosae, Papilionoideae)
Tree 15 = Tree 11.
Tree 16 (*Acacia polyphylla* ; Leguminosae, Mimosoideae)
Tree 17 (*Guarea* sp. ; Meliaceae)
Tree 18 (*Trichilia* sp. ?)
Tree 19 = Tree 17?
Tree 20 = Shrub 19 = Tree 11 = *Rhamnidium* sp.?
Tree 21 (Moraceae)
Tree 22 (*Dipteryx* sp.? ; Leguminosae: Papilinoideae)
Tree 23 (*Neea* sp. 2 ; Nyctaginaceae)
Tree 24 (*Sorocea sprucei* ; Moraceae)
Tree 25 (Annonaceae?)

Appendix III. Notes on the Plants of the Region of Cañada de los Lagartos

Achachairú (*Rheedia* sp. ; Guttiferae). A small tree with a popular, sour yellow fruit (winter and early spring). Common on the wet margins of forest islands. Seeds likely distrbuted by people, other larger mammals, and large birds.

Aceite copaíbo (*Copaifera reticulata* Ducke ; Caesalpinoideae). Very hard heartwood, large diameter. A few individuals have been located in the gallery forests of the cañada.

Aguaí (*Pouteria tortum*?; Sapotaceae). Large tree with large yellow fruits. Reported from gallery forest.

Ajo (*Gallesia integrifolia* (Sprengel) Harms ; Phytolaccaceae). This garlic-scented tree of the gallery forests is typical of the semi-deciduous forests from Santa Cruz to eastern Brazil, where it is considered an indicator of good soils for agriculture.

Alcornoque (*Tabebuia aurea* (A. Silva Manso) Benth. & Hook. f. ex S. Moore, syn. *T. caraiba* (C. Martius) Bureau and *T. suberosa* Rusby) ; Bignoniaceae). A cork-barked, often gnarled tree of the savannas, with large yellow flowers in the late winter and palmate leaves and long, pendulous seedpods in the spring. Winged seeds. Flowering individual observed in March, appeared to have been recently burned. Also in Marajó, Pantanal do Mato Grosso, considered typical of the Brazilian Cerrado.

Aliso (*Vochysia divergens* Pohl ; Vochysiaceae). A rapidly-growing colonizer of the pampas, widely used for firewood. Spikes of yellow flowers. Not present at La Chacra.

Almendrillo (Leguminosae, Papilionoideae (?)). In islas of the bajío. Not observed with flowers or fruits.

Ambaibo (*Cecropia* spp. ; Moraceae). Abundant along parts of the highway and early secondary forest development, these trees are not particularily important at La Chacra. Possibly replaced ecologically by palo diablo (*Triplaris* spp.). Edible fruits, likely with numerous tiny seeds. Small ambaibos (1-2 m) are sometimes found upon flattened termite mounds in semialturas.

Azocaró (*Neea* sp. 1, Nyctanginaceae). A large tree with simple, entire, ovate, alternate leaves. Gallery forests.

Azotocó (*Piptadenia robusta* Pittier ; Mimosoideae). This larger mimosaceous tree with dark green, bi-pinnate foliage (4-7 pairs of pinnae, glands near base of petiole and and end of rachis) and magenta-tinged caterpillar-like (cylindrical spikes) inflorescences (March) is characteristic of the semialtura savannas of the region of La Chacra. Stamens ten, filaments white, then magenta. Anthers with apical gland. Grown as ornamental in Santa Cruz. This species was known only from Venezuela until material from Santa Cruz and La Chacra was identified by New York Botanical Garden specialists.

Bí (*Genipa americana* L. ; Rubiaceae). A very common tree of forest islands, gallery forests, and savanna woodlands. Large bright green leaves and deciduous yellow flowers in the spring make this tree easy to find. Edible fruit. Two varieties (*G. a.* var. *americana* and *G. a.* var. *caruto*) are present, the former being more common. This tree is common throughout the American tropical lowlands, being an important element of Amazon floodplain forest.

Bibosi (*Ficus* spp. ; Moraceae). Several species of figs go by this general name. They range from small stranglers to enormous butress-rooted forest emergents. Some of the stranglers are specific to the motacú. The giant trees are most common along low drainage ways in the gallery forest, although the forest islands also shelter them. Seeds dispersed by defecation by monkeys, bats, and birds.

Ficus eximia = *F. guaranitica*

F. pertusa L.f.

F. trigona L.f.

Blanquillo (*Ampelocera ruizii* Klotzsch ; Ulmaceae). This is a favored firewood tree, also used for axe handles. Very common In the West Ceramic Forest. Slightly butressed when larger. Bark is light beigeish-brown and somewhat scaly-shaggy. Younger individuals very common in the shrub understory.

Caracoré (*Cereus* spp. ; Cactaceae) Candelabra-type cacti, usually found on old termite mounds in semialturas. Used as a medicinal for a variety of ailments.

Cari-cari (*Acacia polyphylla* DC. and/or *A. loretensis* J.F. Macbr. ; Mimosoideae) Weakly spiny-branched tree with smooth grayish to reddish brown, somewhat squamose, bark on trunk. Whitish flowers in February. Produces large quantities of dehiscent, flat, reddish-brown legumes. Gallery forest/savanna woodland. Young individuals more sharply spined. Abundant overall, but absent from the islas of the bajío.

Cedrillo (*Spondias mombin* L. ; Anacardiaceae). "Walnut-leaved" tree with thick, deeply furrowed bark (with transient spines?) of the gallery forest/semialtura transition. Delicious orange drupes in February, eaten by monkeys. Used for refrescos. "Savanna" trees (more open, bifurcating branching pattern) not same as forest trees? (At least four *Spondias* species identified from Bolivia). *S. mombin* is a typical element of tropical deciduous forests.

Cerrate puta (*Mimosa pellita* and other spp. ; Mimosoideae). Spiny and aggressive “sensitive plant” that is a major invader of “overgrazed” semialturas and alturas. Tolerant of seasonal indundation and fire. Can form dense thickets that appear to be only temporary nuisances that eventually give way to semi-deciduous woodland and forest.

Chaaco (*Curatella americana* L. ; Dilleniaceae). TJK considers it to be a trash plant and an indicator of high water tables, but not flooded conditions. Common at Santa Fe/La Envidia along "road" and on camellones. Also present on sandhills west of Piraí. WMD found it to be abundant on camellones near Rogoaguado. Nee found it to be common on the termite mound "pimple savannas" at Flor de Oro (Río Iténez). My few encounters with this plants demonstrate an association with a *Piper* shrub (*ambaibillo*?). Not yet found at La Chacra. Anemophilous. Reported from La Chacra in "chaparral" near highway, but confused with other species, especially a related dilleniaceous vine (*Tetracera* cf. *parviflora*).

Chauchachi (*Geoffroea striata* (Willd.) Morong ; Papilionoideae). A classic and picturesque savanna-type tree, with a flat-topped, broadly spreading crown. Golden yellow faboid flowers in summer. Pinnate leaves. No spines. Semialturas. Also found in Bañados de Izozog. Woody drupe-like fruit eaten by cattle. Larger individuals found in low forest may represent old individuals which were established in former pampa environments. Also common in Chacoan gallery forests.

Chichapí (*Celtis* spp. ; Ulmaceae). Spiny shrubs with small ovate, alternate leaves and orange-red berries. Stems are "zig-zagged." Semialturas, termite mounds. This genus is widespread from temperate North America (the hackberry of Wisconsin is *Celtis occidentalis*) to temperate South America.

Chontilla or Marayaú (*Bactris* sp. ; Palmae). A common spiny understory palm of the gallery forest, flowers early spring, delicious reddish brown fruits in summer.

Cicuana (Nympahaeaceae). Water lilies. Abundant in the bajío, the cañada, and in the inundated zones of the gallery forests.

Coca (*Eugenia biflora*? ; Myrtaceae). Small tree with coca-shaped leaves and a large round edible fruit.

Coco (*Guazuma ulmifolia* Lam. ; Sterculiaceae). A very common tree or shrub in disturbed areas. Has a small, knobby, woody fruit. Flowers early spring through summer. This deciduous tree is widespread in tropical America, being found in wide range of ecological settings.

Conservilla (*Eugenia* aff. *ligustrina* (Sw.) Willd. ; Myrtaceae). An abundant shrub of gallery forest and woodlands. Waxy-looking, ovate acuminate opposite leaves with translucent points.

Consuelta (Loranthaceae). Various species of mistletoes.

Corcho (*Aeschynomene* sp.). A lanky suffrutescent denizen of the junquillares. Small sticking legumes?

Cortadera (Cyperaceae). 1) *Scleria pterota* Presl. A sharp-bladed tussock-forming sedge of the semialtura-bajío transition. 2) *Rhynchospora holoschoenoides* (L.C. Rich.) Herter ? An extremely sharp-bladed, pinkish near base, non-tussock forming sedge of deeper bajíos in summer. Often in association with *C. giganteus*.

Cosorió (*Erythrina* spp. ; Papilionoideae). Said to occur in *bajuras* (depressions) at La Chacra, but very common elsewhere.

Curupaú (*Anadenanthera colubrina* (Vell. Conc.) Benth. ; Mimosoideae; "angico" (Brazil), "cebil", Argentina) A large, bluntly-spiny mimosaceous tree of drier gallery forest alturas and the East Ceramic Forest. Bark used for tanning hides. Hard flat legumes, seed likely distributed by birds and mammals. Favored tree of the silvery marmoset (*Callithrix melanura*), which feeds upon its resin. Prado and Gibbs (1993) take this species as a paradigm for the "residual Pleistocene seasonal formations arc" distribution pattern. *A. colubrina* ranges from the Caatinga of northeastern Brazil, then through the Cerrado toward the southwest, into Misiones-Paraguay, the Pantanal, Chiquitos, Moxos, and then north to Ecuador in the drier Andean valleys and likewise south into Tucumán and eastern Catamarca in Argentina. Andrade-Lima (1982) considered this tree to be indicative of “dry region refuges” in otherwise humid regions of eastern Brazil.

Cuta (*Astronium fraxinifolium* ; Anacardiaceae). Common pinnate-leaved tree with smoother, patchy bark (grey and pinkish/reddish patches) of the savanna woodland, often upon old termite mounds. Used for firewood. Larger trees often with blackened quadrangularly-cracked bark. Seeds are wind-dispersed. Dubs (1992) considers *A. fraxinifolium* to be a cerradao element.

Espino blanco (*Acacia albicorticata* Burkart ; Mimosoideae = "Aromo"?). A common ruderal tree, somewhat similar to "juno" when larger. Semialturas and artificially cleared alturas. The barks is papery and peeling, likely an adaptation for rapid burning at lower temperatures.

Floripondio (*Solanum* aff. *sessiliflorum*? ; Solanaceae) A small, thorny tree with large purple flowers (Sep.) and a green tomato-like fruit. Forest islands. Fruit probably eaten by mammals (foxes, maned wolves?).

Gabetillo (*Mimosa debilis* ; Leguminosae, Mimosoideae). Pink-flowered spiny sub-shrub with dichotomously pinnate leaves. Very abundant on semialturas during the summer, but invisible during the winter.

Gallito (*Erythrina* sp. ; Papilionoideae) A spiny red-orange flowered legume tree common along roadsides and wet areas. Reported, but not observed at La Chacra.

Garabatá (*Bromelia serra* ; Bromeliaceae). An unpleasantly spiny terrestrial bromeliad that often creates dense thickets in forest edges. Can be found in clumps in palmares or semialtura savanna, sometimes upon flattened mounds. Fruit used to make *refresco*.

Gebió (Mimosaceae, *Albizia niopoides* (Spruce ex Benth.) Burkart, also *A. hassleri*?). Smooth to bumpy-barked trees with finely bi-pinnate leaves and no spines. Gallery forest and woodlands. Also in Pantanal do Mato Grosso (semi-deciduous forest and cerradao). Kubitzki (1989) considers *A. niopoides* to be a typical element of white-water várzea forests in central Amazonia. *A. hassleri* is found largely in southern Brazil.

Guapomó (*Salacia elliptica* ; Hippocrateaceae). Forest islands. Edible fruit. Also in cerradao forest in Pantanal do Matto Grosso. *Salacia* also has some woody liana forms.

Guayabillo (*Psidium* spp. ; Myrtaceae). Common ruderal shrub. Edible fruit with many small, hard seeds.

Guayabochi (*Calycophyllum spruceanum* (Benth.) Hook f. ex Schumann. ; Rubiaceae). The peeling reddish bark and the smooth greenish trunk of this tree are easily identifiable in many parts of the gallery forests. Navarro calls it an indicator of humid Amazonian forests. Wood is said to be very hard and used as firewood, even when green. Abundant in SE gallery forest near La Providencia. Also a pioneer tree in flooded semialtura savanna (also in the Humaitá savannas of Brazil, Janssen 1986). Flowers in May, fruits wind dispersed. Common in central Amazonia.

Guayumequi (*Albizia*? *Pithecellobium*? ; Mimosoideae). A finely-pinnate leaved leguminous tree, without spines. Two kinds, one along streams and one in the alturas. Flowers in summer.

Huevo de perro (*Tabernaemontana benthamiana* Müll. Arg. ; Apocynaceae). Tree with shiny dark green leaves, somewhat similar to *Genipa*. Fruits like a dog's scrotum with bright red seeds and white latex. Disturbed savanna and gallery forest.

Japunaqui (*Cordia glabrata* (C. Martius) A. DC. ; Boraginaceae). A simple, glabrous, deciduous-leaved tree with large numbers of white tubular flowers in dense corymbs, which turn reddish brown and helicopter to the ground. The adaxial side of the leaf is characteristically silvery. This tree is abundant in the semialtura savanna woodlands and also as a colonizer of roadsides. The fruits are carried by the wind, the dessicated petals serving as helicopter wings. Also in Pantanal do Mato Grosso (semi-deciduous forest), all the way to northeastern Brazil.

Jarajorechi (*Hippeastrum*? ; Amyrillidaceae). A pretty red lily that blooms in the winter in spring in open gallery forest and semialturas.

Quitachiyú (*Ziziphus* sp. ?) A spiny shrub with white edible fruits. This plant is largely ruderal and an element of the Chaco.

Jorori (*Swartzia jorori* Harms ; Papilionoideae). A small ("guatoquingo") leguminous tree with a bizarre red brain-like mesocarp on the seeds. Savanna woodlands. Not common at La Chacra, but typical of Moxos savannas and woodlands elsewhere.

Juno (*Pithecellobium scalare* Griesb. = *P. tortum* ; Mimosoideae) A common corky-barked savanna tree. Wood said to smell like "menjunje" (that's shit for you and me). Some branches have pairs of short spines, some don't. Flowers in March.

Junquillo (*Cyperus giganteus* ; Cyperaceae). A papyrus-like sedge that creates often vast stands in the wetter portions of bajíos, curiches, cañadas, and lake margins. These formations are often referred to as yomomos. These plants respond well to burning. The stands are composed of individual (likely clonal) clumps of junquillo, which form slight mounds. The clumps are separated by cattle trails and other openings. The soils of the junquillares are generally highly organic, spongy, and permanently wet.

Leche-leche (*Sapium haematospermum* = *S. longifolium* ; Euphorbiaceae). Shrub to tree, linear leaves with a pair of glands near apice of petiole, abundant white latex. Often on termite mounds. Also in Pantanal do Mato Grosso.

Leche-leche (*Thevetia peruviana* ; Apocynaceae). Subshrub to tree with large yellow flowers, linear leaves, and abundant white latex. Along the "floodplain" of the cañada. The leaves and flowers fold up each evening, reopening in the morning.

Mapajo (*Ceiba pentandra* (L.) P. Gaertner (?) ; Bombacaceae). A taller tree with a dark, squarish, spiny trunk. Gallery forest, forest islands, savanna woodlands. Also in Orinoco. This fast-growing tree was introduced to western Africa, where it has become a major invader of savannas under fire suppression. This tree is definitely a *Ceiba*; however there is no real evidence that it is *C. pentandra*. Other workers in Beni may have assigned these trees on the basis of tradition. According to the literature, *C. pentandra* is widespread in the Neotropical lowlands in both the Amazonian Hylaea as well as in dry forest formations. I have not observed large, buttress-rooted specimens of *Ceiba* at La Chacra; nevertheless there are many mature trees as well as saplings. These trees produce large quantities of cotton-tufted black seeds borne in large pods. The ground of the gallery forest near these tree is littered white after seedfall in the early dry season (observed July 1993).

Mechero (*Cordia* spp.). Several species of shrubs and small trees with large ovate entire pubescent leaves. Sweet, grape-like greenish white drupaceous fruits (winter, summer) with largish woody seeds. Disturbed savanna. Several species of the genus *Cordia* (*C. corymbosa*?, *C. insignis*?).

C. tetrandra Aublet = tree mechero?

C. sellowiana = tree mechero?

Momoqui (*Caesalpinia pluviosa* DC = *C. peltophoroides* ; Caesalpinoideae.). Gallery forests in association with *Anadenanthera*.

Mora (*Maclura tinctoria* (L.) D. Don ex Steudel ; Moraceae). Light-barked, straight-trunked gallery forest tree with *Morus*-like dentate leaves and spines on short twigs. Common in Chacoan gallery forests, but widespread throughout lowland tropical America.

Motacú (*Attalea phalerata* Mart. ex Spreng. ; Palmae). The typical palm of gallery forests and islas. In the savannas near San Ignacio, motacú palms can be found either in small clumps or individually in apparently natural pampas. Likewise, we find motacú in the leaf-cutter ant mound islands in the pampas of Santa Cruz (El Cedrito, Viru-Viru). Motacú are also dominants in many smaller islas in the pampas, on abandoned causeways and raised fields, in gallery forests, and as relict forests elements in anthropogenic grasslands. Motacú fruits are large and heavy, yet widely dispersed by animals (TJK thinks that cows eat'm and shit'm. I agree.) and humans. Motacú, however, are notably absent on heavy clay soils and permanently wet sites, being replaced in the former situation by *Copernicia* (and in the latter by *Mauritia*?).

Negrillo (*Nectandra* spp. Lauraceae). Aromatic ("huele lindo" to some, but “hediondo” to others) tree of gallery forest bajuras and along edge of islas in the bajíos, a tree that appears to lie on its side, with numerous small, sweet-smelling white flowers in early spring (late Sept-Oct).

Ochoó (*Hura crepitans* L. ; Euphorbiaceae). This is a large spiny-trunked tree of low-lying, seasonally-flooded gallery forest at La Chacra. This tree is deciduous, but is typical of flooded forests throughout Amazonia and ranges as far north as Mexico. This species appears to be reproducing successfully, as a wide range of tree sizes can be found in a small area. The characteristic leaves of the ochoó dominate the leaf litter composition where the tree is found. At La Chacra, the tree is apparently restricted to a rather limited area of the gallery forest. The root system of the ochoó has thick woody roots that spread widely across the surface and influence the geomorphology by creating barriers and diverisions to surface flows and deposition. According to a 1993 survey, this is third most important timber species in Bolivia. The male inflorescence is "fleshy," red, and closely resembles the fruit of the *Morus*! I found a second ochoó site near the pampa edge of the north gallery forest toward La Providencia.

Pacay (*Inga* spp.; Mimosoideae). These small trees and shrubs are common elements of forest island and gallery forest edges and as isolated individuals in flooded semialtura savanna. They produce sweet fruits. Cultivated species are common in the Andes, but not in the lowlands. Their leaves are winged.

Paichané (*Vernonia* spp.; Compositae). Aromatic composite shrubs which often indicate poor range management practices. Common in semialtura woodland savanna and on termite mounds.

Palmera (*Copernicia alba* C. Martius ex Endl. ; Palmae). Large numbers of these fan palms are harvested for their trunks, which are widely used for posts and construction materials. Split logs are often used as roofing materials. On one occasion, 90 palms were taken for 10-m posts for a mining project in Oruro. 3-m posts are more often taken and used for fence posts. In spite of the cutting which kills the palm, these palms are still abundant and can form extensive stands, such as those on the north side of the bajío in Cáceres. It is believced that repeated burning creates a more durable palm log. Copernicia palms apparently are most abundant on clayey soils with intermediate inundation (semialturas). The diameter and height of the trunk is highly variable and seems dependent on environmental factors. Palms from the gallery forest may be very tall and thin, while cultivated palms in gardens can have extraodinarily thick (>50 cm basal diameter?), stout trunks. Often, these palms are found in small clumps upon termite mounds, with the trunks sometimes nearly horizontal before curving upwards. Dead, hollow Copernicia are probably valuable nesting sites for many birds, including macaws and parrots. The distribution of this palm in Bolivia would present a very informative map. Herzog (1923) erroneously considered this typical palm of Moxos as Mauritia, which does not coexist with Copernicia.

Copernicia is the typical savanna palm of east of the Mamoré, while being of more restricted occurence to the west, although common at Espíritu on the Río Yacuma. Travelling from the east along the Santa Cruz highway, these palms are not frequent until one nears Casarabe.

The distribution of *Copernicia* seems positively correlated with the presence of clayey soils near the surface. These palms are indicators of what has been termed *semialtura*, but occur in three general situations. The first is as an element of a rather open forest or woodland with numerous hardwood species; the second is scattered in open pampa, and the third is dense *palmares*, where they are the sole element. *Islas de semialtura* also exist in the pampas. Beck suggested that these may be eroded remanant of *alturas*; however, they may also represent pampa soils that have experienced changes in local drainage and flooding parameters. Replaced in Orinoco by *C. tectorum*.

Palo bejuco (*Combretum fruticosum* ; Combretaceae). An important invader and thicket former on semialtura pastures.

Palo diablo (*Triplaris* spp.; Polygonaceae). One of the banes of the forest, this tree is the home of inordinately aggressive *Pseudomyrmex* ants, which pack a powerful sting. In the early spring, the palo diablo is aflame with pinkish to reddish trimerous flowers which helicopter to the ground. Although very common in the gallery forests, this tree is pleasantly uncommon in the forest islands.

Palo llave (Shrub 5 ? ; Rubiaceae) An abundant shrub of the gallery forest understory and semialtura woodlands and forest nuclei.

Palo María (*Callophylum brasiliense* Cambess. ; Guttiferae). Wide-spread gallery forest tree harvested for lumber. Not present at La Chacra, but common nearby.

Paquió (*Hymenaea courbaril* L. ; Caesalpinoideae). At La Chacra, this largish tree is restricted to the gallery forest, not being found in the savannas. Leaves are shaped like a cow's hoof. The mealy yellow mass of the fruit is eaten. Also in Orinoco, Pantanal do Mato Grosso.

Patujú (*Heliconia* spp.; Heliconiaceae). Found in wet depressions in the gallery forest. Not common at La Chacra, but elsewhere very abundant locally. Often forms border between forest and wet savanna. Also *Calathea, Canna, Costus,* and *Thalia*.

Peloto (*Sapium glandulosum* = *S. aerum* ; Euphorbiaceae). A common tree in gallery forests, tall, narrow form with ficus-like leaves. Bark is light-colored and has longitudinal ridges. Latex used to make rubber balls.

Pequí (*Pseudobombax marginatum* A. St. Hil., Adr. Juss. & Cambess. ; Bombacaceae). Large 7+ palmate, ambaibo-like leaves, whitish (apetalous?) flowers with numerous long stamens. Wood is bright blood red beneath bark. SE gallery forest. Also in Pantanal do Mato Grosso (semi-deciduous forest and cerradao).

Perotó (*Pseudobombax longiflorum* (C. Martius & Zucc.) Robyns ; Bombacaceae) is a classic savanna tree, with a thick whitish cork bark, stout branches and twigs, and completely deciduous leaves. Its distribution, however, seem rather localized. I have observed it south and west of San Ignacio, but not in the Trinidad region (however the toponym "Perotó" is fairly common elsewhere). Michel found it to be characterisic of abandoned raised fields at El Villar. TJK: "only very small ones (i.e. shrubs) around San Borja). This tree occurs in the semialtura savanna near the forest edge in the far eastern region of La Chacra.

Penoco (*Samanea tubulosa*, formerly known as *Pithecellobium saman.* ; Mimosoideae) is a common element of disturbed savannas, roadsides, palmares, and islas. It has a corky, fire-resistant bark and produces large quantities of sickeningly sweet smelling legumes. Pink mimosaceacous flowers (spring, summer). Seed dispersed by cattle. Its sister species, *S. saman*, is the “rain tree” of Central America.

Picana (*Cordia alliodora* (Ruíz & Pavón) Oken, *Cordia nodosa* Lam. ; Boraginaceae). An abundant tree and shrub of the gallery forests and woodlands. Lanceolate to lanceovate, scabrous leaves, spiral phyllotaxy (?). Characteristic branching pattern with an inflated node in th center containing stinging black ants. Larger trees with dark reddish brown squamose bark. May be several species. *C. alliodora* has smaller flowers (May-June) than *C. glabrata* (August-October), but they are still showy. *C. alliodora* considered to be a complex with *C. trichotoma* (Prado and Gibbs 1993).

Pica-pica (*Urera baccifera* (L.) Gaudich ; Urticaceae). Herbaceous to woody stinging, spiny-stemmed nettles. Common in clearings of West Ceramic Forest and Isla 2.

Piraquina (*Xylopia* sp. ; Annonaceae). Gallery forest tree,

Pitón (*Trichilia* ; Meliaceae, *Talisia* ; Sapindaceae). Trees and shrubs with yellow to orange edible fruit, islas and termite mounds.

Pororó (*Coccoloba* spp. ; Polygonaceae). Common tree of isla. Shrubby species are common on the semialturas. “Fruit” is composed of fleshy calyx which surrounds the hard achene. Bark is rough and leaves are somewhat leathery (somewhat resembling smallish *Curatella* leaves). A round-leafed species is common on termite mounds in savannas. There is a lanceolate-leaved, multiple-trunked species (*C.* aff. *meissneriana*?) which spreads over termite islets.

Sapito (*Sorocea sprucei* (Baillon) J.F. Macbr. ; Moraceae). A common shrub/small tree of savannas and islas with sclerophyllous scrub oak-like leaves and white latex. There are at least two other larger-leaved *Sorocea* species at La Chacra, one a shrub and the other a medium- sized tree.

Saúco (*Zanthoxylum* sp. ; Rutaceae). A spiny-trunked tree with largish pinnate leaves and small fragrant white flowers (May). Pioneer tree in semialtura mounds. Gallery forest, semialtura woodland, and islas.

Sujo (*Sterculia apetala* (Jacq.) Karsten. ; Sterculiaceae). This weakly butress-based tree with large trilobate, deciduous leaves is common in forest islands, gallery forests, and semialtura woodlands where it may create small groves, often growing to great heights (at least 27 m). Also known as *maní*, this tree produces edible seeds enclosed in a woody pod. The branches are usually restricted to the upper canopy. Flowers and friuts in summer to late fall. *S. apetela* also in Orinoco. Considered to be closely related, if not synonomous to *S. chicha* (Lorenzi 1992). *S. striata* also in Pantanal do Mato Grosso and in mesotrophic forest patches throughout the greater Cerrado region ("calcicolous species" Dubs 1992).

Sumuqué (*Syagrus sancona* Karsten ; Palmae) Common palm in gallery forests with thin-skinned, orange fruits that taste somewhat fermented and leave a pleasant warm feeling in the back of the throat (early spring). The Sirionó make chicha (“muy amarga”) with its fruit.

Tajibo (*Tabebuia* spp. ; Bignoniaceae). These trees are deciduous and bear great quantities of birght flowers. They are most common on semialturas and were not identified on any islas at La Chacra. They leaf out rapidly in early spring. These trees are among the most characteristic of the Bolivian Oriente. They are commonly represented on local artwork and handicrafts.

1. *T. heptaphylla.* 3-5 small, nearly entire to serrate, glabrous leaflets, pink flowers, termite mounds.

2. *T. ochracea.* 3-5 densely pubescent, larger leaflets, bark corky, savanna woodlands, yellow flowers.

3. *T. serratifolia.* 4-5 large, entire to serrate leaflets, bark somewhat furrowed, not corky, larger trees of gallery forests and savanna woodlands. Reported to have white flowers?

4. *T. aurea* (Formerly *T. caraiba* and *T. suberosa*). A tree with very corky bark, often a gnarled physiognomy, large bright yellow flowers, and large leaves. Not considered to be a tajibo, bur rather is called the alcornoque (due to its corky bark).

Tajibo morado (*Jacaranda cuspidifolia* C. Martius ; Bignoniaceae). A small to large tree of the gallery forest and semialtura woodland, with large purple flowers, light-colored bark, and opposite bipinnate leaves. Also in Pantanal do Mato Grosso. *Jacaranda* are considered to be heliophiles which are regenerated only by seed in open environments (Hartshorn 1989).

Tarara (*Platymiscium* sp. ; Papilionoideae) Savanna woodland, dark green pinnate, whorled (in threes) leaves. Smaller tree.

Tararaqui (*Ipomoea carnea* ; Convolvulaceae). Common weed in seasonally inundated places. Toxic to livestock. Often occurs on the margins of degraded islas, especially in semialturas. Also common at Marajó.

Tarope (*Eichhornia* spp. ; Pontederidaceae). Found in the deeper portions of the bajío, cañadas, curiches, pozas, and other bodies of water.

Tarope (*Pontederia subovata* ; Pontederiaceae). Very abundant bajío plant, a close relative of the water hyacinth (*Eichhornia*).

Tarumá (*Vitex cymosa* Bert. ex Sprengel ; Verbenaceae) is a common, sometimes large, deciduous tree of islas, gallery forest, and open woodland. Beck says it is typical of fine-sandy alturas. This tree has blue-violet flowers ca 1 cm long that attract a lot of bees during late August and September. The leaves are palmate and acuminate. The wood is used for firewood at La Chacra. Also common as a shrubby element of palmares along with bí. Fruits are said to be highly variable in flavor, but often considered quite edible by humans. May be more than one species at La Chacra. Replaced in Orinoco by *V. capitata* or *orinocensis*. Also in Pantanal do Mato Grosso (“calcicolous species more typical of forest" Dubs 1992).

Toco (*Enterolobium contortisiliquum* (Vell. Conc.) Morong ; Mimosoideae). Bark is reddish on younger trees, black on large trees, leaflets sowewhat angular in appearance. Savanna woodlands and gallery forests. Fruits are toxic to cattle, but eaten by capibaras. Local ranchers claim that animals suffer from severe skin lesions as the result of consuming the fruits. When capybaras population are reduced by shooting, then toco populations increase and cattle suffer. This trunk of this tree reaches great diameters (more than 1.2 m) in old gallery forest trees; greatest DBH of any tree measured at La Chacra, except for the large buttress-rooted *Ficus*.

Totaí (*Acrocomia aculeata* (Jacq.) Lodd. ex C. Martius, = *A. totai* C. Martius = *A. sclerocarpa* Mart.? ; Palmae). Widespread, but not particularily abundant spiny-trunked palm with popular yellow-orange fruit known as "chicle camba." The fronds are harvested and fed to horses. Recruitment appears to be reduced by livestock browsing. Replaced in Orinoco by *A. sclerocarpa* (which may actually be synonymous).

Trompillo (*Guarea* spp. ; Meliaceae). Abundant pinnate-leaved trees in the islas del bajío. Fruits edible.

Turere (*Rhamnidium elaeocarpum* Reissek ; Rhamnaceae). Shrub or tree with dark, opposite, entire, simple, lanceolate, strongly-veined leaves, purple to black fruits. Common on termite mounds. Also in Pantanal do Mato Grosso.

Tusequi (*Machaerium hirtum* (Vell. Conc.) Stellfield ; Papilionoideae). Common along roadsides, on termite mounds, and in salitrales. Ashes once used to make soap.

Additional Notes on the Palms of La Chacra

There are five genera of palms present at La Chacra: *Acrocomia, Bactris, Copernicia, Attalea*, and *Syagrus*, not including the cultivated *Cocos*. Each of these palms has rather different ecological characteristics and human uses.

Acrocomia aculeata (totaí) is a characteristic palm of the Bolivian lowlands and the savanna/semideciduous forest zones of South America in general. The low rate of *Acrocomia* recruitment at La Chacra is likely the result of high levels of browsing by horses. At Ibiato, where livestock populations are neglible, there are abundant juvenile *Acrocomia* in the semialturas. *Acrocomia* fronds are widely harvested for animal fodder in eastern Bolivia. The juvenile fronds, although armed with long spines on the midrib, are attractive food items for hungry horses, especially during the dry season. The adult trees produce large quanties of fruits (sometimes referred to as *chicle camba* or “camba chewing gum”), whose moist mesocarp is consumed by humans and other animals. The seeds, however, are very hard and can be broken only with the force of a hammer blow. These seeds are frequently attacked by beetle larvae. Both the seeds (*carlucha*) and the grubs are consumed by humans.

The adult *Acrocomia* palms on the semialturas at La Chacra might be considered as “living dead” under the present herbivory regime, doomed to die without reproducing themselves. However, the horses not enter the forest, which may indeed function as a “refuge” for palm reproduction.

Bactris major var. *sociabilis*. (“marayaú”) is an important understory component of certain zones of the gallery forest, especially on the anthropogenic surfaces. These small palms (<3 m high, <5 cm dbh) are extremely spiny, both on the stems and frond midribs. They produce large amounts of fruits which are very attractive to people and presumably to other animals. These palms generally exist in small clumps, presumably formed by a group of clones. They are usually associated with *Attalea* palms, which are an important component of the overstory. Rarely, *Bactris* can be found along the forest edge or forming small thickets in the open.

Copernicia alba and *Attalea phalerata* are the most important palms of much of eastern Bolivia. They certainly deserve chapters of their own! These palms are very different in both morphology and ecology, thus are useful indicators of environmental conditions.

Attalea phalerata (motacú) is the most important palm of the forests of Moxos. In the more humid Madre de Dios region of Peru, this palm has been considered a common invader of pastures (Kahn and de Granville 1992, p. 82). This palm is also characteristic of the capões forest islands of the Pantanal of the upper Paraguay where it is known as the acuri.

Syagrus sancona (sumuqué) is a locally dominant, taller palm of the gallery forest and woodlands. The anthers and pollen of this palm carpet the ground and give off a pleasant aroma during the wet season. The orange fruits have a thin exocarp and the mesocarp is rather juicy and generally has a rather fermented flavor. Howler monkeys appear to be especially fond of these fruits. The stem is smooth and thin (generally <30 cm dbh), with the fronds and apical meristem elevated into the forest canopy. This palm is not generally cut or used for any purpose at La Chacra. *Syagrus* appears to fare well under forest fires and is occasionally found in more open woodlands. Elsewhere in South America, other *Syagrus* species are typical of more arid environments and are often acaulescent. On the low and watery surfaces south of the cañada, there are patches of forest where *Syagrus sancona* and *Calycophyllum spruceanum* are the visual dominants.

Kahn and de Granville (1992, p. 89) classify forests co-dominated by *Attalea phalerata* and *Syagrus sancona* as “secondary forest and deforested areas; southern region [of Amazonia].” Although this may is sometimes true, it is difficult to claim that all of the *Attalea-Syagrus* gallery forest at La Chacra (and for that matter all of Eastern Bolivia) as “secondary forest.” This implies some past disturbance and regrowth which deflected development of “primary forest.” Perhaps it would be better to think of these as forests with periodical fires and livestock impacts. These authors (p. 11) also consider these palms to be “particularly abundant in the drier forests and savannahs.”

Typical “Amazonian” palms present in the “terra firme” forest in the northern part of the Beni Department (see Boom 1986) such as *Astrocaryum*, *Euterpe*, *Geonoma*, *Iriartea*, *Jessenia*, *Maximiliana*, *Oenocarpus*, and *Socratea* are absent from the forests in the immediate Chacra region.

Appendix IV. Annotated List of the Vertebrates Identified at La Chacra and its vicinity.

Osteichthyes (Bony Fish)

Callichthyidae

Hoplosternum littorale. Simbao.

Lepthoplosternum beni. Buchere? Small catfish observed in mud of drying bajío.

Erythrinidae

Hoplerythrinus unitaeniatus. Yeyú. Inundated pampa.

Hoplias malabaricus. Bentón. Cañada, channels in gallery forest. Adults estivate in mud during winter and rapidly appear en masse in with the spring rains. Delicious source of protein. Easily caught on hook and line.

Serrasalmidae

Serrasalmus nattereri. Palmometa, yellow-bellied piranha. Abundant in Laguna Santa Rosa.

Synbranchidae

Synbranchus sp. Small brown eel found in muddy pampa.

Amphibia

Bufonidae (Toads)

Bufo granulosus. Common at night around house.

Bufo marinus group. Found under wood in grassy area behind Isla #2.

Bufo paracnemis. Common around the house at night.

Bufo typhonius group sp. 1. Found on forest floor in afternoon of early spring.

Bufo typhonius group sp. 2.

"Sapo bora" A giant toad? One was reported to be found eating an *Ameiva* near Loma 1,

Epipedobates pictus. Poison arrow frog. Common, diurnal, found under wood in channel and on forest floor.

Leptodactylidae

Leptodactylus spp. All environments. Various species.

Hylidae (Tree frogs)

Scinax rubra group. Found most often in the toilet and on bathroom walls.

Hyla spp. All environments, including on the corrals and in the inundated bajío.

Microhylidae

Elachistocleis ovalis. Observed in gallery forest and termite mounds.

Pseudidae

Lysapsus limellus. Very abundant small frog in bajíos and semialtura depressions.

Reptilia

Sauria (Lizards)

Tropiduridae

Chupacoto (*Tropidurus spinulosus*). Difficult to encounter when not in corrals, one juvenile observed on termite mound in semialtura savanna (February), one adult observed on a cari-cari along the cañada (March).

Teiidae

Jaúsi (*Ameiva ameiva*). Forest islands, gallery forest. Terrestrial.

Peni (*Tupinambis teguixin*). Gallery forest. Terrestrial.

Serpentes (Snakes)

Boidae

Eunectes murinus. Anaconda, sicurí. Common in wetlands, watercourses, and forest islands.

Colubridae

Víbora lonja (*Hydrodynastes gigas*). 2+ m. The "false water cobra." Abundant in forest islands of the *bajío*. Semiaquatic, hides in holes in ground under the bases of trees and logs.

Culebra (*Drymarchon corais*). A larger yellow snake, common in the forests. Same species as the North American indigo snake.

Jichi-mora (*Liophis* sp.). A common small, completely inoffensive snake often encountered around the house.

(*Liophis* sp.?). 50 cm. A bright green diurnal terrestrial snake of the bajío. Observed in open grass in mid-afternoon, also on bench near house.

Philodryas sp. ?. 1.5 m. A terrestrial snake of the gallery forest with an olive green dorsum and yellow venter. Long, narrow neck, relatively small head and large eyes. Appears to have distinct vertbral ridge. Scales large and smooth, 13 rows? Rapid movements on ground with head held erect. Observed in late afternoon. Same species also found at Palmar del Oratorio, Santa Cruz. Frequents termite mound trees and shrubs.

Crocodylia

Caiman yacare. Yacare caiman. Largarto. Abundant in artificial ponds and deep sections of the cañada. Reported to pass the dry winter dormant in mud. In wet season, found in the indundated pampas and semialturas. Can be dangerous if accidentally stepped upon (as my assistant Armando did). Nest with egg shells found on small island in inundated prehistoric canals near the big paquió.

Chelonia

Geochelone carbonaria. Peta, jaboty tortoise. Gallery forest. Hunted for meat by residents of La Chacra. Red -legged, light-shelled juvenile (ca. 6 cm) found in *Bromelia serra* thicket in *Anadenanthera colubrina* forest (26.II.94).

Phrynops geoffroanus. Dead and partially eaten individual encountered in gallery forest (2.IX.93).

Aves

Bird taxonomy follows Remsen and Traylor (1989) and Meyer de Schauensee (1970). All identifications are based on sightings I made in the field. Some entire families of small, cryptic, or difficult taxa are omitted completely from the following record.

Rheidae (Rheas)

Piyu (*Rhea americana*). Semialturas, bajíos, islas. Flocks (or subadults with parent) in summer. A group of 15 was observed near the potreros of the Chacra. Found in junquillares and islas del bajío even in the deepest water of the summer. They can run well through deep water and dense aquatic vegetation. Not hindered by fences. They sometimes killed for their gizzards (*churiqui de piyu*), which are sold in town for medicinal purposes ($150 bs each in early 1994). This large bird is an important for dispersal for semialtura and isla de bajío species. Local informants claim that rheas are especially fond of the fruits of *Vitex cymosa.*

Tinamidae (Tinamous)

Unidentified species.

Anhingidae (Anhingas)

Anhinga anhinga.
Ardeidae (Herons)
Tigrisoma lineatum. Rufescent Tiger-Heron.
Ardea cocoi. Cocoi Heron.
Bulbucus ibis. Cattle Egret.
Egretta thula. Snowy Egret.
Casmerodius albus. Great Egret.
Agamia agami. Chestnut-bellied Heron.
Nycticorax nycticorax. Black-crowned Night-Heron.
Threskiornithidae (Ibises)
Phimosus infuscatus. Bare-faced Ibis.
Theristicus caerulescens. Plumbeus Ibis.
Theristicus caudatus. Buff-necked Ibis.
Mesembrinibis cayennensis. Green Ibis.
Platalea ajaja. Roseate Spoonbill.
Ciconiidae (Storks)
Mycteria americana. Wood stork. Cabeza seca.
Ciconia maguari. Maguari stork.
Jabiru mycteria. Jabiru stork. Bato colorao. Nests in islas in winter.
Cathartidae (American vultures)

Coragyps atratus. Black Vulture. Sucha. Black vultures seem to congregate from diverse and distant locations when there is a large dead animal to feed upon. A dead mare attracted perhaps 200 individuals where none had been previously observed.

Anhimidae (Screamers)

Chauna torquata. Southern Screamer. Tapacaré. Congregates in flocks in winter (10-15 birds).

Anatidae (Ducks)
Dendrocygna spp. Whistling ducks. Putirí. Observed near artificial ponds in summer.

Cairina moschata. Muscovy duck (wild type). Pato negro. Observed near artificial ponds in summer.

Accipitridae (Hawks and Kites)
Elanus caeruleus. Black-shouldered Kite.
Rostrhamus sociabilis. Snail kite.
Busarellus nigricollis. Black-collared hawk. Nests in Isla #2.
Various unidentified hawks. Collectively referred to as “Chuubis.”
Falconidae (Falcons)

Polyborus plancus. Crested Caracara. Carcaña. Common in semialtura woodland, forest edges, islas.

Various unidentified falcons.
Cracidae (Guans, Chacalacas)
Ortalis motmot. Speckled Chachalaca.
Penolope jacquacu. Spix’s Guan.
Rallidae (Rails)
Various species.
Eurypygidae (Subitterns)
Eurypyga helias. Sunbittern.
Aramidae (Limpkins)
Aramus guarauna. Limpkin. Carau.

Charadriidae (Plovers)

Vanellus chilensis. Southern Lapwing. Leque-leque, Tero-tero.

Charadrius collaris. Collared Plover.

Recurvostridae (Avocets)

Himantopus mexicanus. Black-necked Stilt.

Jacanidae (Jacanas)

Jacana jacana. Wattled Jacana. Gallareta. One of the most common birds of the Moxos wetlands and cañadas.

Scolopacidae (Sandpipers)

Various species.

Columbidae (Pigeons)

Various species of doves known as torcazas or chai..

Psitaccidae (Parrots)

Ara ararauna, paraba, blue and gold macaw.

Ara glaucogularis. An edangered, endemic species of the eastern Llanos de Moxos savannas. Nests only in *Attalea*-dominated islas, not in gallery forests. Not observed at La Chacra, but likely to be present locally.

Various other species species of smaller macaws, parrots, and parakeets.

Cuculidae (Cuckoos)

Crotophagus major. Greater Ani. Tordo. Abundant.

Nyctibiidae (Potoos)

Nyctibeus grisaceous. Common Potoo. Guajojó.

Caprimulgidae (Nightjars)

Chordeiles sp. Nighthawk.

Caprimulgus spp. Nightjars.

Hydropsalis brasiliana. Scissor-tailed Nightjar. Cuyabo.

Trochilidae (Hummingbirds)

Various species.

Trogonidae (Trogons)

Trogon sp. Trogon. One individual observed in Isla #4a (AUG-93)

Alcedinidae (Kingfishers)

Ceryle torquata. Ringed Kingfisher.

Chloroceryle spp. Kingfishers.

Galbulidae (Jacamars)

Galbula ruficauda. Rufous-tailed Jacamar.

Rhamphastidae (Toucans)

Rhamphastos toco. Toco Toucan. Tucán. Observed in Isla #2.

Various other smaller toucanets or aracaris.

Picidae (Woodpeckers)

Colaptes campestris. Campo flicker.

Various species of woodpeckers.

Dendrocolaptidae (Woodcreepers)

Various species.

Furnariidae (Ovenbirds)

Furnarius rufus. Ovenbird. Tiluchi or Hornero. Very common throughout the savannas, farmlands, and cities of Beni and Santa Cruz. One of the symbols of the region. Builds oven-like nests of mud.

Various other genera.

Tyrranidae (Tyrant flycatchers)

Pyrrhocephalus rubinus. Vermillion Flycatcher. Hijo del Sol.

Pitangus sulphuratus. Greater Kiskidee. Frío. Very common.

Various other genera of Flycatchers.

Fringillidae (Seed-eaters)

Paroaria coronata. Red-crested Cardinal. Cardenal.

Many other genera.

Icteridae (Blackbirds)

Psarocolius decumanus (or *Cacicus cela*?). Crested Oropendola. Tojo. A common large and noisy icterid that builds large hanging nests in large trees such as *Ficus.*

Mammalia

Rodentia

Sciuridae (Squirrels)

Sciurus sp. Masi. A red squirrel that feeds on motacú fruits. Gallery forest. Not considered good eating becaues it smells like motacú oil.

Dasyproctidae (Agoutis)

Dasyprocta sp. Agouti, jochi colorao, jochi carlucha. An abundant diurnal rodent of the gallery forest and woodlands. A popular food item for people of the Neotropical lowlands, but not hunted at La Chacra.

Cuniculidae

Cuniculus paca. Paca, jochi pintao. A large nocturnal rodent occasionally hunted for food at La Chacra. During the dry season, they are ambushed when the emerge from the forest to drink from the artificial watering holes.

Hydrochoeridae (Capybaras)

Hydrochoerus hydrochoeris. Capybara, capibara. Pampa, islas, gallery forest. The world's largest rodent. This is the principal native grazer of the wetlands and savannas. Shot occasionally as vermin which compete for grass with the livestock. Not taken as food in Moxos due to the belief that these rodents carry tuberculosis. Some informant consider that the skin lesions these animals often bear are the result of feeding on the seeds of *Enterolobium contortisiliquum,* which are considered to be toxic to livestock. When capibaras are exterminated from a ranch, the numbers of *Enterolobium* increase and cattle ingest more seeds and suffer the consequences.

Erithizontidae (New World porcupines)

Coendou sp. Prehensile-tailed porcupine, puerco espín. Gallery forest and woodland.

There is a noticeable absence of mice and rats, at least ones that leaves obvious signs of life.

Artiodactyla

Cervidae (Deer)

Blastoceros dichotomus. Swamp deer, ciervo. Inhabits the junquillares of neighboring Cáceres, occasionally visiting La Chacra. This is the largest of the Neotropical deer.

Mazama americana. Red brocket deer, hurina. Observed once in the pampa near Isla #1.

Mazama gouazoubira. Brown brocket deer, hurina. Common. Gallery forest, islas, pampa.

Tayassuidae

Tayassu pecari. Taitetú. Occasional in gallery forest.

Perissodactyla

Tapiridae (Tapirs)

Tapirus terrestris. Tapir, anta. These are the largest native mammals of the Neotropical lowlands. Wandering individuals occasionally pass through. Tracks observed in gallery forest. Heavily hunted for meat and hide.

Xenarthra (Edentata)

Bradypodidae (Sloths)

Bradypus sp. Three-toed sloth. Perico. Gallery forest. Small individuals observed near ground during the day. Not observed on cecropias!

Dasypodidae (Armadillos)

Euphractes sexcinctus. Peji. Abundant, diurnal, not considered palatable by many people. Considered to be "quiabó" (fishy-smelling).

Dasypus novemcinctus. Nine-banded armadillo. Tatú. Abundant, diurnal, widely eaten by people.

Carnivora

Felidae (Cats)

Felis yaguarundi. Yaguarundi, gato gris. Gallery forest. I observed one during the day as I sat atop Loma 1. I first saw a terrified agouti bolting through the groundcover. Moments later, a disappointed-looking yaguarundi came ambling by, looked at me briefly, then ran off to find something more interesting to do.

Felis concolor. Puma, león. Reported. This big cat is apparently more adept in keeping low and living around humans than are jaguars; their persistence in suburban California bears this out.

Primates

Cebidae (New World monkeys)

Alouatta caraya. Black howler, manechi. Gallery forest. Female yellow, male black. Feeds on *Syagrus* palms fruits (winter). Baby observed in winter. According to Terborgh (1985) howlers are lethargic and sedentary, feeding largely upon leaves and figs. Howlers can eat toxic leaves and unripe fruit that other primates cannot.

Aotus azarai. Night monkey, mono nocturno. Gallery forest, reported from islas del bajío. Feeds on motacú fruits (Jan). An inquisitive monkey that is often found low in the trees. Most often observed in around sunset. Kavanagh (1983) reported that night monkey nest trees may be as close as 130 m. At Cocha Cashu (Peru: Madre de Dios), Terborgh (1985) reports an average territory size of 10 ha (2-5 individuals per group).

Callicebus donacophilus. Dusky titi monkey. Gallery forest, woodland. There are numerous families on both sides of the cañada and they can often be heard in "shouting matches." Babies observed in winter. Known as "faca-faca" in the San Borja region if not elsewhere, due to sound of one its vocalizations. I observed this abundant monkey in *Copernicia* palm woodland as well as gallery forest. Kinzey (1982) concluded that each of the member of the *C. molloch* group corresponds with a Pleistocene refuge as proposed by Brown (based on butterflies). The species *C. donacophilus* is found east of the Mamoré, in the Iténez Valley, the Bolivian Precambrian region, and the Pantanal. Kinzey claims that this subspecies underwent differentiation in the "Guaporé Refuge" during the Pleistocene. However, it appears that the "center" of *C. donacophilus* is the semi-deciduous forest and woodlands of the Bolivian Precambrian shield. Kinzey was obviously unaware that this is the most abundant primate of the gallery forest fragments and semi-deciduous woodlands (even observed on *Copernicia* palms in open stands) at La Chacra. Unfortunately for the refuge model, *Callicebus donacophilus* is quite at home in "non-rain forest" environments. There is no need to invoke a Guaporé forest refuge for a species which is highly abundant in the very types of environments hypothesized for "glacial" Amazonia: tiny relict gallery forest islands and savanna woodlands.

Callicebus territories are known to be as small as 0.5 ha in flooded forests. 75% of diet is fruit, remainder foliage (Kavanagh 1983). Terborg (1985) considers tiitis to be "diminutive counterparts of howlers." A species of *forest edges*. Territories are from six to eight hectares (2-5 individuals). Found in early successional vegetation, not mature forest, due to the availability of young leaves and bamboo.

Cebus apella. Capuchin monkey, mono silbador. Gallery forest. Baby observed in summer. Capuchins are omnivores, but cannot digest leaves. These are not common at La Chacra, being far outnumbered by *Aotus* or *Callicebus.*

Saimiri boliviensis. Squirrel monkey, mono chichilo. Reported from gallery forest. This small monkey is locally very common along permanent watercourses such as the Ibare.

Callitrichidae (Marmosets and tamarins)

Callithrix melanura. Silvery marmoset, mono isá, monito león. Found in *Anadenanthera colubrina* woodlands and galley forest. Feeds on sap exudates of *A. colubrina*. The smallest primate of La Chacra and the most difficult to observe. This marmoset does not stick around long once disturbed and jumps rapidly from tree to tree. Not encountered until May 1994; however, we found three separate occurrences (all with babies) in two days, all on the south side of the cañada. Given their small range size, there are likely many families of these tiny sprites in the drier parts of La Chacra.

Terborgh (1985) noted that callitrichids utilize vertical trunk niches not used by other monkeys. Engage in "cling-and-leap" locomotion. *Cebuella* is a sap specialist with ranges as small as 0.1 hectare! Field data for *Callithrix* are "extremely scanty"! These observations are born out by my own observations of *C. melanura* at La Chacra. These tiny primates make use of the lowest strata of the forest and woodlands as well as the higher ones by leaping from trunk to trunk, not just from branch to branch (or canopy to canopy as it may be). The genus *Callithrix* is largely restricted to the “Brazilian Shield Region” and Southeastern Brazil; that is, they are not true “Amazonian” creatures.

Additional Notes on the Primates of La Chacra

Ojasti (1990) lists five genera of Neotropical “savanna” primates -- *Callithrix, Aotus, Callicebus, Cebus*, and *Alouatta* -- all of which are present at La Chacra. All five were also present at Fazenda Acurizal in the Pantanal (Schaller 1983).

The Chacra primates, while essentially are all arboreal, are not significantly limited in any sense by the stretches of non-forest environments between forest islands. The capuchin and the night monkey appear most adept at savanna travel, as these sometimes visit the islas del bajío which are accesible only by crossing over a kilometer of herbaceous savanna. The area of most forest islands is not large enough to indefinitely maintain a group of *Alouatta* or *Cebus*, but a 500 x 200 m stretch of gallery forest is enough to support groups of the smaller species.

The carrying capacity of the vegetation is influenced by its botanical composition and age, which are influenced by livestock and human activity. The increased abundance and distribution of the palms fostered by livestock and humans is certainly beneficial to the primates. *Attalea phalerata* provides a rich foodsource with its nearly year-round production of fruits. *Callicebus*, which feeds upon young leaves and shoots, is said to be most abundant in "early succesional vegetation" (Terborgh 1985) and thus may benefit from a human disturbance generated mosaic of uneven aged stands, as well as the young woodlands developing on the semialturas. *Cebus* is notorious as a bold pillager of garden and field. In the Beni they often enter gardens to steal mangoes and bananas.

The persisting preference for beef over wild game instilled in the Moxos natives by the Jesuits has certainly helped conserve monkeys and other mammals. None of the Chacra resident men were willing to eat an *Aotus* shot by one of my assistants; however, all of the women wanted to eat the dead primate. The women, however, were raised in the "traditional" Isiboro-Sécure region, while the men were from the more "urban" regions (San Borja, Santa Ana, Trinidad). Small numbers of armadilloes and pacas are hunted by local folk, but these are still abundant. At Ibiato, where the Sirionó subsist almost soley upon wild game, the abundance of mammals has been decreasing recently.

Cattle ranching has also helped to maintain low human population densities in the savannas. Only with the construction of the highway has any intenisification of activity occurred in the zone between Trinidad and the San Pablo. Ranch owners are hesistant to allow "squatters" or use by small farmers. The most significant activity in recent years has been the establishment of small dairies along the highway, but this still has not led to dramatic increases in local population pressure. In contrast, the northern forest districts of the Beni where rubber and Brazil nut collection occurs are more heavily populated and largely devoid of wild game.

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