STEVEN NELSON PANFIL

Late Holocene Forest and Savanna Diversity and Dynamics Across An Amazonian Ecotone

(Under the Direction of Chris J. Peterson)

I used floristic inventory, plant demographic, and paleoecological methods to examine the modern and historical distribution of vegetation at Noel Kempff Mercado National Park in northeastern Bolivia. This park covers 1.5 M ha and spans the ecotone between moist evergreen forest, dry forest, and savanna formations at the southern margin of the Amazon Basin. Floristic analysis of the forest and savanna formations of the region shows that high β-diversity is responsible for very high numbers of species. Forest formations have low to moderate richness at the 1 ha plot scale, but species overlap between plots is also low. Twenty-nine 1 ha plots contained 896 species of trees ≥ 10 cm dbh. Savanna formations were sampled with the line intercept technique and have habitat heterogeneity similar to the forests. Nine savanna plots contained 662 herbaceous and woody plant species.

I investigated the history of vegetation change at my site with carbon isotope analysis of soil organic matter. This technique compares the isotopic composition of carbon in the soil with that of standing vegetation. My results indicate that areas that are presently forested have been continuously forested for more than 3,000 years. The savanna is near its maximum extent, and it has experienced at least one episode of increased woodiness during this time.

Plant demographic plots at the edge of forest islands show that the boundary between forest and savanna is abrupt and that the density of woody stems in the savanna rapidly increases in the absence of fire. Natural burns occur at 2-3 year intervals at some locations, and these fires cause high levels of mortality of small woody stems in the savanna. These results suggest that reduced fire frequency would allow the establishment of large trees and shrubs that are resistant to fire, eventually leading to a greater density of woody stems in the savanna and the possible conversion to forest.

INDEX WORDS: Forest/savanna boundary, Ecotone, Carbon isotope analysis, Paleoecology, Amazon, Biodiversity, Bolivia, Cerrado, Tropical forest

# LATE HOLOCENE FOREST AND SAVANNA DIVERSITY AND DYNAMICS ACROSS AN AMAZONIAN ECOTONE

by

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# DEDICATION

*For Jessica:*

> *For your patience, your encouragement, and your sense of adventure.*

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# CHAPTER 1

# INTRODUCTION AND LITERATURE REVIEW

The Amazon Basin contains more species than any other region on earth, yet surprisingly little is known about the current or past distribution of species in the region. Though few would expect that an area this large is homogeneous, few studies have been able to quantify the distribution of species over a large scale in the Amazon, largely because the species are so numerous and systematists are so few.

The past distribution of species is even less well documented. Even a question as basic as whether forest or savanna was dominant in the region during the last ice age is still debated in the literature (Colinvaux et al. 2000). Yet an understanding of how vegetation in the Amazon has changed in response to climate is crucial not only for species conservation, but also for understanding global change, since the Amazon basin is one of the largest terrestrial carbon reservoirs on earth.

This dissertation examines the current and past distribution of vegetation at Noel Kempff Mercado National Park in eastern Bolivia. This 1.5 M ha park spans the ecotone between moist evergreen forest to the north, and dry forest and savanna formations to the south and east. From previous pollen analysis (Mayle et al. 2000), it is known that the region has experienced vegetation change since the Pleistocene, with some savanna formations being replaced with moist forest.

In the present study, I analyze large floristic datasets that represent inundated and upland forest (Chapter 2) and savanna (Chapter 3) formations in this region. One ha permanent tree inventory plots were installed in 19 sites around the park, and line intercept plots were installed to sample the savanna vegetation at 9 sites. These plots serve to document the local (α-diversity), the species turnover between sites (β-diversity) and the total regional diversity (γ-diversity).

I also present the results of an analysis of carbon isotopes in soil organic matter (Chapter 4) to document the past vegetation along the ecotone between forest and savanna. This is a little used paleoecological technique with relatively low taxonomic and temporal resolution, but with high spatial resolution, and widespread applicability, since it depends on soil, and not pollen preserving sediments. In contrast to previous applications of this technique, I used a density and fractionation protocol to isolate the humin fraction of soil organic matter. This fractionation protocol helps to circumvent the problem of bioturbation, whereby carbon of different ages is mixed in the soil. Fractionation serves to remove young organic matter, whose isotopic composition can mask the paleoecological signal of old organic matter.

In Chapter 5, I present the results of repeat inventories of shrubs and trees in strip-plots that are oriented perpendicular to the modern forest/savanna boundary. These inventories document the contemporary dynamics of vegetation, and illustrate one possible mechanism that determines forest/savanna conversion. The rate of colonization of the savanna by trees and shrubs in the absence of fire is compared to the fire-induced rate of mortality.

Together, these studies illustrate the extremely high diversity of plant species and the dynamic nature of the vegetation in this region. Both paleoecology and floristic research are still in their infancy in the Amazon Basin. The present study illustrates that species diversity has important spatial and temporal components in this region. These components have important implications for our understanding of how species are distributed, and for long-term efforts to conserve the richness of the most biologically diverse place on earth.

# CHAPTER 2

# REGIONAL PATTERNS OF TREE DIVERSITY AT THE EDGE OF THE AMAZON (SANTA CRUZ, BOLIVIA)[1]

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[1] Panfil, S.N., T.J. Killeen, L. Arroyo, M. Saldías, R. Guillén, T. Grimwood, P.F. Foster, G. Sánchez, J. Caballero, and A. Jardim. To be submitted to *Conservation Biology*.

# ABSTRACT

Landscape-scale patterns in the distribution of tropical forest species have been difficult to discern because most tropical tree inventories are done at small spatial scales. Without understanding how species are distributed at larger scales, it is impossible to characterize the conservation status of individual species or to forecast the long-term success of protected areas. Here we present inventory data from 29-one ha tree plots in the Noel Kempff Mercado National Park region of Bolivia. These plots represent 5 physiognomic classes of forest and we show that species overlap both within and among forest classes is low. The total richness of these plots (896 species) is large despite relatively low levels of alpha-diversity measured for individual plots. This overall richness is the result of high levels of beta-diversity that can be attributed to habitat heterogeneity.

The region lies at the southern edge of the Amazon basin and spans the ecotone between moist Amazonian forest and tropical dry Chiquitano forest. This region is known to have experienced dramatic vegetation change in the recent past and future climate change may cause additional shifts in vegetation. Because overlap among forest types is so low, climate change that favors any single forest type will force a loss in regional species richness.

## ***Keywords***

AMAZON, CHIQUITANÍA, BOLIVIA, ECOTONE, CLIMATE CHANGE, BIODIVERSITY, TROPICAL FOREST, PERMANENT FOREST PLOT

# INTRODUCTION

Ecologists have a limited ability to predict how the biodiversity of tropical areas is likely to respond to future climate change. This is because we have a coarse understanding of the environmental requirements of tropical species and because the large- or meso-scale distribution of tropical species remains poorly known (Pitman et al. 1999, Pitman et al. 2001). We also have inadequate knowledge of the vegetative history for most tropical sites, so we cannot assess the role of history in determining species distributions or make meaningful predictions about the future. Yet to ensure the long-term success of conservation efforts, we must develop an understanding of the factors that determine the distribution of species across regional and continental landscapes. To accomplish this, we must develop an understanding of the current distribution of species and environmental conditions, and couple that information with knowledge of how vegetation has responded to climate change in the past.

Most floristic inventories in the tropics are done on small geographic scales, where it is difficult to distinguish between species distributions resulting from random processes and those caused by environmental gradients. Floristic inventories are costly and time consuming due to the scarcity of taxonomists who are able to quickly identify the large number of species found in these forests. The most common inventories are based on general collections without plots, or on small (<1 ha) isolated plots. When done by a skilled botanist, the general collection method can be an efficient way to sample the floristic variation of an area, but it is often difficult to describe species assemblages or species-environment associations with this type of study. Small plot sampling allows for a more precise description of assemblages, but rarely provides insight into regional variation in species composition or species-environment associations. Information about soil conditions is frequently not collected in these studies, making it difficult to describe the habitat preferences of a species even on a local scale. Multi-plot studies over a large area are now beginning to reveal patterns that have been hidden (Clinebell et al. 1995, Terborgh and Andresen 1998, Pitman et al. 1999, Ter Steege et al. 2000, de Oliveira and Nelson 2001, Pitman et al. 2001, Malhi et al. in press).

Even with a good understanding of the flora of a tropical region, it is difficult to predict the impact of future climate change without an understanding of past vegetation dynamics. For most tropical sites, there are no paleoecological data. Arguments about whether moist forest covered the Amazon during the Pleistocene have lasted for decades because data are available for so few sites (Haffer 1969, Colinvaux et al. 2000). Basic information about how vegetation has responded to past shifts in climate would make it much easier to forecast the future response of vegetation.

Multidisciplinary datasets from Noel Kempff Mercado National Park in eastern Bolivia allow us to begin to make predictions about the response of vegetation and diversity to climate change. An intensive floristic inventory of the Noel Kempff region has documented nearly 3000 species of vascular plants to date (Killeen and Schulenberg 1998). Extensive geomorphological research (Litherland and Power 1989) and soil analyses (present study) allow us to relate species distributions to environmental conditions. New paleoecological work demonstrates that this region is highly susceptible to fluctuations in climate (Mayle et al. 2000, Killeen et al. *In press*). This unique combination of datasets allows us to address questions that are unanswerable for most tropical sites. How is the total diversity of the system likely to shift in response to climate change? Can we predict which species or groups of species are likely to benefit or be hurt by climate change?

In this paper, we characterize the distribution of tree species in the forest formations of the Noel Kempff region with data from a network of 29, one-ha plots. We then relate this distribution to a broad range of environment variables and to our understanding of the past vegetation dynamics of the region. Based on these analyses, we discuss the possible consequences of climate change on the diversity of this region.

# METHODS

## ***Site Description***

### **Location**

The study sites lie between 13° 30’ and 15° 15’ S and between 60° 20’ and 61° 30’ W. This study area closely fits Gosz’s concept of the biome ecotone (Gosz 1993), where continental scale biomes meet. Moist Amazonian forest lies to the north of the area and Chiquitano deciduous tropical forest (Killeen et al.

1998a) lies to the south. The region also includes the western-most limit of cerrado-type savanna vegetation, and a variety of wetland habitats.

The majority of the study area lies within the borders of Noel Kempff Mercado National Park, a 1.5 M ha protected area situated along Bolivia’s northeast border with Brazil. This park was created to protect the Huanchaca Plateau, a sandstone table-mountain that was the inspiration for Sir Arthur Conan Doyle’s book, *The Lost World* (Fawcett 1988). The park was subsequently enlarged to include the surrounding lowlands. Seasonally inundated and upland forest formations dominate these lowlands, while the vegetation of the plateau contains a mix of upland forest and savanna (Figure 1). Human habitation in the region has been sparse and no permanent settlements are known to have existed on top of the plateau. The surrounding lowlands were selectively harvested for mahogany (*Swietenia macrophylla* King), but total structural damage due to this type of logging is relatively low (Gullison and Hardner 1993, Panfil and Gullison 1998).

The geomorphology of Noel Kempff Park is described in detail in Litherland and Power (Litherland and Power 1989). The region lies on the Brazilian Shield and is dominated topographically by the Huanchaca Plateau, which rises to a maximum height of 950 m above sea level. The plateau is predominantly sandstone, with dolerite and quartzite intrusions underlying some areas. The lowlands surrounding the plateau range from 150 to 300 m in

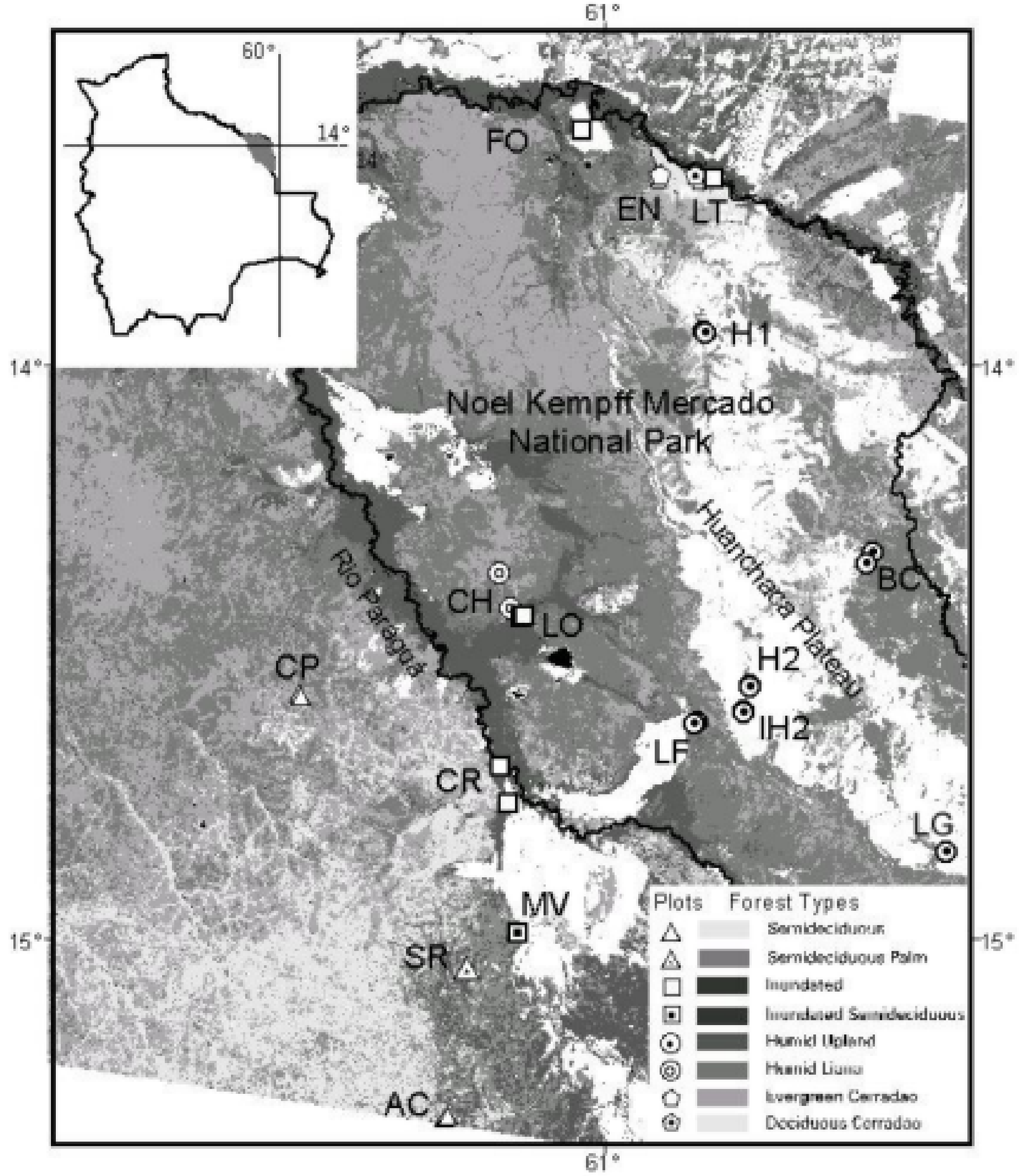

**Figure 1. The vegetation of the Noel Kempff Mercado National Park region. Plots used in this study are labeled with their two letter prefix. Modified from (Killeen et al. 1998b).**

elevation and include seasonally inundated floodplains of the Paraguá River to the west and of the Itenez or Guaporé River to the North. Several granite outcrops rise to a maximum elevation of 500 m to the west of the Paraguá River.

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### Climate

The Noel Kempff region is characterized by a warm tropical climate with strong seasonality in precipitation. Climate information is inferred from meteorological stations located 160-200 km to the southwest and 150–200 km northwest of the park. Mean annual temperature is 25-26º C with a mean annual minimum of 10º C (Roche and Rocha 1985). Frost is unknown in the area. During the austral summer, the inter-tropical convergence zone (ITCZ) brings warm moist Amazonian air masses to the region. Total mean annual precipitation is approximately 1500 mm, with almost all falling between October and June (Killeen et al. *In press*). The northern parts of the park receive two to several hundred mm more of precipitation per year than those to the south (Roche and Rocha 1985). During the austral winter, the ITCZ shifts to the north and dry weather patterns replace the moist air masses.

### Paleoecology

The paleoecology of this region is being documented through palynological work and through $\delta^{13}C$ and radiocarbon analysis of soil organic matter. Pollen cores collected from two lakes located in the lowlands 25-60 km to the west of the Huanchaca Plateau show that moist forest formations now surrounding these lakes are relatively new arrivals. At the northernmost lake these communities developed only about 3000 years B.P. The other lake is located 100 km to the south and moist tropical forest formed there approximately 1000 years B.P. At both sites, the pollen record indicates a drier climate with a predominance of savanna taxa prior to the arrival of the moist forest species (Mayle et al. 2000).

Isotope analysis of soil organic matter can provide evidence of vegetation change at fine spatial resolutions. The carbon isotope compositions of $C_3$ and $C_4$ plant tissue differ and the decomposition of these tissues influences the isotopic composition of soil organic matter. A difference between the isotopic composition of soil organic matter and the isotopic composition of modern vegetation is thus an indicator of vegetation change (Boutton and Yamasaki 1996). Carbon isotope data from sites on the Huanchaca plateau show that forest and savanna have coexisted for several thousand years. However, the extent of these formations has shifted, with alternate periods of forest and savanna expansion (Killeen et al. *In press*). In summary, the paleoecological data show that vegetation in the region has been highly dynamic, with the geographic extent of habitats changing with time.

### ***Vegetation Sampling***

We sampled the vegetation in the park between 1993 and 2000. Individual plot sites were chosen in order to represent the range of forest formations that were identified by field expeditions, over-flights, and LandSat images (Killeen et al 1998b). The study plots are distributed across the landscape (Figure 1) and represent a range of physiognomic and geomorphological features (Table 1). We sampled evergreen, semi-deciduous, and deciduous forest types, in upland and seasonally inundated landscapes, and in continuous forests and forest islands. Plots are grouped within the tables of this paper according to this *a priori* classification.

We sampled the vegetation at each site within one-hectare plots. In order to minimize within plot heterogeneity, we installed the plots in visually homogeneous forest. The form of plots at most sites was a rectangle measuring 500 m x 20m, though at five sites, (CP-1, CP-2, CR-1, IH2-3, and IH2-4) the plot shape was altered to fit the 1 ha study area into forest patches that were not long enough for the 500 m design. We installed one-hectare plots at 19 different sites, and to document within forest-type (local) variation, we installed an additional plot

**Table 1. Plot characteristics. Sites sharing the same two-letter prefix are located at the same site.**

| Plot | Site Name | Physiognomic Forest Class | Substrate | Slope (degrees) | Inundation | Forest Setting | Latitude (S) | Longitude (W) | Altitude (m) | Year Sampled |
|---|---|---|---|---|---|---|---|---|---|---|
| EN-1 | Enano | Dwarf Evergreen / Cerradão | Tertiary Laterite | 0 | Xeric | Continuous | 13.38.34 | 60.53.31 | 550 | 1996 |
| EN-2 | Enano | Dwarf Evergreen / Cerradão | Tertiary Laterite | 0 | Xeric | Continuous | 13.38.39 | 60.53.31 | 550 | 1996 |
| LT-1 | Los Torres | Deciduous / Cerradão | Sandstone | 20 | Xeric | Continuous | 13.39.08 | 60.49.46 | 300 | 1993 |
| LT-2 | Los Torres | Deciduous / Cerradão | Sandstone | 20 | Xeric | Continuous | 13.39.14 | 60.49.52 | 300 | 1993 |
| AC-1 | Aquario | Semideciduous | Granitic | 0 | Xeric | Continuous | 15.14.46 | 61.14.34 | 300 | 1996 |
| AC-2 | Aquario | Semideciduous | Granitic | 0 | Xeric | Continuous | 15.14.46 | 61.14.34 | 300 | 1996 |
| CP-1 | Cerro Pelao | Deciduous | Granitic | 20 | Xeric | Continuous | 14.32.28 | 61.29.53 | 400 | 1993 |
| CP-2 | Cerro Pelao | Deciduous | Granitic | 10 | Xeric | Continuous | 14.32.16 | 61.30.02 | 400 | 1993 |
| SR-1 | San Roque | Semideciduous Palm | Quaternary | 0 | Mesic | Continuous | 14.59.59 | 61.13.17 | 300 | 1995 |
| BC-1 | Rio Verde | Semi-Evergreen | Quaternary | 0 | Mesic | Continuous | 14.18.42 | 60.32.14 | 800 | 1999 |
| BC-2 | Rio Verde | Semi-Evergreen | Sandstone | 0 | Mesic | Continuous | 14.17.26 | 60.31.39 | 800 | 1999 |
| H1-1 | Huanchaca I | Semi-Evergreen | Sandstone | 0 | Mesic | Island | 13.54.49 | 60.48.58 | 500 | 1994 |
| H1-2 | Huanchaca I | Semi-Evergreen | Sandstone | 0 | Mesic | Island | 13.54.49 | 60.48.58 | 500 | 1994 |
| H2-1 | Huanchaca II | Semi-Evergreen | Dolerite | 10 | Mesic | Island | 13.53.09 | 60.04.00 | 700 | 1996 |
| H2-2 | Huanchaca II | Semi-Evergreen | Dolerite | 10 | Mesic | Island | 13.53.09 | 60.04.00 | 700 | 1996 |
| IH2-3 | Huanchaca II | Semi-Evergreen | Dolerite | 15 | Mesic | Island | 14.33.39 | 60.44.55 | 700 | 1999 |
| IH2-4 | Huanchaca II | Semi-Evergreen | Dolerite | 15 | Mesic | Island | 14.34.03 | 60.44.52 | 700 | 1999 |
| LF-1 | Los Fieros | Semi-Evergreen | Tertiary Laterite | 0 | Mesic | Continuous | 14.36.57 | 60.52.16 | 225 | 1993 |
| LF-2 | Los Fierros | Semi-Evergreen | Tertiary Laterite | 0 | Mesic | Continuous | 14.36.53 | 60.51.59 | 225 | 1993 |
| LG-b | Las Gamas | Semi-Evergreen | Sandstone | 5 | Mesic | Island | 14.48.11 | 60.23.33 | 850 | 1993 |

| Plot | Site Name | Physiognomic Forest Class | Substrate | Slope (degrees) | Inundation | Forest Setting | Latitude (S) | Longitude (W) | Altitude (m) | Year Sampled |
|---|---|---|---|---|---|---|---|---|---|---|
| CH-1 | Chore | Semi-Evergreen Liana | Tertiary Laterite | 5 | Mesic | Continuous | 14.23.08 | 61.08.52 | 250 | 1995 |
| CH-2 | Chore | Semi-Evergreen Liana | Tertiary Laterite | 0 | Mesic | Continuous | 14.20.56 | 61.09.39 | 250 | 1995 |
| CR-1 | Monte Cristo | Seasonally Inundated Riverine | Quaternary | 0 | Seasonal | Continuous | 14.38.30 | 61.09.30 | 225 | 1995 |
| CR-2 | Monte Cristo | Seasonally Inundated Riverine | Quaternary | 0 | Seasonal | Continuous | 14.42.40 | 61.09.15 | 225 | 1995 |
| LT-3 | Los Torres | Swamp Forest | Quaternary | 0 | Permanent | Continuous | 13.39.20 | 60.49.08 | 200 | 1993 |
| MV-1 | Monte Verde | Seasonally Inundated | Quaternary | 0 | Seasonal | Continuous | 14.56.27 | 61.07.59 | 230 | 1995 |
| LO-2 | Las Londras | Seasonally Inundated | Quaternary | 0 | Seasonal | Continuous | 14.24.15 | 61.08.38 | 225 | 1996 |
| LO-1 | Las Londras | Seasonally Inundated | Quaternary | 0 | Seasonal | Continuous | 14.24.15 | 61.08.38 | 225 | 1996 |
| FO-b | Flor de Oro | Seasonally Inundated | Quaternary | 0 | Seasonal | Island | 13.34.15 | 61.01.29 | 210 | 1994 |

at 10 of these sites, yielding a total of 29 one ha plots. At the locations where we installed two plots, these were placed parallel to each other 200 m apart within a 500 x 500 m study area, with the exception of CH and CR where plots are approximately 8 km apart. We installed a grid of stakes at 20 m intervals to mark the border of each plot and determined the location of plots with a global positioning system receiver. All freestanding plants greater than 10cm dbh (1.4 m above ground level, or above buttresses) were registered with unique identification numbers using aluminum tags; diameter, height (triangulated using a clinometer), position within the plot, and species name were recorded. We excluded lianas but included palms in this portion of the study.

Voucher specimens are on deposit at the herbarium of the Museo de Historia Natural Noel Kempff Mercado in Santa Cruz, Bolivia (USZ). We made specimen determinations by comparison with specimens in the collection at USZ, at the Missouri Botanical Garden (MO), and with the assistance of many family specialists (see (Killeen and Schulenberg 1998)) for a list of specialists consulted.) Primary data from the voucher collections are available at http://www.mobot.org.

We used the Importance Value Index (IVI) as described by Dallmeier et al. (Dallmeier et al. 1992) to rank the relative importance of species in each plot. This index is the sum of the percent relative values for density, dominance, and frequency of a species and carries a maximum value of 300.

In 17 of the 29 plots, we examined the composition of the understory by measuring, mapping, and identifying all woody individuals with dbh ≥2.5cm in a

500m x 2m subset of the plots (0.1ha). These “Gentry transects” (Clinebell et al. 1995) follow the methodology used by Alwyn Gentry throughout the Neotropics and allow for comparison of data among studies and sites. Lianas were recorded in the Gentry transects, but tags were not attached to any individuals smaller than 10cm dbh.

### ***Soil Analysis***

We characterized the soil profile in 28 of the study plots during field expeditions made in June and October of 1995, 1996, 1997, and 2000. Visual assessments were made with pits; soil samples were collected for later analysis at the Centro de Investigaciones para la Agricultura Tropical (CIAT) in Santa Cruz, Bolivia. Soil analysis methods are described in (Cochrane and Barber 1993) but are summarized here. The pH and electro-conductivity of the soil were determined by water extract at a soil-water ratio of 1:5 (Page et al. 1982, Van Reeuwijk 1987). Total nitrogen was determined by the Kjeldahl method (Varley 1966, Page et al. 1982, Van Reeuwijk 1987), and the organic matter content was measured using a modified Walkley-Black procedure (Metson 1956, Van Reeuwijk 1987). A modified version of the Olsen method was used to determine the soluble phosphorous content (Van Reeuwijk 1987). The exchangeable bases Ca, Mg, K, and Na were extracted with ammonium acetate at pH 7.0 and measured with atomic absorption (Begheyn 1981, 1982, Van Reeuwijk 1987). Exchangeable acidity and aluminum were determined by titration after extraction with potassium chloride (Mclean 1965). The hydrometer method was used for determining sand, silt, and clay percentages (Day 1965). Total exchangeable base content was calculated by summing the values for Ca, Mg, Na and K. Cation exchange capacity was calculated by summing the values for total exchangeable bases and acidity.

### ***Multivariate Analysis***

We assessed the relationship between floristic composition and environmental conditions using canonical correspondence analysis (CCA) (Terbraak 1986). Basal area is used to quantify species abundance in the ordination, as this better represents the relative importance of species than simple counts. We included 28 of the 29 study plots in the CCA. We excluded the IH2-4 plot because it lacks soil chemistry data. The environmental data that we used in the analysis included latitude (as a surrogate for precipitation), altitude, and soil characters (pH, total exchangeable bases, percent base saturation, percent sand and clay, and the concentrations of aluminum, phosphorous, and organic matter in the A horizon of the soils) as continuous variables. We used dummy variables to code for the following categorical conditions: the type of geological substrate, soil moisture regime, and whether a plot is situated in an island or continuous forest.

The multivariate analysis was performed with the CANOCO for Windows v.4.02 statistical software package. Though CCA can serve for hypothesis testing, in this case it must be considered an exploratory analysis because we subjectively assigned the location of the plots and thus violate the assumption of random sampling that is required for hypothesis testing.

## RESULTS

### ***Structure***

The forest types differ significantly for all structural measures except density ($p<.001$, Table 2). For all plots, the mean density of stems ≥ 10cm dbh was 593 trees/ha, ranging from 387 stems/ha in a forest island that is lightly inundated during the wet season (FO-b) to 923 stems/ha in a continuously inundated swamp forest (LT-3). Mean basal area in the plots was 23 $m^2$/ha and ranged from 9.9 $m^2$/ha in *cerrado* transition forest (LT-1) to 34.5 $m^2$/ha in a seasonally inundated evergreen forest plot (CR-1).

The *cerrado* transition plots are characterized by low basal area and low stature, but differ in density, with EN plots forming a closed canopy on flat terrain and LT plots forming an open canopy on a rocky hillside. Plots in Chiquitano dry forest have moderate stature, density, and basal area when compared with the tall upland forest plots. The CH liana forest plots were similar to tall upland forest plots in density, but were smaller in stature and basal area. Inundated plots are intermediate in structure to tall upland and dry forest plots for basal area and stature, but have markedly greater stand density.

Density correlated poorly with basal area across all plots ($\rho=.21$) and within each forest type. Density correlated strongly with height among all plots (ρ=.92), but the correlation was poor within forest types. Basal area and height correlated well across forest types (ρ=.73) but poorly within forest types.

We found substantial structural differences between pairs of plots at the same site. Plot pairs differed in density by between 2.4% (LT) and 34.5% (CH). In basal area, within site plot differences were also substantial, ranging from 0.5% (AC) to 36.1% (CH). Mean height differences between pairs of plots differed somewhat less, ranging from 3.1% (H2) to 25.3% (CP).

### ***Species Composition***

The relative importance of individual families and species shows that the composition of the plots is highly variable. Only one plant family, the Rubiaceae, was represented in each of the 29 study plots, though the Annonaceae, Euphorbiaceae, and Caesalpinaceae were found in 28 of the plots. Among species, the maximum number of plots in which any single species occurred was 17 for the neotropically widespread tree *Tapirira guianensis* Aublet

**Table 2. The structure and diversity of the forest in each study plot. Differences among groups of plots were assessed with ANOVA for each column, with the exception of Simpson's (1-D). For (1-D) values violated assumptions of normality and a Kruskal-Wallis test was performed instead of ANOVA.**

| Forest Type | Plot | Density | | Basal Area | Mean height | Mean height | Richness | | Diversity | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | >=2.5cm dbh (stems/0.1ha) | >=10cm dbh (stems/ha) | >=10cm dbh ($m^2$/ha) | >=10cm dbh (m) | of 1st branch (m) | >=2.5cm dbh (spp/0.1ha) | >=10cm dbh (spp/ha) | (1-D) (>=10cm dbh) | H' | α |
| Cerrado Transition | EN-1 | 377 | 750 | 14.3 | 10.0 | 6.5 | 32 | 49 | 0.87 | 3.75 | 11.74 |
| | EN-2 | - | 674 | 14.0 | 11.8 | 7.8 | - | 51 | 0.88 | 4.00 | 12.81 |
| | LT-1 | - | 456 | 9.9 | 7.1 | - | - | 47 | 0.92 | 4.41 | 13.15 |
| | LT-2 | - | 467 | 11.0 | 6.2 | - | - | 37 | 0.92 | 4.20 | 9.43 |
| Dry Forest | AC-1 | 127 | 478 | 19.2 | 13.8 | 6.7 | 57 | 65 | 0.96 | 5.11 | 20.31 |
| | AC-2 | 122 | 452 | 19.1 | 13.0 | 6.4 | 55 | 67 | 0.95 | 5.01 | 21.74 |
| | CP-1 | 102 | 559 | 20.3 | 10.5 | 5.6 | 36 | 51 | 0.93 | 4.52 | 13.65 |
| | CP-2 | 117 | 492 | 24.6 | 13.1 | 6.9 | 46 | 65 | 0.96 | 5.10 | 20.07 |
| | SR-1 | 271 | 427 | 19.9 | 10.8 | 5.9 | 45 | 36 | 0.55 | 2.41 | 9.37 |
| Tall Upland Forest | BC-1 | - | 532 | 26.8 | 19.0 | - | - | 71 | 0.95 | 4.92 | 21.56 |
| | BC-2 | - | 543 | 23.6 | 19.7 | - | - | 60 | 0.95 | 4.73 | 16.84 |
| | H1-1 | - | 582 | 31.1 | 16.6 | - | - | 123 | 0.95 | 4.95 | 47.65 |
| | H1-2 | - | 725 | 31.2 | 15.7 | - | - | 102 | 0.96 | 5.30 | 32.36 |
| | H2-1 | 271 | 539 | 27.5 | 14.4 | 9.1 | 63 | 76 | 0.95 | 5.31 | 24.13 |
| | H2-2 | 300 | 654 | 30.5 | 14.9 | 9.3 | 62 | 90 | 0.97 | 5.40 | 28.27 |
| | IH2-3 | - | 718 | 28.0 | 15.0 | - | - | 97 | 0.97 | 6.00 | 30.03 |
| | IH2-4 | - | 599 | 25.5 | 17.8 | - | - | 78 | 0.96 | 5.30 | 23.93 |

| Forest Type | Plot | Density | | Basal Area | Mean height | Mean height | Richness | | Diversity | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | >=2.5cm dbh | >=10cm dbh | >=10cm dbh | >=10cm dbh | of 1st branch | >=2.5cm dbh | >=10cm dbh | (1-D) | H' | α |
| | | (stems/0.1ha) | (stems/ha) | ($m^2$/ha) | (m) | (m) | (spp/0.1ha) | (spp/ha) | (>=10cm dbh) | | |
| | LF-1 | 223 | 626 | 25.3 | 14.5 | 9.4 | 83 | 107 | 0.95 | 5.15 | 37.15 |
| | LF-2 | 226 | 589 | 30.0 | 17.5 | 9.4 | 62 | 85 | 0.95 | 5.01 | 27.26 |
| | LG-b | - | 665 | 34.3 | 15.5 | - | - | 85 | 0.96 | 5.26 | 25.89 |
| Liana Forest | CH-1 | 447 | 733 | 16.3 | 10.7 | 6.2 | 125 | 109 | 0.85 | 4.69 | 35.44 |
| | CH-2 | 473 | 545 | 12.0 | 12.0 | 7.3 | 122 | 109 | 0.98 | 5.86 | 40.97 |
| Seasonally Inundated Forest | CR-1 | 302 | 592 | 34.5 | 14.3 | 6.8 | 59 | 67 | 0.93 | 4.59 | 19.42 |
| | CR-2 | 308 | 651 | 27.9 | 14.9 | 7.6 | 62 | 78 | 0.96 | 5.02 | 23.13 |
| | LT-3 | - | 923 | 23.3 | 15.0 | - | - | 76 | 0.87 | 4.07 | 19.63 |
| | MV-1 | 299 | 629 | 21.7 | 11.6 | 6.1 | 70 | 98 | 0.92 | 4.90 | 32.56 |
| | FO-b | - | 387 | 25.0 | 18.4 | - | - | 31 | 0.82 | 3.20 | 9.33 |
| | LO-1 | 435 | 574 | 20.6 | 12.0 | 6.8 | 87 | 83 | 0.96 | 5.21 | 26.64 |
| | LO-2 | 410 | 650 | 21.0 | 13.2 | 9.4 | 67 | 73 | 0.94 | 4.88 | 21.10 |
| Means | Transition | 377.0 | 586.8 | 12.3 | 8.8 | 7.2 | 32.0 | 46.0 | 0.90 | 4.09 | 11.78 |
| | Dry | 147.8 | 481.6 | 20.6 | 12.3 | 6.3 | 47.8 | 56.8 | 0.87 | 4.43 | 17.03 |
| | Tall | 255.0 | 615.6 | 28.5 | 16.4 | 9.3 | 67.5 | 88.5 | 0.95 | 5.21 | 28.64 |
| | Liana | 460.0 | 639.0 | 14.1 | 11.4 | 6.7 | 123.5 | 109.0 | 0.91 | 5.28 | 38.21 |
| | Inundated | 350.8 | 629.4 | 24.9 | 14.2 | 7.3 | 69.0 | 72.3 | 0.91 | 4.55 | 21.69 |
| **Forest Types Differ?** | | **yes** | **no** | **yes** | **yes** | **yes** | **yes** | **yes** | **no** | **yes** | **yes** |
| p-value | | <.001 | =0.187 | <.001 | <.001 | =.002 | <.001 | <.001 | =.064 | =.032 | <.001 |

(Anacardiaceae). Other widespread species include *Didymopanax morototoni* (Aubl.) Decne. & Planch. (Araliaceae), *Machaerium acutifolium* Vogel (Papilionaceae), and *Physocalymma scaberrimun* Pohl (Lythraceae), each of which were present in 15 plots.

The most speciose families varied by vegetation type (Table 3). The Papilionaceae was the most speciose family in 11 of the plots, including 4 of the 5 dry forest plots and 4 of the 7 seasonally inundated plots. The Mimosaceae was the most speciose in 6 of the plots including 4 of the 13 tall upland plots. The Moraceae was the most speciose in 5 of the plots, 3 times in the tall upland plots and 3 times in the seasonally inundated plots.

The most important species and the degree of importance varied considerably between plots. The highest importance value (172.3) was registered for the palm *Attalea speciosa* (Aublet) Mart. in the SR-1 plot, which is representative of a dry forest type that is common in the south of this region. Another high importance value (109.5) was recorded for an undetermined *Qualea* species (Vochysiaceae) in a seasonally inundated forest island (FO-b). Importance values of the top species in other plots were lower, indicating a more even distribution of species. *Erisma uncinatum* Warm. (Vochysiaceae) was the only species to rank the highest in terms of importance at more than one site. It was the top ranked species in 5 plots, all in the tall upland forest class. The IVI for the top species averaged 45.0 across all 29 plots. The lack of widespread importance of a single species among sites is an indication of the heterogeneous nature of the region.

**Table 3. The most speciose families and the 12 most important species in each plot as determined by the importance value index (IVI). See text or (Dallmeier et al. 1992) for an explanation of how IVI is calculated.**

| Plot | Most Speciose Families | Spp. | Most Important Species | IVI |
|---|---|---|---|---|
| AC-1 | Papilionaceae | 11 | Pseudobombax marginatum (A. St.-Hil.) Robyns | 25.2 |
| | Bignoniaceae | 5 | Anadenanthera colubrina (Vell.) Brenan | 22.8 |
| | Palmae | 4 | Casearia gossypiosperma Brig. | 18.7 |
| | Caesalpiniaceae | 4 | Tabebuia impetiginosa (Mart. ex DC.) Standl. | 18.1 |
| | | | Simira cordifolia (Hook. f.) Steyerm. | 17.9 |
| | | | Tabebuia roseo-alba (Ridley) Sandwith | 17.7 |
| | | | Attalea speciosa (Aubl.) C. Mart. | 11.2 |
| | | | Combretum leprosum Mart. | 10.9 |
| | | | Caesalpinia floribunda Tul. | 9.3 |
| | | | Apuleia leiocarpa (Vogel) J. F. Macbr. | 7.4 |
| | | | Psidium sp. 1 | 6.9 |
| | | | Hymenaea courbaril L. | 6.0 |
| AC-2 | Papilionaceae | 12 | Caesalpinia floribunda Tul. | 36.9 |
| | Bignoniaceae | 6 | Anadenanthera colubrina (Vell.) Brenan | 26.4 |
| | Mimosaceae | 5 | Tabebuia roseo-alba (Ridley) Sandwith | 19.8 |
| | Caesalpiniaceae | 5 | Attalea speciosa (Aubl.) C. Mart. | 17.3 |
| | | | Casearia gossypiosperma Brig. | 15.0 |
| | | | Combretum leprosum Mart. | 13.9 |
| | | | Sterculia apetala (Jacq.) Karsten | 10.9 |
| | | | Cordia alliodora (Ruíz & Pavón) Oken | 9.8 |
| | | | Bauhinia rufa (Bong.) Steud. | 9.8 |
| | | | Chorisia integrifolia Ulbr. | 9.6 |

| Plot | Most Speciose Families | Spp. | Most Important Species | IVI |
|---|---|---|---|---|
| | | | Attalea phalerata C. Martius ex Sprengel | 8.6 |
| | | | Guazuma ulmifolia Lam. | 8.0 |
| BC-1 | Mimosaceae | 6 | Erisma uncinatum Warm. | 32.0 |
| | Lauraceae | 5 | Pourouma minor | 25.4 |
| | Sapotaceae | 5 | Hieronima oblonga (Tul.) Müll. Arg. | 20.6 |
| | Moraceae | 5 | Euterpe precatoria Mart. | 18.7 |
| | | | Pseudolmedia laevis (Ruiz & Pav.) J. F. Macbr. | 16.2 |
| | | | Endichleria sp. 2 | 15.7 |
| | | | Miconia chrysophylla (Rich.) Urban | 14.9 |
| | | | Matayba guianensis Aubl. | 12.8 |
| | | | Qualea paraensis Ducke | 11.7 |
| | | | Sloanea eichleri K. Schum. | 8.6 |
| | | | Sclerolobium rugosum Mart. ex Benth. | 6.6 |
| | | | Desco 4 | 5.9 |
| BC-2 | Melastomataceae | 7 | Erisma uncinatum Warm. | 37.5 |
| | Mimosaceae | 5 | Pourouma minor | 25.3 |
| | Sapotaceae | 5 | Hieronima duquei Cuatrec. | 23.5 |
| | Moraceae | 5 | Miconia chrysophylla (Rich.) Urban | 21.2 |
| | | | Endichleria sp. 3 | 17.0 |
| | | | Euterpe precatoria Mart. | 17.0 |
| | | | Guatteria hyposericea Diels | 13.6 |
| | | | Pseudolmedia laevis (Ruiz & Pav.) J. F. Macbr. | 12.7 |
| | | | Vochysia obidensis Ducke | 12.2 |
| | | | Miconia sp. 5 | 9.5 |
| | | | Helicostylis tomentosa (Poepp.& Endl.) Rusby | 8.9 |
| | | | Socratea exorrhiza (Mart.) H. L. Wendl. | 7.8 |

| Plot | Most Speciose Families | Spp. | Most Important Species | IVI |
|---|---|---|---|---|
| CH-1 | Mimosaceae | 14 | Phenakospermum guianensis Aubl. | 65.4 |
|  | Moraceae | 10 | Astronium fraxinifolium Schott ex Sprengel | 11.6 |
|  | Papilionaceae | 7 | Crepidospermum goudotianum (Tul.) Triana & Planch. | 9.5 |
|  |  |  | Cecropia palmata Willd. | 8.3 |
|  |  |  | Amburana caerensis (Allemão) A.C. Sm. | 8.0 |
|  |  |  | Apuleia leiocarpa (Vogel) J. F. Macbr. | 7.3 |
|  |  |  | Pseudolmedia laevis (Ruiz & Pav.) J. F. Macbr. | 6.8 |
|  |  |  | Pseudolmedia macrophylla Trécul | 6.4 |
|  |  |  | Pourouma guianensis Aubl. | 6.4 |
|  |  |  | Helicostylis tomentosa (Poepp.& Endl.) Rusby | 6.2 |
|  |  |  | Ocotea sp. 1 | 6.0 |
|  |  |  | Sloanea eichleri K. Schum. | 5.8 |
| CH-2 | Papilionaceae | 13 | Erythrina sp. 1 | 24.7 |
|  | Moraceae | 11 | Leguminosae-Mim Indet. 2 | 15.2 |
|  | Mimosaceae | 9 | Talisia sp. 2 | 14.2 |
|  |  |  | Astronium fraxinifolium Schott ex Sprengel | 13.8 |
|  |  |  | Crepidospermum goudotianum (Tul.) Triana & Planch. | 13.5 |
|  |  |  | Platypodium elegans Vogel | 11.1 |
|  |  |  | Ocotea guianensis Aubl. | 9.3 |
|  |  |  | Talisia angustifolia Radlk. | 8.0 |
|  |  |  | Mabea fistulifera Mart. | 7.5 |
|  |  |  | Dendropanax arboreus (L.) Decne. & Planch. | 7.2 |
|  |  |  | Cordia alliodora (Ruíz & Pavón) Oken | 6.7 |
|  |  |  | Cecropia palmata Willd. | 6.4 |
| CP-1 | Papilionaceae | 8 | Combretum leprosum Mart. | 37.6 |
|  | Annonaceae | 4 | Anadenanthera colubrina (Vell.) Brenan | 29.9 |

| Plot | Most Speciose Families | Spp. | Most Important Species | IVI |
|---|---|---|---|---|
| | Sapindaceae | 3 | Aspidosperma cylindrocarpon Müll. Arg. | 23.7 |
| | | | Spondias mombin L. | 22.9 |
| | | | Aspidosperma macrocarpon Mart. | 17.6 |
| | | | Luehea candicans Mart. | 16.9 |
| | | | Tabebuia impetiginosa (Mart. ex DC.) Standl. | 15.6 |
| | | | Callisthene fasciculata Mart. | 14.4 |
| | | | Pseudobombax longiflorum (Mart. & Zucc.) Robyns | 9.0 |
| | | | Sebastiania huallagensis Croizat | 8.4 |
| | | | Amburana caerensis (Allemão) A.C. Sm. | 8.4 |
| | | | Casearia gossypiosperma Brig. | 8.2 |
| CP-2 | Mimosaceae | 5 | Combretum leprosum Mart. | 28.2 |
| | Caesalpiniaceae | 5 | Chorisia integrifolia Ulbr. | 25.5 |
| | Flacourtiaceae | 4 | Spondias mombin L. | 22.6 |
| | | | Trichilia elegans A. Juss. | 19.3 |
| | | | Simira sp. 1 | 15.6 |
| | | | Talisia esculenta (A. St.-Hil.) Radlk. | 11.2 |
| | | | Guazuma ulmifolia Lam. | 11.0 |
| | | | Neea amplifolia Donn. Sw. | 10.7 |
| | | | Casearia gossypiosperma Brig. | 9.7 |
| | | | Inga cylindrica (Vell.) Mart. | 9.2 |
| | | | Aspidosperma cylindrocarpon Müll. Arg. | 8.6 |
| | | | Machaerium acutifolium Vogel | 8.5 |
| CR-1 | Moraceae | 8 | Brosimum lactescens (S. Moore) Bergius | 54.2 |
| | Sapotaceae | 6 | Maquira coriacea (Karsten) Bergius | 39.6 |
| | Mimosaceae | 6 | Trichilia inaequilatera T. D. Penn. | 19.1 |
| | | | Annonaceae Indet. 1 | 18.6 |

| Plot | Most Speciose Families | Spp. | Most Important Species | IVI |
|---|---|---|---|---|
| | | | Symmeria paniculata Benth. | 18.0 |
| | | | Diospyros pseudoxylopia Mildbr. | 13.0 |
| | | | Annonaceae Indet. 2 | 11.2 |
| | | | Micropholis venulosa (Mart. & Eichl.) Pierre | 9.6 |
| | | | Pouteria cuspidata (A. DC.) Baehni | 8.7 |
| | | | Derris sp. 1 | 8.4 |
| | | | Mouriri acutiflora Naudin | 7.9 |
| | | | Abarema jupunba (Willd.) Britton & Killip | 6.5 |
| CR-2 | Mimosaceae | 7 | Brosimum lactescens (S. Moore) Bergius | 39.0 |
| | Moraceae | 7 | Maquira coriacea (Karsten) Bergius | 29.9 |
| | Sapotaceae | 6 | Hevea brasiliensis (Willd. ex Juss.) Müll. Arg. | 18.0 |
| | | | Micropholis venulosa (Mart. & Eichl.) Pierre | 15.9 |
| | | | Inga laurina (Sw.) Willd. | 14.7 |
| | | | Annonaceae Indet. 1 | 14.4 |
| | | | Trichilia inaequilatera T. D. Penn. | 13.2 |
| | | | Derris sp. 1 | 12.3 |
| | | | Pouteria cuspidata (A. DC.) Baehni | 11.9 |
| | | | Casearia sp. 1 | 11.5 |
| | | | Licania kunthiana Hook. f. | 10.6 |
| | | | Abarema jupunba (Willd.) Britton & Killip | 8.2 |
| EN-1 | Sapotaceae | 4 | Chrysobalanaceae Indet. 1 | 58.6 |
| | Chrysobalanaceae | 4 | Sacoglottis mattogrossensis Malme | 45.7 |
| | Melastomataceae | 4 | Xylopia sp. 1 | 41.0 |
| | | | Siphoneugena occidentalis Legrand | 15.9 |
| | | | Alchornea schomburgkii Klotzsch | 15.4 |
| | | | Palicourea sp. 1 | 13.3 |

| Plot | Most Speciose Families | Spp. | Most Important Species | IVI |
|---|---|---|---|---|
| | | | Humiria balsamifera A. St.-Hil. | 10.9 |
| | | | Calophyllum longifolium Willd. | 10.2 |
| | | | Emmotum nitens (Benth.) Miers | 9.6 |
| | | | Roupala montana Aubl. | 7.4 |
| | | | Guatteria sp. 1 | 7.1 |
| | | | Endlicheria paniculata (Spreng.) J. F. Macbr. | 6.6 |
| EN-2 | Lauraceae | 3 | Chrysobalanaceae Indet. 1 | 56.9 |
| | Caesalpiniaceae | 3 | Sacoglottis mattogrossensis Malme | 44.4 |
| | Vochysiaceae | 3 | Xylopia sp. 1 | 30.3 |
| | Melastomataceae | 3 | Alchornea schomburgkii Klotzsch | 17.6 |
| | Rubiaceae | 3 | Siphoneugena occidentalis Legrand | 17.5 |
| | Sapotaceae | 3 | Ocotea guianensis Aubl. | 10.6 |
| | | | Calophyllum longifolium Willd. | 8.5 |
| | | | Pouteria bangii (Rusby) T. D. Penn. | 8.3 |
| | | | Palicourea sp. 1 | 8.1 |
| | | | Humiria balsamifera A. St.-Hil. | 7.0 |
| | | | Miconia myriantha Benth. | 7.0 |
| | | | Sclerolobium rugosum Mart. ex Benth. | 5.1 |
| FO-b | Moraceae | 4 | Qualea sp. 1 | 109.5 |
| | Rubiaceae | 3 | X-indet. Indet. 4 | 58.0 |
| | Myristicaceae | 3 | Hirtella sp. 1 | 23.7 |
| | Caesalpiniaceae | 3 | Brosimum guianense (Aubl.) Huber | 18.5 |
| | | | Rubiaceae Indet. 1 | 16.1 |
| | | | Moraceae Indet. 2 | 12.1 |
| | | | Alibertia edulis (Richard) A. Richard ex A. DC. | 10.4 |
| | | | Virola elongata (Benth.) Warb. | 7.3 |

| Plot | Most Speciose Families | Spp. | Most Important Species | IVI |
|---|---|---|---|---|
| | | | Xylopia sp. 3 | 4.7 |
| | | | Virola sebifera Aubl. | 3.8 |
| | | | Pagamea guianensis Aubl. | 3.7 |
| | | | Copaifera reticulata Ducke | 3.2 |
| H1-1 | Caesalpiniaceae | 8 | Cheiloclinium cognatum (Miers) A. C. Sm. | 18.9 |
| | Papilionaceae | 8 | Erisma uncinatum Warm. | 16.8 |
| | Moraceae | 8 | Talisia angustifolia Radlk. | 11.9 |
| | | | Miconia holosericea (L.) A. DC. | 11.5 |
| | | | Leguminosae-Mim Indet. 5 | 10.5 |
| | | | Qualea paraensis Ducke | 9.1 |
| | | | Apuleia leiocarpa (Vogel) J. F. Macbr. | 7.4 |
| | | | Sclerolobium bracteosum Harms | 7.4 |
| | | | Pera sp. 1 | 7.1 |
| | | | Euterpe precatoria Mart. | 7.1 |
| | | | Pseudolmedia laevis (Ruiz & Pav.) J. F. Macbr. | 6.5 |
| | | | Sloanea eichleri K. Schum. | 6.4 |
| H1-2 | Moraceae | 9 | Erisma uncinatum Warm. | 30.7 |
| | Caesalpiniaceae | 6 | Euterpe precatoria Mart. | 22.8 |
| | Sapotaceae | 5 | Cheiloclinium cognatum (Miers) A. C. Sm. | 19.1 |
| | Rubiaceae | 5 | Pseudolmedia laevis (Ruiz & Pav.) J. F. Macbr. | 15.1 |
| | Palmae | 5 | Pourouma guianensis Aubl. | 12.3 |
| | Bignoniaceae | 5 | Rinoreocarpus ulei (Melchior) Ducke | 11.5 |
| | Sapindaceae | 5 | Xylopia sp. 2 | 10.9 |
| | | | Inga thibaudiana A. DC. | 9.6 |
| | | | Apuleia leiocarpa (Vogel) J. F. Macbr. | 8.8 |
| | | | Qualea paraensis Ducke | 8.2 |

| Plot | Most Speciose Families | Spp. | Most Important Species | IVI |
|---|---|---|---|---|
| | | | Socratea exorrhiza (Mart.) H. L. Wendl. | 7.7 |
| | | | Eugenia sp. 1 | 6.7 |
| H2-1 | Mimosaceae | 6 | Metrodorea flavida K. Krause | 24.8 |
| | Palmae | 5 | Sloanea gracilis Uittien | 22.3 |
| | Moraceae | 5 | Pouteria glomerata (Pohl ex Miq.) Radlk. | 20.6 |
| | Papilionaceae | 5 | Inga marginata Willd. | 15.3 |
| | | | Socratea exorrhiza (Mart.) H. L. Wendl. | 14.9 |
| | | | Conceveiba sp. 1 | 14.6 |
| | | | Pourouma guianensis Aubl. | 14.0 |
| | | | Jacaranda glabra (A. DC.) Bureau & K. Schum. | 13.6 |
| | | | Apuleia leiocarpa (Vogel) J. F. Macbr. | 11.0 |
| | | | Alchornea glandulosa Poepp. & Endl. | 10.4 |
| | | | Erisma uncinatum Warm. | 9.7 |
| | | | Xylopia sericea A. St.-Hil. | 9.6 |
| H2-2 | Mimosaceae | 6 | Socratea exorrhiza (Mart.) H. L. Wendl. | 22.2 |
| | Bignoniaceae | 5 | Metrodorea flavida K. Krause | 18.2 |
| | Papilionaceae | 5 | Conceveiba sp. 1 | 14.0 |
| | Palmae | 5 | Pouteria glomerata (Pohl ex Miq.) Radlk. | 13.8 |
| | | | Sloanea gracilis Uittien | 13.8 |
| | | | Pourouma guianensis Aubl. | 12.4 |
| | | | Pseudolmedia laevis (Ruiz & Pav.) J. F. Macbr. | 12.2 |
| | | | Erisma uncinatum Warm. | 9.7 |
| | | | Inga marginata Willd. | 9.2 |
| | | | Aspidosperma cylindrocarpon Müll. Arg. | 9.0 |
| | | | Turpinia occidentalis (Sw.) G. Don | 8.3 |
| | | | Alibertia verrucosa S. Moore | 8.2 |

| Plot | Most Speciose Families | Spp. | Most Important Species | IVI |
|---|---|---|---|---|
| IH2-3 | Myrtaceae | 6 | Metrodorea flavida K. Krause | 26.0 |
| | Bignoniaceae | 6 | Socratea exorrhiza (Mart.) H. L. Wendl. | 23.4 |
| | Sapotaceae | 5 | Ecclinusa lanceolata (Mart. & Eichler) Pierre | 15.8 |
| | Mimosaceae | 5 | Didymopanax morototoni (Aubl.) Decne. & Planch. | 15.3 |
| | | | Matayba guianensis Aubl. | 11.6 |
| | | | Pourouma cecropiifolia | 10.0 |
| | | | Attalea maripa (Aubl.) Mart. | 8.2 |
| | | | Guarea macrophylla Vahl. | 8.1 |
| | | | Pouteria macrophylla (Lam.) Eyma | 8.1 |
| | | | Virola sebifera Aubl. | 7.8 |
| | | | Apuleia leiocarpa (Vogel) J. F. Macbr. | 7.7 |
| | | | Guatteria hyposericea Diels | 5.7 |
| IH2-4 | Moraceae | 6 | Socratea exorrhiza (Mart.) H. L. Wendl. | 19.3 |
| | Lauraceae | 5 | Matayba guianensis Aubl. | 17.7 |
| | Melastomataceae | 5 | Aspidosperma multiflorum A. DC. | 13.0 |
| | | | Sloanea eichleri K. Schum. | 11.1 |
| | | | Physocalymma scaberrimun Pohl | 11.1 |
| | | | Pourouma cecropiifolia | 10.7 |
| | | | Miconia chrysophylla (Rich.) Urban | 10.2 |
| | | | Indet. 2 | 9.7 |
| | | | Enterolobium schomburgkii (Benth.) Benth. | 9.5 |
| | | | Virola sebifera Aubl. | 8.9 |
| | | | Nectandra sp. 2 | 8.7 |
| | | | Guatteria hyposericea Diels | 8.2 |
| LF-1 | Melastomataceae | 12 | Erisma uncinatum Warm. | 38.0 |
| | Papilionaceae | 11 | Qualea paraensis Ducke | 22.6 |

| Plot | Most Speciose Families | Spp. | Most Important Species | IVI |
|---|---|---|---|---|
| | Moraceae | 8 | Pseudolmedia laevis (Ruiz & Pav.) J. F. Macbr. | 20.9 |
| | | | Phenakospermum guianensis Aubl. | 19.8 |
| | | | Capirona decorticans Spruce | 15.6 |
| | | | Euterpe precatoria Mart. | 14.3 |
| | | | Sloanea eichleri K. Schum. | 10.5 |
| | | | Hyeronima oblonga (Tul.) Müll. Arg. | 10.5 |
| | | | Pseudolmedia macrophylla Trécul | 10.3 |
| | | | Amaioua guianensis Aubl. | 8.1 |
| | | | Miconia pyrifolia Naudin | 6.6 |
| | | | Socratea exorrhiza (Mart.) H. L. Wendl. | 6.4 |
| LF-2 | Moraceae | 10 | Erisma uncinatum Warm. | 40.7 |
| | Melastomataceae | 9 | Qualea paraensis Ducke | 25.4 |
| | Lauraceae | 7 | Sloanea eichleri K. Schum. | 19.5 |
| | | | Euterpe precatoria Mart. | 19.4 |
| | | | Hyeronima oblonga (Tul.) Müll. Arg. | 19.3 |
| | | | Pseudolmedia laevis (Ruiz & Pav.) J. F. Macbr. | 18.1 |
| | | | Pseudolmedia macrophylla Trécul | 13.3 |
| | | | Phenakospermum guianensis Aubl. | 13.1 |
| | | | Socratea exorrhiza (Mart.) H. L. Wendl. | 8.9 |
| | | | Capirona decorticans Spruce | 8.8 |
| | | | Vochysia obidensis Ducke | 8.2 |
| | | | Helicostylis tomentosa (Poepp.& Endl.) Rusby | 7.7 |
| LG-b | Annonaceae | 7 | Pseudolmedia laevis (Ruiz & Pav.) J. F. Macbr. | 23.9 |
| | Melastomataceae | 7 | Erisma uncinatum Warm. | 22.9 |
| | Lauraceae | 6 | Lauraceae Indet. 1 | 21.4 |
| | Sapotaceae | 6 | Aspidosperma rigidum Rusby | 18.5 |

| Plot | Most Speciose Families | Spp. | Most Important Species | IVI |
|---|---|---|---|---|
| | | | Guatteria sp. 3 | 15.7 |
| | | | Miconia chrysophylla (Rich.) Urban | 14.3 |
| | | | Qualea paraensis Ducke | 13.5 |
| | | | Miconia bulbalina (Don) Naudin | 12.6 |
| | | | Hyeronima oblonga (Tul.) Müll. Arg. | 12.0 |
| | | | Pourouma guianensis Aubl. | 10.4 |
| | | | Amaioua guianensis Aubl. | 10.2 |
| | | | Vochysia sp. 2 | 10.1 |
| LO-1 | Papilionaceae | 8 | Miconia poeggigii Triana | 26.7 |
| | Moraceae | 7 | Inga capitata Desv. | 25.1 |
| | Palmae | 5 | Rinoreocarpus ulei (Melchior) Ducke | 21.2 |
| | | | Pouteria caimito (Ruíz & Pavón) Radlk. | 18.8 |
| | | | Xylopia sp. 4 | 13.7 |
| | | | Brosimum guianense (Aubl.) Huber | 12.2 |
| | | | Sloanea gracilis Uittien | 11.6 |
| | | | Helicostylis sp. 1 | 9.9 |
| | | | Guarea guidonia (L.) Sleumer | 9.9 |
| | | | Inga laurina (Sw.) Willd. | 9.4 |
| | | | Buchenavia tomentosa Eichler | 8.7 |
| | | | Vochysia mapirensis Rusby | 7.0 |
| LO-2 | Papilionaceae | 7 | Rinoreocarpus ulei (Melchior) Ducke | 37.9 |
| | Moraceae | 7 | Miconia poeggigii Triana | 36.1 |
| | Melastomataceae | 5 | Xylopia sp. 4 | 16.8 |
| | | | Miconia sp. 4 | 14.5 |
| | | | Euterpe precatoria Mart. | 14.3 |
| | | | Vochysia mapirensis Rusby | 13.1 |

| Plot | Most Speciose Families | Spp. | Most Important Species | IVI |
|---|---|---|---|---|
| | | | Pseudolmedia laevis (Ruiz & Pav.) J. F. Macbr. | 11.9 |
| | | | Sloanea gracilis Uittien | 9.1 |
| | | | Hevea brasiliensis (Willd. ex Juss.) Müll. Arg. | 7.2 |
| | | | Pouteria caimito (Ruíz & Pavón) Radlk. | 7.2 |
| | | | Tapirira guianensis Aubl. | 6.4 |
| | | | Inga laurina (Sw.) Willd. | 5.6 |
| LT-1 | Papilionaceae | 4 | Terminalia sp. 1 | 60.7 |
| | Caesalpinaceae | 4 | Poeppigia sp. 1 | 24.0 |
| | Apocynaceae | 4 | Leguminosae Indet. 3 | 22.8 |
| | Burseraceae | 4 | Copaifera langsdorffii Desf. | 15.2 |
| | | | Terminalia fagifolia (Cambess.) Mart. & Zucc. | 14.8 |
| | | | Ormosia sp. 3 | 11.4 |
| | | | Aspidosperma macrocarpon Mart. | 10.3 |
| | | | X-indet Indet. | 10.3 |
| | | | Vochysia haenkeana Mart. | 9.9 |
| | | | Qualea parviflora Mart. | 9.7 |
| | | | Pterodon emarginatus Vogel | 9.6 |
| | | | Simarouba amara Aubl. | 7.4 |
| LT-2 | Papilionaceae | 4 | Terminalia sp. 1 | 51.4 |
| | Vochysiaceae | 4 | Leguminosae Indet. 3 | 36.7 |
| | Caesalpiniaceae | 3 | Qualea parviflora Mart. | 23.3 |
| | | | Vochysia haenkeana Mart. | 19.4 |
| | | | Pseudobombax longiflorum (Mart. & Zucc.) Robyns | 18.0 |
| | | | Hexachlamys sp. 2 | 16.3 |
| | | | Bowdichia sp. 1 | 15.2 |
| | | | Ormosia sp. 3 | 11.7 |

| Plot | Most Speciose Families | Spp. | Most Important Species | IVI |
|---|---|---|---|---|
| | | | Byrsonima orbignyana A. Juss. | 11.6 |
| | | | Norantea guianensis Aubl. | 10.5 |
| | | | Copaifera langsdorffii Desf. | 8.6 |
| | | | Eriotheca sp. 1 | 8.3 |
| LT-3 | Papilionaceae | 6 | Pseudolmedia rigida (Klotzsch & H. Karst.) Cuatrec. | 60.1 |
| | Euphorbiaceae | 5 | Euterpe precatoria Mart. | 35.9 |
| | Annonaceae | 5 | Lauraceae Indet. 1 | 22.2 |
| | Moraceae | 5 | Protium spruceanum (Benth.) Engl. | 18.2 |
| | Chrysobalanaceae | 5 | Xylopia emarginata Mart. | 16.1 |
| | | | Eschweilera parvifolia Mart. ex A. DC. | 15.8 |
| | | | Pouteria cuspidata (A. DC.) Baehni | 9.9 |
| | | | Protium heptaphyllum (Aubl.) Marchand. | 9.3 |
| | | | Prunus sp. 1 | 7.8 |
| | | | Licania apetala (E. Meyer) Fritsch | 7.0 |
| | | | Brosimum utile (Kunth) Pittier | 7.0 |
| | | | Meriania urceolata Triana | 5.6 |
| MV-1 | Papilionaceae | 11 | Physocalymma scaberrimun Pohl | 47.1 |
| | Malpighiaceae | 6 | Hirtella gracilipes (Hook. f.) Prance | 42.4 |
| | Moraceae | 6 | Inga ingoides (L. C. Rich.) Willd. | 18.9 |
| | | | Qualea cordata (Mart.) Spreng. | 17.1 |
| | | | Inga laurina (Sw.) Willd. | 13.9 |
| | | | Xylopia sericea A. St.-Hil. | 8.9 |
| | | | Hymenaea courbaril L. | 7.7 |
| | | | Cecropia concolor Willd. | 6.8 |
| | | | Terminalia amazonia (J.F. Gmel.) Exell | 6.2 |
| | | | Tabebuia serratifolia (Vahl.) G. Nicholson | 5.4 |

| Plot | Most Speciose Families | Spp. | Most Important Species | IVI |
|---|---|---|---|---|
| | | | Ceiba samauma (Mart.) K. Schum. | 5.0 |
| | | | Pera barbinervis (Klotz.) Pax & K. Hoffm. | 4.8 |
| SR-1 | Papilionaceae | 5 | Attalea speciosa (Aubl.) C. Mart. | 172.3 |
| | Anacardiaceae | 3 | Astronium urundeuva (Allemão) Engl. | 13.2 |
| | Chrysobalanaceae | 3 | Astrocaryum chonta Mart. | 12.6 |
| | Mimosaceae | 3 | Machaerium acutifolium Vogel | 12.0 |
| | | | Physocalymma scaberrimun Pohl | 7.1 |
| | | | Tabebuia roseo-alba (Ridley) Sandwith | 6.8 |
| | | | Pseudobombax marginatum (A. St.-Hil.) Robyns | 6.4 |
| | | | Platymiscium ulei Harms | 5.3 |
| | | | Dilodendron bipinnatum Radlk. | 5.1 |
| | | | Chaetocarpus echinocarpus (Baill.) Ducke | 4.9 |
| | | | Sacoglottis mattogrossensis Malme | 4.9 |
| | | | Astronium lecointei Ducke | 4.5 |

### *Alpha Diversity*

Measures of alpha diversity (Whittaker 1975) show similar results for each of the different indices calculated (richness, Simpson's 1-D, Shannon's H', and Fisher's $\alpha$; Table 2). Species richness among trees 10cm ≥ dbh ranged from 31 to 123 species in one ha. The richest plots were found at the tall forest and the liana forest sites. The seasonally inundated plots were the next richest, followed by the dry forest and the transition forest. Among plots that were sub-sampled for individuals ≥ 2.5 cm dbh, the richness ranged from 32 to 125 species in 0.1 ha.

The liana forest plots were the richest among those sampled, though the richest of the tall forest plots (H1-1) was not sampled using this methodology.

Simpson’s (1-D) represents the probability of picking two trees at random that are of different species (Krebs 1989). With the exception of plot SR-1, (1-D) ranged from 0.82 - 0.98 among the plots studied. The value for plot SR-1 was 0.55, which is indicative of the high frequency of the palm *Attalea speciosa*.

Shannon’s H’ ranged from 2.41 (SR-1) to 6.00 (IH2-3). H’ is sensitive to rare species (Krebs 1989) and low values in these plots indicate that these plots have relatively few rare species. The highest values for H’ were recorded in the tall forest and the liana forest, which have large numbers of species represented by a single individual.

Fisher’s $\alpha$ approximates the number of species represented by a single individual (Hayek and Buzas 1997). It ranged from 9.3 (SR-1) to 47.7 (H1-1). As with the other measures of diversity, the liana forest and the tall upland forest had the greatest values for Fisher’s $\alpha$.

The rate of species accumulation also differed markedly between plots (Figure 2.) The highest rates of species accumulation were found in the tall upland plots. The slope of the curve is steep even after several hundred individuals have been sampled. In contrast, the species accumulation curves for the dry forest and transitional plots begin to level out after 100 to 200 individuals sampled.

Figure 2

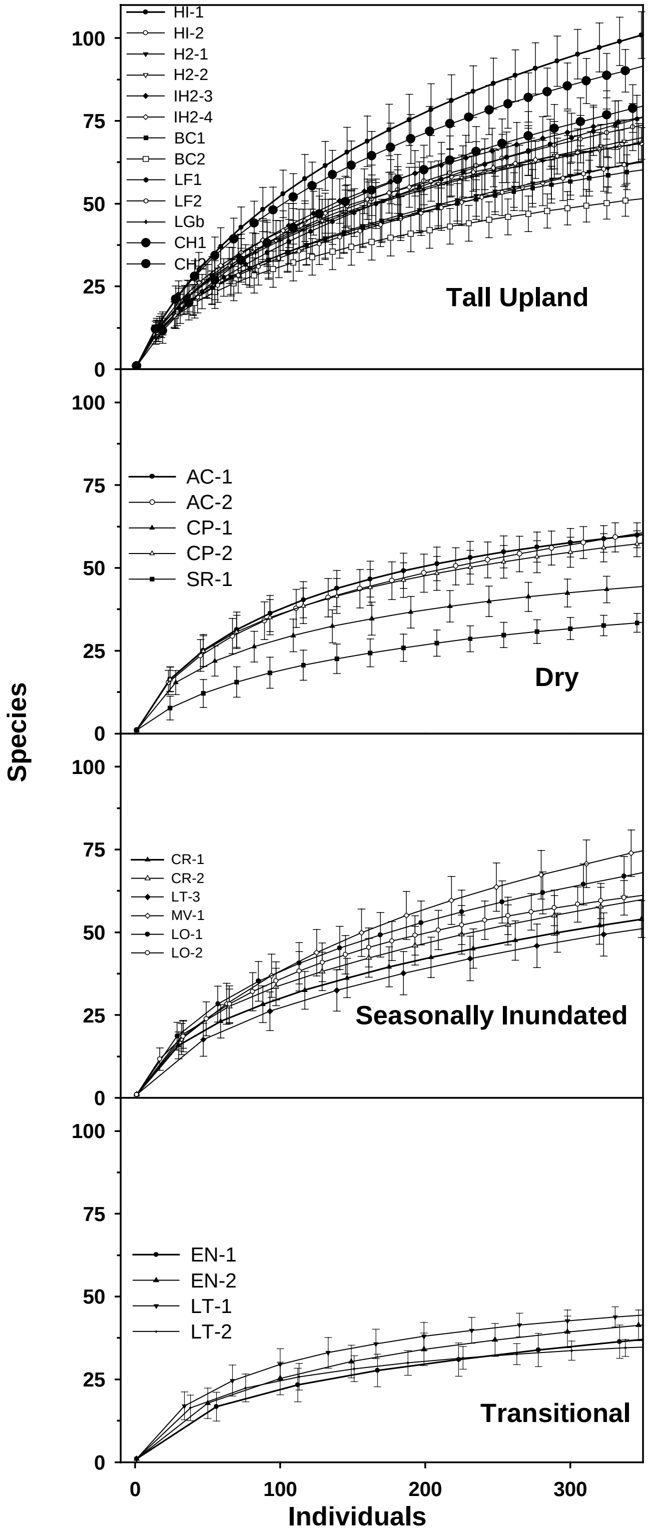

**Figure 2. Species accumulation curves for each of the 29 plots. For ease of comparison, the horizontal axis of each plot has been truncated at 387, which is the number of stems found in the plot with the lowest density (FO-b).**

### ***Beta Diversity***

Multiple analyses highlight the large level of between-habitat (beta) diversity as defined by (Whittaker 1975). As shown in Table 3, no species are universally common and only 4 out of 896 total species recorded are present in more than half of the plots. We used Sorensen's similarity index to further illustrate that the overlap in species composition of the study plots was low.

Sorensen's index is a measure of the number of species shared between two sites relative to the total combined number of species at both sites (Magurran 1988). We computed pair-wise comparisons for all sites for both Sorensen's presence/absence index and Sorensen's abundance index (Table 4). We found that the only plots that share more than half of their species are plots that are located at the same site. Among sites of the same forest type, we found moderate amounts of species overlap only in the dry forest and tall upland forest groups. Between forest types, there was very little species overlap. The *cerrado* transition class had few species in common with any of the other forest types and the overlap among dry forest plots and seasonally inundated forests plots was minimal. The liana forest had moderate amounts of overlap with the tall upland forest and somewhat less overlap with the dry forest.

### ***Soils***

The edaphic conditions in the park range from very young, seasonally deposited alluvium (Entisols and Inceptisols) to well-drained and highly weathered upland soils (Ultisols and Oxisols)(Table 5). At most sites, the soils are sandy, though the seasonally inundated sites CR-1 and CR-2 have silty clays and the seasonally inundated sites LO-1, LO-2, and FO-b are loamy. The H2-2 site is also a silty loam despite its upland setting. Organic matter ranges from 0.4% to 21.2 %. Because most of these soils are low in clays and have low amounts of organic matter, cation exchange capacity (CEC) is generally low, ranging from 1.3 to 11.7. The percent base saturation (PBS) of these soils is low in many of the plots, ranging from 8% in the swamp forest plot (LT-3) to greater than 90% in five of the upland plots. As is typical for many tropical areas, the soils are acidic, with pH values ranging from 4 to 6.3, and the soils are free of carbonates.

On average, the soils in the dry forest plots were the most fertile, though two of the dry forest plots (CP-2 and SR-1) had moderate to low values for CEC. Mean CEC for the dry forest plots was nearly double that of the cerrado transition plots and the liana forest plots. Soils in the tall upland forest and the seasonally inundated forests were intermediate to the dry forests and cerrado transition plots. For plots in each of these classes the soil conditions varied considerably. The H2-1 and H2-2 plots had soils that are among the richest of any site, with comparable CEC and base saturation levels to the dry forest sites. In contrast, other tall upland forest plots, LF-1, LF-2, H1-1 and H1-2, showed modest CEC levels with low percent base saturation. Among the inundated plots, we found similar variation. Variability among soil types can be attributed to geological substrate in upland plots and the variable nature of inundation and sedimentation in riparian habitats

**Table 4. Sorensen’s similarity index calculated for all plots. The value above the diagonal is the Sorensen’s abundance index and the value below the diagonal Sorensen’s incidence index for presence/absence data. Values greater than 0.25 are in bold and a box surrounds values greater than 0.5.**

| | | Cerrado Transition | | | | Dry Forest | | | | | Tall Upland Forest | | | | | | | | | | | | | Seasonally Inundated Forest | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | EN1 | EN2 | LT1 | LT2 | AC1 | AC2 | CP1 | CP2 | SR1 | H11 | H12 | H21 | H22 | IH23 | IH24 | BC1 | BC2 | LF1 | LF2 | LGb | CH1 | CH2 | CR1 | CR2 | LT3 | MV1 | LO1 | LO2 | FOb |
| Cerrado Transition | EN1 | | **0.79** | 0.02 | 0.02 | - | - | - | - | 0.02 | 0.02 | 0.03 | - | - | 0.01 | 0.04 | 0.04 | 0.03 | 0.01 | 0.01 | 0.04 | 0.02 | 0.04 | 0.01 | 0.02 | 0.02 | 0.02 | 0.01 | 0.02 | 0.02 |
| | EN2 | **0.64** | | 0.02 | 0.01 | - | - | - | - | 0.02 | 0.04 | 0.04 | - | - | 0.03 | 0.04 | 0.08 | 0.07 | 0.03 | 0.03 | 0.03 | 0.04 | 0.06 | 0.01 | 0.03 | 0.03 | 0.02 | 0.03 | 0.03 | 0.02 |
| | LT1 | 0.15 | 0.08 | | **0.55** | 0.02 | - | 0.07 | 0.04 | 0.01 | 0.02 | - | 0.01 | - | 0.03 | 0.03 | - | 0.01 | 0.01 | - | 0.01 | - | 0.01 | - | - | 0.02 | 0.03 | 0.01 | - | 0.02 |
| | LT2 | 0.09 | 0.07 | **0.6** | | 0.02 | - | 0.06 | 0.02 | 0.01 | 0.01 | - | 0.01 | 0.01 | 0.02 | 0.02 | - | 0.01 | 0.01 | - | 0.01 | - | 0.01 | - | - | 0.01 | 0.02 | 0.01 | - | 0.01 |
| Dry Forest | AC1 | 0.02 | - | 0.09 | 0.1 | | **0.61** | **0.34** | **0.26** | 0.12 | 0.03 | 0.02 | 0.07 | 0.09 | 0.04 | 0.03 | 0.01 | 0.01 | 0.02 | 0.01 | 0.02 | 0.05 | 0.08 | 0.01 | 0.01 | - | 0.09 | 0.02 | 0.02 | - |
| | AC2 | 0.02 | - | 0.04 | 0.04 | **0.64** | | **0.33** | **0.33** | 0.12 | 0.03 | 0.02 | 0.08 | 0.08 | 0.03 | 0.02 | - | 0.01 | 0.01 | 0.01 | 0.01 | 0.04 | 0.09 | - | 0.01 | - | 0.09 | 0.03 | 0.01 | - |
| | CP1 | - | - | 0.08 | 0.11 | **0.45** | **0.44** | | **0.35** | 0.05 | 0.01 | - | 0.03 | 0.05 | 0.01 | 0.01 | - | - | 0.01 | 0.01 | 0.02 | 0.05 | 0.06 | - | 0.01 | - | 0.05 | 0.02 | 0.01 | - |
| | CP2 | 0.02 | - | 0.09 | 0.08 | **0.34** | **0.44** | **0.5** | | 0.06 | 0.03 | 0.03 | 0.09 | 0.11 | 0.07 | 0.05 | - | 0.01 | 0.01 | 0.01 | 0.04 | 0.04 | 0.1 | - | 0.01 | 0.02 | 0.07 | 0.03 | 0.01 | - |
| | SR1 | 0.07 | 0.07 | 0.05 | 0.08 | **0.28** | **0.27** | 0.18 | 0.2 | | 0.04 | 0.04 | 0.03 | 0.02 | 0.04 | 0.03 | 0.01 | 0.01 | 0.03 | 0.02 | 0.01 | 0.02 | 0.05 | 0.01 | 0.01 | 0.01 | 0.05 | 0.02 | 0.02 | - |
| Tall Upland Forest | H11 | 0.09 | 0.09 | 0.06 | 0.04 | 0.07 | 0.08 | 0.05 | 0.07 | 0.09 | | **0.51** | 0.08 | 0.13 | 0.13 | 0.17 | 0.21 | 0.21 | **0.26** | 0.23 | 0.17 | 0.16 | 0.15 | 0.01 | 0.03 | 0.06 | 0.04 | 0.09 | 0.13 | 0.01 |
| | H12 | 0.07 | 0.05 | 0.01 | 0.01 | 0.1 | 0.09 | 0.04 | 0.06 | 0.09 | **0.61** | | 0.15 | 0.23 | 0.11 | 0.15 | **0.25** | **0.25** | **0.3** | **0.31** | 0.23 | 0.12 | 0.12 | 0.01 | 0.03 | 0.12 | 0.04 | 0.13 | 0.19 | 0.01 |
| | H21 | 0.02 | 0.03 | 0.05 | 0.07 | 0.18 | 0.15 | 0.11 | 0.2 | 0.13 | 0.19 | 0.18 | | **0.61** | 0.23 | 0.13 | 0.05 | 0.06 | 0.09 | 0.08 | 0.15 | 0.08 | 0.12 | 0.02 | 0.01 | 0.01 | 0.06 | 0.07 | 0.06 | - |
| | H22 | 0.01 | 0.01 | 0.03 | 0.05 | 0.19 | 0.15 | 0.13 | 0.17 | 0.1 | 0.2 | 0.19 | **0.54** | | **0.25** | 0.2 | 0.09 | 0.09 | 0.15 | 0.15 | 0.21 | 0.11 | 0.14 | 0.01 | 0.01 | 0.01 | 0.05 | 0.07 | 0.08 | 0.01 |
| | IH23 | 0.05 | 0.05 | 0.06 | 0.07 | 0.1 | 0.11 | 0.04 | 0.11 | 0.11 | 0.24 | 0.15 | 0.16 | 0.16 | | **0.5** | 0.17 | 0.17 | 0.1 | 0.1 | 0.11 | 0.09 | 0.12 | 0.02 | 0.02 | 0.02 | 0.05 | 0.03 | 0.03 | 0.01 |
| | IH24 | 0.11 | 0.09 | 0.08 | 0.09 | 0.11 | 0.1 | 0.05 | 0.1 | 0.11 | **0.25** | 0.16 | 0.21 | 0.18 | **0.58** | | **0.29** | **0.28** | 0.2 | 0.19 | 0.24 | 0.13 | 0.14 | 0.01 | 0.02 | 0.03 | 0.08 | 0.03 | 0.06 | 0.01 |
| | BC1 | 0.18 | 0.2 | 0.02 | - | 0.04 | 0.01 | - | - | 0.06 | **0.25** | **0.25** | 0.14 | 0.1 | **0.27** | **0.38** | | **0.66** | **0.4** | **0.42** | **0.29** | 0.11 | 0.08 | 0.02 | 0.03 | 0.09 | 0.03 | 0.06 | 0.15 | - |
| | BC2 | 0.15 | 0.16 | 0.04 | 0.04 | 0.08 | 0.05 | - | 0.03 | 0.06 | **0.32** | **0.33** | 0.12 | 0.12 | **0.29** | **0.36** | **0.55** | | **0.32** | **0.33** | 0.23 | 0.12 | 0.08 | 0.01 | 0.02 | 0.08 | 0.02 | 0.06 | 0.18 | - |
| | LF1 | 0.06 | 0.08 | 0.04 | 0.04 | 0.08 | 0.07 | 0.04 | 0.07 | 0.11 | **0.35** | **0.33** | 0.14 | 0.17 | 0.19 | **0.27** | **0.3** | **0.32** | | **0.7** | **0.34** | **0.29** | 0.11 | 0.01 | 0.02 | 0.08 | 0.04 | 0.07 | 0.15 | - |
| | LF2 | 0.06 | 0.07 | - | 0.02 | 0.07 | 0.07 | 0.03 | 0.05 | 0.1 | **0.28** | **0.27** | 0.12 | 0.16 | 0.19 | 0.22 | **0.28** | **0.3** | **0.64** | | **0.29** | 0.24 | 0.1 | 0.01 | 0.03 | 0.1 | 0.03 | 0.07 | 0.15 | - |
| | LGb | 0.13 | 0.1 | 0.06 | 0.02 | 0.08 | 0.05 | 0.04 | 0.05 | 0.05 | **0.25** | 0.22 | **0.26** | **0.26** | 0.22 | **0.29** | 0.24 | 0.22 | **0.35** | **0.28** | | 0.11 | 0.1 | 0.02 | 0.02 | 0.1 | 0.02 | 0.06 | 0.1 | - |
| Liana For. | CH1 | 0.05 | 0.09 | 0.01 | 0.03 | 0.14 | 0.16 | 0.11 | 0.16 | 0.12 | **0.28** | **0.26** | 0.22 | 0.23 | 0.18 | 0.19 | 0.14 | 0.22 | **0.28** | **0.28** | 0.2 | | **0.36** | - | 0.01 | 0.01 | 0.05 | 0.04 | 0.06 | 0.01 |
| | CH2 | 0.1 | 0.1 | 0.04 | 0.04 | 0.17 | 0.19 | 0.14 | 0.18 | 0.15 | **0.25** | 0.23 | **0.25** | **0.26** | 0.2 | 0.21 | 0.16 | 0.2 | 0.2 | 0.23 | 0.19 | **0.51** | | 0.02 | 0.02 | 0.02 | 0.09 | 0.04 | 0.05 | 0.02 |

| | | Cerrado Transition | | | | Dry Forest | | | | | Tall Upland Forest | | | | | | | | | | | | | Seasonally Inundated Forest | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | EN1 | EN2 | LT1 | LT2 | AC1 | AC2 | CP1 | CP2 | SR1 | H11 | H12 | H21 | H22 | IH23 | IH24 | BC1 | BC2 | LF1 | LF2 | LGb | CH1 | CH2 | CR1 | CR2 | LT3 | MV1 | LO1 | LO2 | FOb |
| Seasonally Inundated Forest | CR1 | 0.05 | 0.03 | - | - | 0.03 | 0.01 | 0.02 | 0.02 | 0.04 | 0.04 | 0.06 | 0.06 | 0.05 | 0.07 | 0.06 | 0.06 | 0.03 | 0.07 | 0.08 | 0.04 | 0.01 | 0.06 | | **0.54** | 0.04 | 0.04 | 0.02 | 0.03 | 0.01 |
| | CR2 | 0.11 | 0.09 | 0.02 | - | 0.06 | 0.06 | 0.03 | 0.03 | 0.05 | 0.09 | 0.1 | 0.09 | 0.07 | 0.09 | 0.1 | 0.12 | 0.09 | 0.11 | 0.13 | 0.07 | 0.04 | 0.1 | **0.55** | | 0.05 | 0.11 | 0.1 | 0.05 | 0.04 |
| | LT3 | 0.14 | 0.09 | 0.05 | 0.05 | 0.04 | 0.01 | 0.02 | 0.03 | 0.05 | 0.14 | 0.11 | 0.05 | 0.04 | 0.07 | 0.09 | 0.11 | 0.1 | 0.13 | 0.14 | 0.15 | 0.06 | 0.08 | 0.07 | 0.1 | | 0.04 | 0.04 | 0.07 | 0.02 |
| | MV1 | 0.07 | 0.07 | 0.08 | 0.09 | **0.25** | 0.23 | 0.13 | 0.21 | 0.19 | 0.13 | 0.14 | 0.13 | 0.14 | 0.13 | 0.11 | 0.08 | 0.1 | 0.12 | 0.12 | 0.05 | 0.14 | 0.19 | 0.07 | 0.18 | 0.17 | | 0.1 | 0.05 | 0.02 |
| | LO1 | 0.06 | 0.06 | 0.03 | 0.03 | 0.11 | 0.11 | 0.06 | 0.08 | 0.07 | 0.17 | 0.21 | 0.16 | 0.14 | 0.1 | 0.12 | 0.13 | 0.13 | 0.18 | 0.17 | 0.14 | 0.15 | 0.15 | 0.04 | 0.15 | 0.14 | 0.23 | | **0.52** | 0.05 |
| | LO2 | 0.08 | 0.08 | 0.02 | 0.02 | 0.07 | 0.06 | 0.03 | 0.03 | 0.11 | 0.17 | 0.19 | 0.12 | 0.11 | 0.11 | 0.12 | 0.17 | 0.17 | 0.18 | 0.22 | 0.16 | 0.14 | 0.14 | 0.09 | 0.12 | 0.16 | 0.15 | **0.59** | | 0.01 |
| | FOb | 0.18 | 0.17 | 0.1 | 0.09 | - | 0.02 | - | 0.02 | 0.03 | 0.03 | 0.05 | - | 0.02 | 0.03 | 0.04 | 0.02 | - | 0.03 | 0.03 | 0.02 | 0.01 | 0.04 | 0.04 | 0.06 | 0.11 | 0.05 | 0.05 | 0.04 | |

### *Factors affecting composition and diversity*

To examine the importance of geographic distance in determining floristic composition, we plotted the similarity between pairs of plots against the geographic distance between the plots (Figure 3). Even among plots with similar physiognomic characteristics, we found that geographic proximity was not correlated with floristic similarity. Paired plots located only two hundred meters apart share less than 2/3 of their species. At greater distances between-plot similarity was even lower, but there is no discernable trend at increased distance.

We included all 890 species from 28 plots in the canonical correspondence analysis; however, the interpretation is based only on the more common species. More than half (475) of all species in the dataset are represented by five or fewer individuals and because of their rarity, are less useful as indicators of specific habitats. We chose to consider the species scores

**Table 5. Soil characteristics of the A horizon for 28 of the study plots.**

| | Plot | pH$_w$ | Elec. Cond. 1:5 uS cm$^{-1}$ | K (cmol/kg) | Na (cmol/kg) | Ca (cmol/kg) | Mg (cmol/kg) | Total Exch. Bases (cmol/kg) | C.E.C. (cmol/kg) | % Base Sat | Acidity cmol/kg | Al cmol/kg | Al/CEC | P, Olsen (mg/kg) | O.M. % | Total N % | Sand% | Silt% | Clay% | Soil Order |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Cerrado Transition | EN-1 | 4.5 | 32 | 0.06 | 0.02 | 0.2 | 0.1 | 0.4 | 1.9 | 20 | 1.5 | 1.3 | 0.68 | 21 | 0.4 | 0.07 | 85 | 1 | 14 | Inceptisol |
| | EN-2 | 5.1 | 24 | 0.05 | 0.05 | 0.1 | 0.1 | 0.3 | 1.3 | 23 | 1 | 0.6 | 0.46 | 1 | 0.9 | 0.03 | 73 | 6 | 21 | Inceptisol |
| | LT-1 | 4.3 | 70 | 0.44 | 0.09 | 0.2 | 0.2 | 0.9 | 5 | 18 | 4.1 | 3 | 0.6 | 3 | 2.7 | 0.25 | 72 | 8 | 20 | Inceptisol |
| | LT-2 | 4.3 | 35 | 0.17 | 0.05 | 0.2 | 0.2 | 0.6 | 3.8 | 16 | 3.2 | 2.6 | 0.68 | 7 | 2.5 | 0.22 | 79 | 3 | 18 | Entisol |
| Dry Forest | AC-1 | 6.1 | 64 | 0.5 | 0.11 | 5.5 | 2.2 | 8.3 | 8.7 | 95 | 0.4 | | 0 | 3 | 4.4 | 0.33 | 63 | 14 | 23 | Alfisol |
| | AC-2 | 6.3 | 44 | 0.53 | 0.11 | 4.3 | 1.4 | 6.3 | 6.5 | 97 | 0.2 | | 0 | 2 | 2.9 | 0.22 | 47 | 20 | 33 | Alfisol |
| | CP-1 | 5.9 | 50 | 0.22 | 0.08 | 5.2 | 1.2 | 6.7 | 6.9 | 97 | 0.2 | | 0 | 6 | 3.3 | 0.25 | 55 | 20 | 25 | Entisol |
| | CP-2 | 5.4 | 33 | 0.2 | 0.07 | 1.7 | 0.4 | 2.4 | 3.2 | 75 | 0.8 | 0.2 | 0.06 | 3 | 4.4 | 0.52 | 64 | 24 | 12 | Entisol |
| | SR-1 | 5.8 | 20 | 0.1 | 0.03 | 0.6 | 0.4 | 1.1 | 1.3 | 85 | 0.2 | | 0 | 1 | 0.8 | 0.07 | 85 | 5 | 10 | Alfisol |
| Tall Upland Forest | BC-1 | 3.4 | 81 | 0.07 | 0.05 | 0.1 | 0.1 | 0.32 | 3.1 | 10 | 2.8 | 1.9 | 0.61 | 3 | 3.2 | 0.22 | 39 | 46 | 15 | Oxisol |
| | BC-2 | 3.8 | 60 | 0.1 | 0.05 | 0.1 | 0.1 | 0.35 | 2.7 | 13 | 2.3 | 2 | 0.74 | 2 | 2.7 | 0.18 | 77 | 9 | 14 | Oxisol |
| | H1-1 | 4 | 55 | 0.09 | 0.05 | 0.2 | 0.1 | 0.4 | 2.5 | 16 | 2.1 | 1.7 | 0.68 | 3 | 1 | 0.09 | 74 | 4 | 22 | Ultisol |
| | H1-2 | 4.3 | 33 | 0.1 | 0.04 | 0.2 | 0.1 | 0.4 | 2.1 | 19 | 1.7 | 1.1 | 0.52 | 1 | 0.9 | 0.07 | 74 | 6 | 20 | Ultisol |

|  | Plot | $pH_w$ | Elec. Cond. 1:5 uS $cm^{-1}$ | K (cmol/kg) | Na (cmol/kg) | Ca (cmol/kg) | Mg (cmol/kg) | Total Exch. Bases (cmol/kg) | C.E.C. (cmol/kg) | % Base Sat | Acidity cmol/kg | Al cmol/kg | Al/CEC | P, Olsen (mg/kg) | O.M. % | Total N % | Sand% | Silt% | Clay% | Soil Order |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
|  | H2-1 | 5.4 | 40 | 0.26 | 0.07 | 2.4 | 0.7 | 3.4 | 3.7 | 92 | 0.3 |  | 0 | 2 | 2.4 | 0.19 | 58 | 17 | 25 | Alfisol |
|  | H2-2 | 5.5 | 87 | 0.75 | 0.13 | 7.1 | 3.3 | 11.3 | 11.7 | 97 | 0.4 |  | 0 | 1 | 21.2 | 1.2 | 33 | 59 | 8 | Alfisol |
|  | IH2-3 | 4.2 | 86 | 0.21 | 0.13 | 0.1 | 0.1 | 0.54 | 3.6 | 15 | 3 | 2.2 | 0.61 | 3 | 5.1 | 0.32 | 33 | 18 | 49 | Alfisol |
|  | LF-1 | 4.4 | 41 | 0.09 | 0.05 | 0.3 | 0.1 | 0.5 | 2.6 | 19 | 2.1 | 1.6 | 0.62 | 2 | 1.2 | 0.1 | 64 | 8 | 28 | Oxisol |
|  | LF-2 | 4.2 | 34 | 0.09 | 0.04 | 0.4 | 0.1 | 0.6 | 2.3 | 26 | 1.7 | 1.3 | 0.57 | 2 | 1.1 | 0.09 | 77 | 1 | 22 | Ultisol |
|  | LG-b | 4.1 | 81 | 0.13 | 0.04 | 0.2 | 0.1 | 0.5 | 4.6 | 11 | 4.1 | 3.3 | 0.72 | 5 | 3.1 | 0.36 | 63 | 12 | 25 | Ultisol |
| Liana Forest | CH1 | 4.4 | 82 | 0.2 | 0.07 | 0.4 | 0.8 | 1.5 | 2.8 | 54 | 1.3 | 0.7 | 0.25 | 2 | 2.9 | 0.19 | 51 | 9 | 40 | Alfisol |
|  | CH2 | 5.5 | 49 | 0.32 | 0.05 | 1.1 | 1 | 2.5 | 2.8 | 89 | 0.3 |  | 0 | 1 | 2.2 | 0.16 | 65 | 8 | 27 | Alfisol |
| Seasonally Inundated Forest | CR-1 | 4.3 | 65 | 0.43 | 0.17 | 1.1 | 0.9 | 2.6 | 9.1 | 29 | 6.5 | 5.3 | 0.58 | 7 | 3.4 | 0.3 | 6 | 58 | 36 | Entisol |
|  | CR-2 | 4.8 | 63 | 0.66 | 0.21 | 2.8 | 2.4 | 6.1 | 8.9 | 69 | 2.8 | 1.9 | 0.21 | 3 | 3.2 | 0.31 | 2 | 29 | 69 | Entisol |
|  | LT-3 | 4.3 | 36 | 0.17 | 0.05 | 0.2 | 0.1 | 0.5 | 6.4 | 8 | 5.9 | 5 | 0.78 | 3 | 1.3 | 0.15 | 47 | 24 | 29 | Entisol |
|  | MV-1 | 5.1 | 22 | 0.26 | 0.05 | 0.5 | 0.3 | 1.1 | 1.8 | 61 | 0.7 | 0.4 | 0.22 | 1 | 1.4 | 0.1 | 60 | 20 | 20 | Entisol |
|  | LO-1 | 4.8 | 18 | 0.19 | 0.09 | 0.1 | 0.1 | 0.5 | 1.6 | 31 | 1.1 | 0.6 | 0.38 | 3 | 10.5 | 0.63 | 33 | 57 | 10 | Entisol |
|  | LO-2 | 4.8 | 21 | 0.37 | 0.08 | 0.1 | 0.2 | 0.8 | 3.2 | 25 | 2.4 | 1.8 | 0.56 | 1 | 5.5 | 0.45 | 31 | 39 | 30 | Entisol |
|  | FO-b | 4.9 | 18 | 0.11 | 0.04 | 0.2 | 0.1 | 0.5 | 2.5 | 20 | 2 | 1.3 | 0.52 | 1 | 2.7 | 0.26 | 27 | 46 | 27 | Entisol |

|  | Plot | $pH_w$ | Elec. Cond. 1:5 uS $cm^{-1}$ | K (cmol/kg) | Na (cmol/kg) | Ca (cmol/kg) | Mg (cmol/kg) | Total Exch. Bases (cmol/kg) | C.E.C. (cmol/kg) | % Base Sat | Acidity cmol/kg | Al cmol/kg | Al/CEC | P, Olsen (mg/kg) | O.M. % | Total N % | Sand% | Silt% | Clay% | Soil Order |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Means | Cerrado | 4.6 | 40.3 | 0.2 | 0.1 | 0.2 | 0.2 | 0.6 | 3.0 | 19.2 | 2.5 | 1.9 | 0.6 | 8.0 | 1.6 | 0.1 | 77.3 | 4.5 | 18.3 |  |
|  | Dry | 5.9 | 42.2 | 0.3 | 0.1 | 3.5 | 1.1 | 5.0 | 5.3 | 89.8 | 0.4 | 0.2 | 0.0 | 3.0 | 3.2 | 0.3 | 62.8 | 16.6 | 20.6 |  |
|  | Humid | 4.3 | 59.8 | 0.2 | 0.1 | 1.1 | 0.5 | 1.8 | 3.9 | 31.8 | 2.1 | 1.9 | 0.5 | 2.4 | 4.2 | 0.3 | 59.2 | 18.0 | 22.8 |  |
|  | Liana | 5.0 | 65.5 | 0.3 | 0.1 | 0.8 | 0.9 | 2.0 | 2.8 | 71.4 | 0.8 | 0.7 | 0.1 | 1.5 | 2.6 | 0.2 | 58.0 | 8.5 | 33.5 |  |
|  | Inundated | 4.8 | 29.7 | 0.3 | 0.1 | 0.7 | 0.5 | 1.6 | 4.1 | 35.6 | 2.5 | 1.8 | 0.4 | 2.0 | 4.1 | 0.3 | 33.3 | 35.8 | 30.8 |  |

of only those species that were represented by more than 50 individuals among all plots, yielding a total of 99 species. For clarity, we present these species on separate biplots from the environmental factors (Figure 4).

One end of the first axis of the CCA is characterized by soils with high pH, high percent base saturation, and a granite substrate. This combination of conditions represents richer soils typical of the dry forest plots that are found in the south of the region. The axis is heavily weighted by *Attelea speciosa*, an unidentified sp. of *Terminalia*, and an unidentified Fabaceous species. The other end of this axis is heavily weighted by species found in seasonally inundated forest islands, particularly *Qualea sp. 1*, *Virola elongata*, and *Brosimum guianense*. The eigenvalue for this axis is 0.897 and it accounts for 7.2% of the variance of the species data.

The second CCA axis is characterized most strongly by sandy soils and higher altitude at one end. Sandy soils are present at many, though not all of the plots located on the plateau, so these conditions are generally representative of many of the tall forest plots and of the plots at the EN transitional forest site. None of the common species have values that correspond strongly to this end of the axis. Those with the most negative values are *Attalea speciosa*., *Siphoneugena occidentalis* Legrand, and an unidentified Chrysobalanaceae. Inundated plots with high aluminum concentrations, higher percentages of clay, and higher cation exchange capacity characterize the other end of this axis.

Figure 3

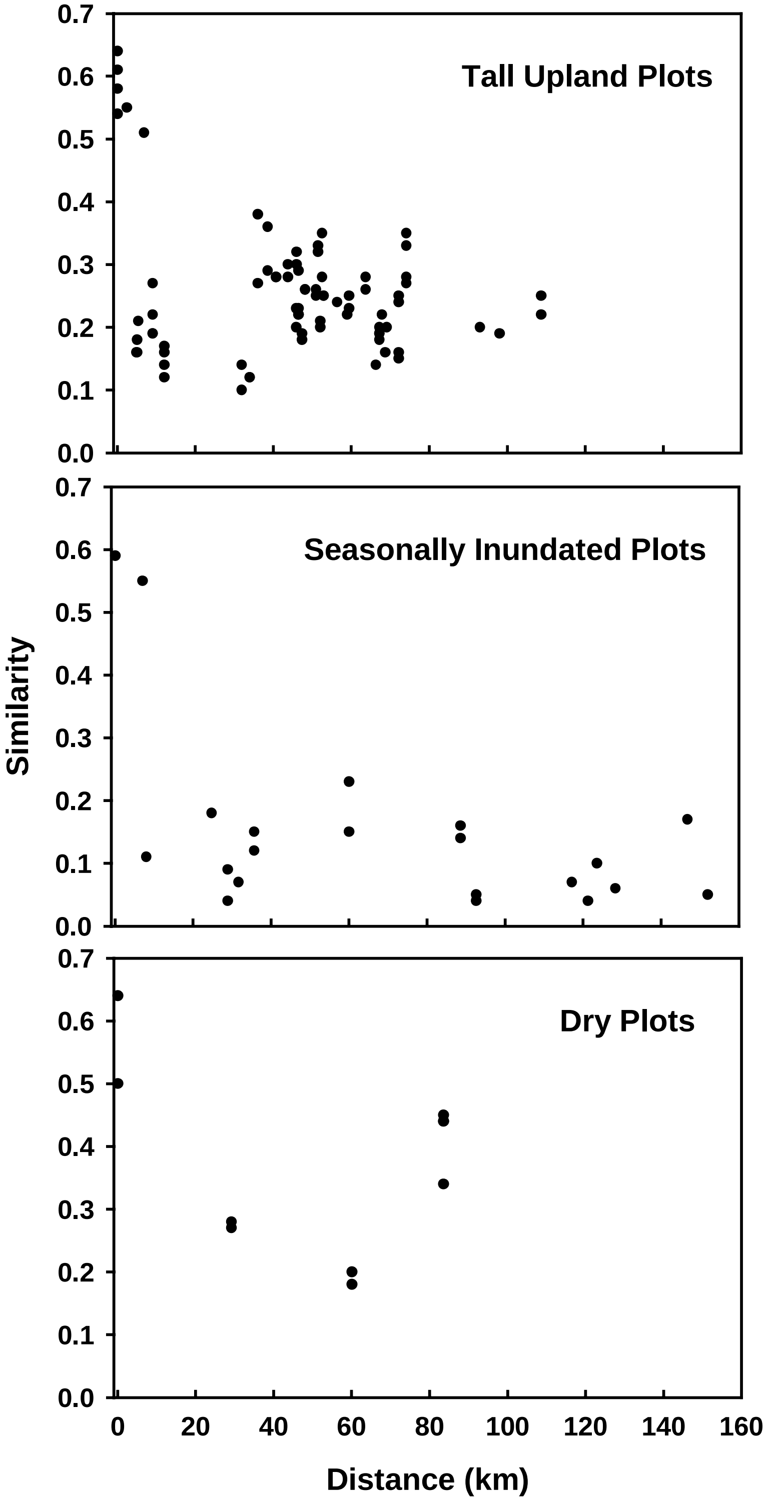

**Figure 3. The relationship between Sorensen's presence/absence similarity index and geographic distance between plots. The plots are separated by forest type.**

These conditions are all found at the CR inundated forest site, and none of the other inundated sites have this combination of features. Species that correspond well to this combination of characters include two unidentified species of Annonaceae, *Symmeria paniculata* Benth., and *Maquira coriacea* (Karsten) Bergius. Each of these species is found exclusively at the CR site. The eigenvalue for this axis is 0.885 and it explains 7% of the variance of the species data.

The third CCA axis is aligned with percent base saturation, pH, granite substrate, and total exchangeable bases at one end. These characters typify richer soils and also were grouped at one end of the first CCA axis. They are typical of the dry forest plots, and the species associated with this end of the axis are typical dry forest species, including *Caesalpinia floribunda*, *Tabebuia roseo-alba*, and *Bauhinia rufa*. The other end of this axis is strongly defined by phosphorous content, with latitude, tertiary laterite substrate, and sandy soil as secondary factors. This combination of characters is found in the EN transitional forest plots. The species most strongly associated with these conditions are unidentified species of *Palicourea*, Chrysobalanaceae, and *Xylopia*. The *Palicourea* and the chrysobalanaceous species were only found in the EN plots, while the *Xylopia* was found in both the EN plots and the BC-1 plot. The eigenvalue for this axis is 0.852 and it explains 6.8% of the variance in species data.

Figure 4

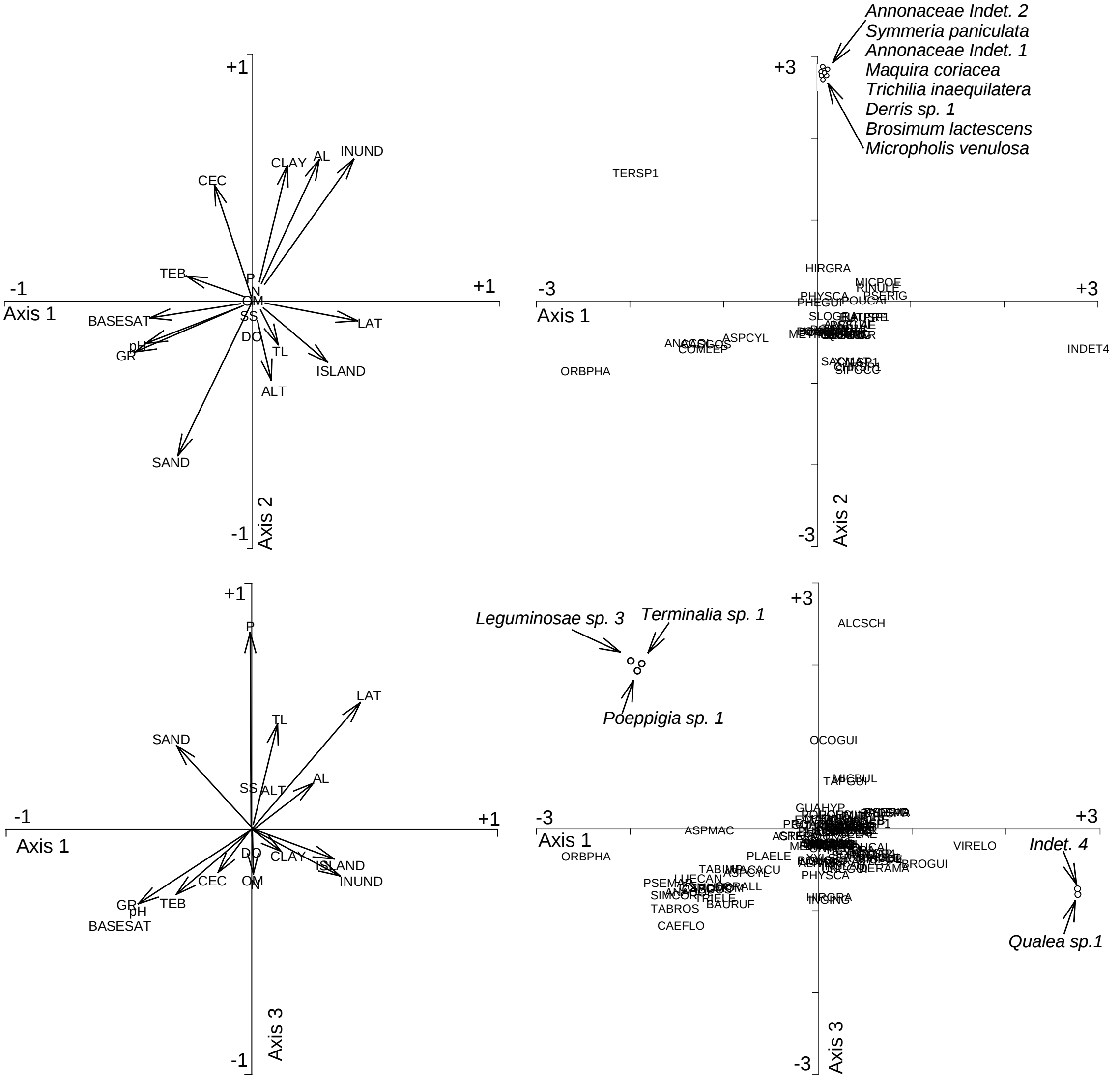

**Figure 4. CCA biplots. The plots on the left show the scores of 18 environmental variables used in the analysis. The plots on the right show the scores of all species which were represented by more than 50 individuals in the total dataset. Species names are represented by a six letter code that includes the first three letters of the genus and species names. Tightly clumped species that are distant from the centroid have been marked with a circle for clarity.**

The Fourth axis (not shown in Figure 4) is weighted by altitude and sandstone substrate, but is particularly associated with a suite of taxa with

Amazonian distributions, such as *Phenakospermum guianensis*, *Pourouma cecropiifolia*, *Pourouma minor, Ecclinusa lanceolata, Matayba guianensis, Miconia chrysophylla, Erisma uncinatum,* and *Vochysia obidensis.* On the other end of the axis, an assortment of factors and taxa are associated with either dry forest or wetland forest. The eigenvalue for this axis is 0.815 and it explains 6.5% of the variance in the species data.

Some of the most common species (in terms of total frequency over all plots) were not associated with any axis, indicating that they are widely distributed among several forest types. *Metrodorea flavida* and *Physocalymma scaberrimun* are found in both dry forest and humid tall forest communities, and *Pseudolmedia laevis* and *Euterpe precatoria* are common in both humid upland forest forest and inundated forest.

## DISCUSSION

We recorded 896 species of trees with a minimum diameter of 10 cm in the 29 one-hectare plots sampled. Comparisons among datasets are difficult, but this species total is high for a relatively small geographic area. A much larger sample of 1 ha plots (48) scattered across South America, from the Atlantic rainforest of Brazil to the Guyana shield, contained 1951 species (Terborgh and Andresen 1998). This is only slightly more than double the number of species documented for the Noel Kempff plots in the present study. This shows the impressive levels of diversity found in this ecotonal region.

Despite great total richness at Noel Kempff, alpha diversity is low for Amazonian forest. The 0.1 ha plots that Gentry sampled across Amazonia ranged in richness from 33 to 276 species (Clinebell et al. 1995). In our dataset, we found 32 to 125 species in the 0.1 ha subplots. Regression and correlation analysis of the Gentry dataset suggests that high precipitation and aseasonality are the best predictors of species richness (Clinebell et al. 1995), so it is not surprising that plots at Noel Kempff are at the lower end of the range of species richness, given their position at the dry end of a precipitation gradient for Amazonian forest.

At the 1 ha scale, where we sampled only individuals $\geq 10$ cm dbh, the Noel Kempff plots are also relatively species poor. Our richest plot contained 109 species. By comparison, 1 ha plots in the Iquitos region of Perú were found to contain nearly 300 species (Gentry 1988). Though low relative to other locations in Amazonia, alpha diversity was sufficiently high that species accumulation curves were not saturated at the scale of one ha for any of the plots. Accordingly, we found that plots located only a few hundred meters from each other at the same site differed substantially in composition. Across all forest types, plots at the same site shared between 50 and 64% of their species. Comparison with other sites is difficult because species turnover at this scale is not commonly reported in the literature. We expect that high rates of turnover within forest types are typical in the Amazon.

If alpha diversity is relatively low, then the high total species count for the Noel Kempff region must be due to rapid species turnover within and/or among forest types. We had expected a high degree of dissimilarity among forest types, but we also found considerable variation within each forest type, suggesting that our *a priori* classification was insufficient to characterize the composition of these communities. Structurally, our classifications reasonably circumscribed distinct forest types in terms of basal area and height, though the density of stems was highly variable within each group. Our classifications also were reasonably good at grouping forest types with similar species richness.

Our classification was less precise for describing species composition. The two sites categorized as cerrado transition forest shared very few species and therefore do not constitute a natural group. We found the same to be true for the five sites in the inundated forest group. Among the plots in the tall upland forest class, we found a greater proportion of shared species, with many pairs of plots in this group sharing between one quarter and one third of their species based on the Sorensen's presence/absence index. However, Sorensen's quantitative index shows less similarity in the relative abundances of these species, again highlighting the importance of beta diversity. We measured the highest levels of within-group overlap among the dry forest sites. The proportion of shared species between the AC sites and the CP sites approaches the proportion of species shared between plots at each of those sites. Nevertheless, it is clear that similar physiognomies do not imply highly similar composition.

From forest type to forest type, we found very low (<10%) species overlap, with a few exceptions. The cerrado transition plots had low overlap with other groups except for the EN plots and the BC tall forest plots, which shared 15-20 %

of their species and which are both located on top of the Huanchaca Plateau. Interestingly, the EN plots also have moderate overlap with two of the inundated plots LT-3 (14%) and FO-b (18%); an oddity that begs an explanation considering the contrasting edaphic conditions of those sites. The dry forest plots share few species with other plots, with the exception of the H2 tall forest site (10-19%), which is situated on similarly mesotrophic soils and the inundated forest at MV (13-25%), which is situated in the southern sector of the study area where dry forest types predominate on upland landscapes. Similarly, liana forest plots have substantial overlap with both humid forest plots (14-28%) and dry forest plots (11-19%), indicating that liana forests may represent a transitional or successional phase between the Amazonian and Chiquitano dry forest ecosystems

Upland forest plots have generally low overlap with the inundated plots. Exceptions to this are the MV and LO plots (8-22%), which are situated on landscapes with considerable topographic variability associated with termite mounds and offer upland species microhabitats that are normally above the level of maximum inundation. In all cases of moderate between-habitat similarity, we found Sorensen’s quantitative index to be substantially lower when compared to the presence/absence index, indicating that though two plots had species in common, the abundance of those species differed between plots.

Our multivariate analysis suggests that there is not a single gradient that can explain a large proportion of the variance in species distribution. Each of the first three axes explains a similar, small proportion of the total variance in the system. The first axis shows that soil fertility is important and that it is associated with the dry forest formations in the region. This finding is similar to that documented for other dry forests in central South America (Ratter et al. 1978). The other end of this axis and the ends of the other axes represent composites of environmental conditions not found together in a single plot. This indicates that each of the plots contains a distinct combination of conditions and species and it reflects high beta diversity.

We expected certain factors like latitude (precipitation) and inundation to correlate more strongly than they did with species composition. Heterogeneity in the other factors appears to diminish the importance of these conditions. Because of the dynamic nature of the vegetation in the region, it is also likely that site history has influenced composition, and we did not include historical variables in the CCA analysis. Latitude can also be considered a surrogate for recent vegetation change (Mayle et al 2000); northern Amazonian forest communities (H1) are probably older than southern Amazonian forest communities (LF, H1 LG). Evidence to support this hypothesis can be found by comparing species diversity and composition of the plots, with H1 plots being both more diverse and incorporating more Amazonian taxa, particularly in the Sapotaceae and Moraceae.

The degree of isolation of forests in this region does not seem to be important for determining species composition or diversity and this also suggests that history is important in determining species composition. Island biogeography theory suggests that the highest levels of diversity should be found in continuous forest, but we found the richest plots at a forest island (H1). This could be explained by unknown site-specific factors or by historical reasons, where this forest island could be the result of relatively recent fragmentation of continuous forest.

How will future climate change affect the diversity of this region? We believe that the low degree of similarity between forests makes the total diversity of this system highly sensitive to changes in climate. A shift in climate that results in one vegetation type subsuming another will cause an entire suite of species to be eliminated from the system. The fact that there are relatively low amounts of similarity between plots of the same forest type means that even the loss of isolated patches of any forest type will lead to a loss of species from the system.

Even changes in the extent of a single habitat type will have consequences for diversity. We found that within-site species turnover is high over short distances. For a patch of habitat to maintain its richness when it decreases in size, the density of species must increase. We consider this unlikely, so the result of a decrease in patch size will more likely be a decrease in species numbers.

Conversion of one habitat to another does not inherently cause the extinction of species, as many species are simply displaced by changing conditions to areas that are newly suitable. Some of the forest formations at Noel Kempff appear to be quite young (<3000 yr) (Mayle et al. 2000) and in light of the young nature of these forests, the alpha diversity could be considered to be quite high. Nevertheless, the rapid accumulation of species will become increasingly difficult in the future, as the landscapes surrounding Noel Kempff are converted to other uses. Human settlement is likely to present barriers to plant migration that will result in the complete loss of some species from the system.

In addition to causing change in biodiversity, climate change will influence the structure and therefore the amount of carbon sequestered in these forests. Stem density, basal area, and mean height are extremely variable among forest types. The basal area in the tall upland forest and in the seasonally inundated forest plots is similar to that found in other forests distributed around the Amazon basin (Malhi et al. in press). Basal area values for the other forest types are much lower resulting in substantially lower biomass in these forests. A shift from one forest type to another that is caused by climate change will therefore result in changes in above and belowground carbon stocks.

## CONCLUSION

We recorded a total of 896 tree species with diameters of 10cm and greater in 29 ha of study plots in this region. The floristic similarity of the plots was low for all plots except those located at the same site. Local environmental conditions across the region are also highly variable, and there are no simple environmental gradients that explain the species distributions observed.

# CHAPTER 3

# STRUCTURE, COMPOSITION, AND BIODIVERSITY OF SAVANNA FORMATIONS ACROSS THE SOUTHERN LIMIT OF AMAZONIAN FOREST IN BOLIVIA[2]

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[2] Panfil, S.N., T.J. Killeen, B. Mostacedo, E. Gutierrez, T. Grimwood, J. Caballero, G. Sánchez, M. Menacho. To be submitted to *Biological Conservation*.

# ABSTRACT

Landscape-scale patterns of diversity are poorly documented in the most species-rich ecosystem on earth, the Amazon basin. A lack of understanding of how species are distributed over large geographic areas and how this distribution relates to environmental conditions makes the long-term conservation of diversity difficult in the face of shifting conditions that are due to climate change.

We used line-intercept and point-intercept techniques to describe the composition and structure of savanna habitats in Noel Kempff Mercado National Park in northeastern Bolivia. This park spans the ecotone between moist evergreen forest, dry forest, and savanna formations at the edge of the Amazon basin. Because of its geographic position between biomes, the vegetation in the region has been sensitive to changes in climate during the Holocene. We sampled variations on upland, cerrado-type savanna as well as seasonally inundated savanna types. Our plots contained a total of 662 species. The upland formations generally contained greater richness than the seasonally inundated ones, and the richest plots of all were found on the Huanchaca Plateau, an ancient sandstone table-mountain that lies at the center of the park. The level of species overlap among the study sites was low and there was also considerable variation in the structural characteristics of the vegetation in the plots. The high regional species richness for this area is the result of high levels of habitat heterogeneity, a result we previously found in a separate analysis of the forest formations of the region. The long-term conservation of biodiversity in this region will require an understanding of the conditions responsible for this habitat heterogeneity, and active maintenance of these conditions may be necessary in the face of climate change.

**Keywords**: Amazon, Bolivia, Ecotone, Climate Change, Biodiversity, Savanna, Cerrado

# INTRODUCTION

Biological reserves are typically designed so that they contain large total numbers of species. At a landscape level, high richness could be achieved through the inclusion of few habitats that contain many species (high $\alpha$-diversity), or through the inclusion of many habitats that have moderate $\alpha$-diversity but which have few species in common with one another (high $\beta$-diversity). These two scenarios could have very different implications for the long-term conservation of the species currently present. For reserves with high $\beta$-diversity, management must focus on understanding and maintaining the environmental conditions that promote habitat heterogeneity.

There are few, if any, large tropical reserves where the geographic distribution of the flora is well documented. Tropical floristic studies are costly and time consuming because very few taxonomists are able to rapidly identify the many species found in these regions. The species composition of vegetation at some field stations is well known, but these studies are confined to small geographic areas (Croat 1978, Ribeiro et al. 1999). Floras for larger protected areas are rare and those that exist are generally not plot-based, making quantitative comparisons of local ($\alpha$) and between habitat ($\beta$) diversity difficult.

In previous research (Panfil et al. Chapter 2, this dissertation), we found that the forests of the Noel Kempff Mercado National Park region contained moderate levels of $\alpha$ diversity, but very high levels of $\beta$ diversity, resulting in a total ($\gamma$) floristic diversity that is among the highest of any protected area in the world. We argued that this diversity makes the park extremely valuable for conservation, but that it may also make the diversity of the park susceptible to climate change, as changing conditions cause some habitats to be lost.

Noel Kempff Park also contains large areas of savannas. Neotropical savannas are often overlooked in discussions of diversity, because they are considered to be species poor when compared to forests. Nevertheless, savanna vegetation occupies 700,000 $km^2$ of the Amazon basin, and approximately 40% of all cerrado vegetation (Amazonian and southern Brazilian) has been converted to agricultural use (Ratter et al. 1997). This rapid rate of conversion to agriculture makes remaining tracts especially important for conservation.

In this paper, we report on the landscape-level patterns of diversity in the savanna formations of Noel Kempff Mercado National Park in eastern Bolivia. We apply a similar analysis to one done for the forests of the region in order to quantify the local diversity, to compare the diversity of different savanna formations and to correlate diversity with environmental conditions (Panfil et al. Chapter 4 this dissertation). While physiognomic and sampling differences preclude direct comparison with our forest results, we nevertheless present our findings in parallel fashion to highlight analogous landscape-scale patterns in the two vegetation types.

## SITE DESCRIPTION

Noel Kempff Park lies on Bolivia’s northeastern border with Brazil and spans the ecotone between evergreen tropical forest, dry forest, and savanna at the southwestern edge of the Amazon basin. The main geomorphological feature of the park is the Huanchaca Plateau (maximum elevation 950 m), a sandstone table-mountain that was the inspiration for Sir Arthur Conan Doyle's book, *The Lost World* (Fawcett 1988). The region lies on the Brazilian Shield, and the lowlands surrounding the plateau range in elevation from 150 m to 300 m. These lowlands include seasonally inundated floodplains of the Paraguá River to the west and of the Itenez or Guaporé River to the north. Details about the geomorphology of the area can be found in Litherland and Power (1989).

Human influence appears to have been minimal in the region. Human habitation has been sparse in the lowlands, and no permanent settlements are known to have existed on top of the plateau. Currently, only three small villages exist at the edge of the park, and these are located on high ground that was once forested. The lowlands surrounding the plateau were selectively harvested for mahogany (*Swietenia macrophylla* King) in the 1980's and 1990's, but total structural damage due to this type of logging is relatively low (Gullison and Hardner 1993, Panfil and Gullison 1998).

The climate of Noel Kempff Park is tropical with strongly seasonal precipitation. Local weather data is not available, but conditions can be inferred from meteorological stations located 160-200 km to the southwest and 150–200 km northwest of the park. Mean annual temperature is 25-26º C with a mean annual minimum of 10º C (Roche and Rocha 1985). Frost is unknown in the area. During the austral summer, the inter-tropical convergence zone (ITCZ) brings warm moist Amazonian air masses to the region. Total mean annual precipitation is approximately 1500 mm, with almost all precipitation falling between October and June (Killeen et al. *In press*). The northern parts of the park receive two to several hundred mm more of precipitation per year than those to the south (Roche and Rocha 1985). During the austral winter, the ITCZ shifts to the north and dry weather patterns replace the moist air masses.

### ***Vegetation***

The vegetation of the park includes upland and seasonally inundated forest and savanna vegetation (Figure 5). On the Huanchaca plateau, a mosaic of upland forest and savanna exists on well-drained soils. The surrounding lowlands include upland formations as well as seasonally inundated forests and savannas and permanently inundated swamps and lakes.

The savannas are typical of cerrado vegetation and include campo rupestre, campo sujo, cerrado, and cerradão. These savanna types represent a continuum of upland formations with increasing amounts of woody vegetation (Eiten 1978). Seasonally inundated formations are also present and include termite savannas, which have raised mounds that remain dry while the remainder of the savanna floods annually. A separate savanna formation, pampa inundada, also floods annually, with no portions remaining above the water line.

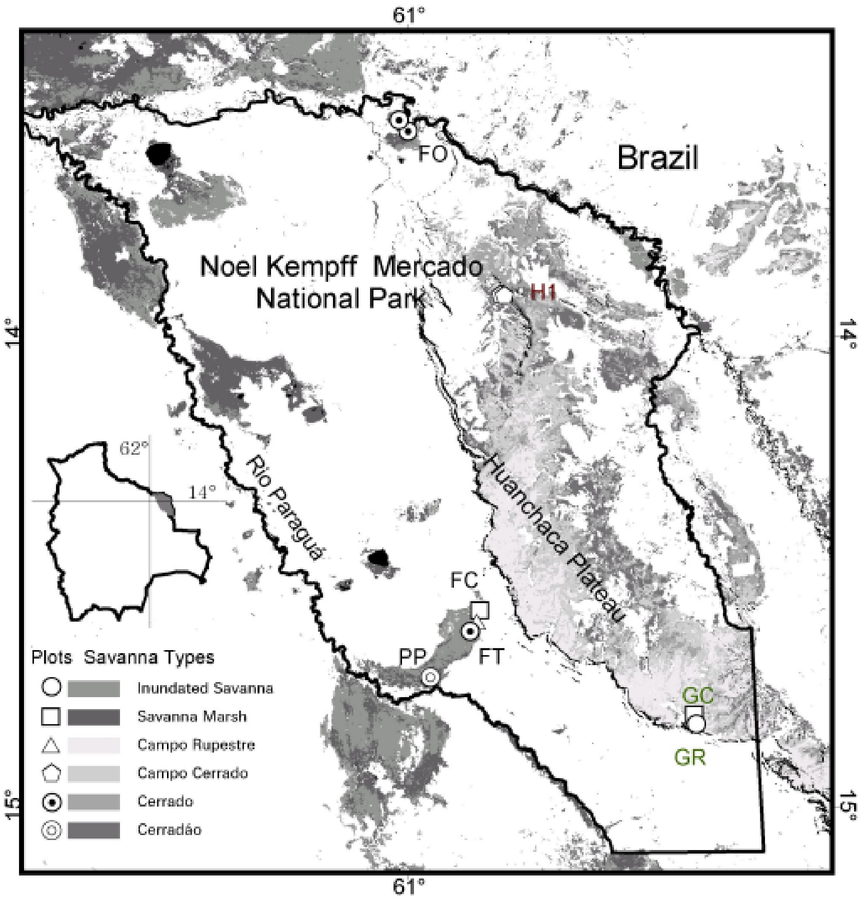

**Figure 5. The savanna formations of Noel Kempff Mercado National Park. Forest formations have been left blank for clarity.**

## METHODS

### *Vegetation Sampling*

We selected 9 savanna formations based on LandSat imagery and aerial reconnaissance (Table 6). The sites represent both seasonally inundated and upland formations and within each of these groups, we selected sites with differing physiognomic characteristics, from rocky grassland (campo rupestre) to tall woodland (cerradão) (Table 6). These plots are widely distributed around the park, with a maximum distance of 192 km between plots (Figure 5).

We used line intercept and point intercept techniques to sample the composition and structure of the vegetation. We marked a 500 m baseline at each site and randomly located between nine and fifteen 20 m lines perpendicular to this baseline. For the line intercept sampling, we recorded the horizontal coverage of each plant along these 20 m lines, yielding a total linear coverage of 180 to 300 m for each site. A botanical voucher collection was made the first time that a species was encountered in each plot. Voucher specimens are on deposit at the herbarium of the Museo de Historia Natural Noel Kempff Mercado in Santa Cruz, Bolivia (USZ). Specimen determinations were made by comparison with specimens in the collection at USZ, at the Missouri Botanical Garden (MO), and with the assistance of many plant family specialists (see Killeen et al (1998) for a list of specialists consulted). In some cases, determination to the species level was not possible. Incompletely determined specimens from all plots were compared and morphospecies names were standardized to allow among-plot comparisons of composition. Specimen label information is available at http://www.mobot.org.

**Table 6. The 9 plots inventoried for this study.**

| Plot | Site Name | Savanna Type | Substrate | Slope | Inundation | Latitude | Longitude | Altitude (m) | Year Sampled |
|---|---|---|---|---|---|---|---|---|---|
| FC2 | Los Fierros | cerradão | Granitic | < 1º | none | 14.34.45 S | 60.50.29 W | 200 | 1993 |
| FC1 | Los Fierros | cerrado | Tertiary Laterite | 0º | none | 14.36.25 S | 60.51.23 W | 200 | 1993 |
| GC | Las Gamas | cerrado | Sandstone | < 1º | none | 14.48.11 S | 60.23.33 W | 850 | 1993 |
| H1 | Huanchaca I | campo sujo | Tertiary Laterite | < 1º | none | 13.53.55 S | 60.48.46 W | 550 | 1994 |
| GR | Las Gamas | campo rupestre | Quartzite | < 1º | none | 14.48.11 S | 60.23.33 W | 900 | 1993 |
| FO1 | Flor de Oro | termite savanna | Quaternary sediments | 0º | seasonal (~30 cm) | 13.32.41 S | 61.01.23 W | 120 | 1993 |
| FO2 | Flor de Oro | termite savanna | Quaternary sediments | 0º | seasonal (~30 cm) | 13.33.50 S | 61.01.02 W | 120 | 1994 |
| FT | Los Fierros | termite savanna | Quaternary sediments | 0º | seasonal (~30 cm) | 14.36.53 S | 60.51.59 W | 200 | 1993 |
| PP | Puerto pasto | pampa inundada | Quaternary sediments | 0º | seasonal (1-2 m) | 14.44.37 S | 60.57.38 W | 200 | 1993 |

We used some or all of the same 20 m lines described above to document the vertical structure of vegetation with the point intercept method. At one-meter intervals along the lines, we recorded the height at which any plants intersected the vertical line described by the sampling point. We also recorded the life form for each of these plants. We sampled between 5 and 13 lines at each site this way (the number of lines per plot is indicated in Figure 3). We did not record species names during this part of the study because compositional data was recorded during the line intercept inventory.

### *Soil analysis*

We characterized the soil profile in each of the study plots during field expeditions made in the dry season of 1995, 1996, and 1997. Soil samples were collected with pits, dried in the field, and analyzed later at the Centro de Investigaciones para la Agricultura Tropical (CIAT) in Santa Cruz, Bolivia. Soil analysis methods are described in Cochrane and Barber (1993) but are summarized here. The pH and electro-conductivity of the soil were determined by water extraction at a soil-water ratio of 1:5 (Page et al. 1982, Van Reeuwijk 1987). Total nitrogen was determined by the Kjeldahl method (Varley 1966, Page et al. 1982, Van Reeuwijk 1987), and the organic matter content was measured using a modified Walkley-Black procedure (Metson 1956, Van Reeuwijk 1987). A modified version of the Olsen method was used to determine the soluble phosphorous content (Van Reeuwijk 1987). The exchangeable bases Ca, Mg, K, and Na were extracted with ammonium acetate at pH 7.0 and measured with atomic absorption (Begheyn 1981, 1982, Van Reeuwijk 1987). Exchangeable acidity and aluminum were determined by titration after extraction with potassium chloride (Mclean 1965). The hydrometer method was used for determining sand, silt, and clay percentages (Day 1965). Total exchangeable base content was calculated by summing the values for Ca, Mg, Na and K. Cation exchange capacity (CEC) was calculated by summing the values for total exchangeable bases and acidity.

## RESULTS

### ***Diversity***

The number of species in each plot ranged from 64 to 167 (Table 7). These counts are based on different sample sizes, however, making direct comparison difficult. Better indicators of the relative diversity are diversity indices or species accumulation curves. Fisher's $\alpha$ is a number close to the number of species represented by a single individual and is less influenced by sample size than other indices (Hayek and Buzas 1997). It ranges from 14.59 in the PP plot to almost 41 in the GC and H1 plots. Since $\alpha$ is less commonly reported than other indices, we also present H' and 1-D to facilitate comparison with other studies (Table 7). Shannon's H' is a measure of evenness and large numbers of species with similar abundances result in high values of H'. H' ranges from 2.64 in the FC2 plot to 3.39 in the H1 plot. Simpson's 1-D represents the probability of picking two individuals at random that are different species (Krebs 1989). This index ranges from 0.80 in the FC2 plot to 0.94 in the FT and PP plots.

**Table 7. Plot diversity measured with different indices, including Fisher's $\alpha$, Shannon's H', and Simpson's 1-D. Lines sampled refers to the number of 20 m intercept lines used to inventory each plot.**

| Plot | Lines sampled | Plants | Density (plants/line) | Richness | $\alpha$ | H' | 1-D |
|---|---|---|---|---|---|---|---|
| FC2 | 12 | 1541 | 128.4 | 106 | 25.82 | 2.64 | 0.80 |
| FC1 | 12 | 1481 | 123.4 | 113 | 28.46 | 3.09 | 0.90 |
| GC | 15 | 2376 | 158.4 | 167 | 40.95 | 3.27 | 0.88 |
| H1 | 14 | 1682 | 120.1 | 158 | 40.96 | 3.39 | 0.91 |
| GR | 9 | 1816 | 201.8 | 76 | 16.04 | 2.78 | 0.89 |
| FO1 | 13 | 1750 | 134.6 | 92 | 20.67 | 2.91 | 0.89 |
| FO2 | 13 | 2947 | 226.7 | 90 | 17.54 | 3.19 | 0.91 |
| FT | 13 | 1616 | 124.3 | 93 | 21.45 | 3.33 | 0.94 |
| PP | 10 | 1159 | 115.9 | 64 | 14.59 | 3.18 | 0.94 |
| Means | 12.3 | 1818.7 | 147.9 | 106.6 | | | |
| Total | 111 | 16368 | | 662 | | | |

Species accumulation curves provide a direct way to compare the richness of samples of different sizes. New species were encountered at the highest rates in the GC and H1 plots (Figure 6). The FC1 and FC2 plots also show a more rapid rate of species accumulation than the remaining plots, though at a considerably slower rate than the GC and H1 plots. The FT, FO1, and FO2 plots all showed similar rates of accumulation, and greater richness than the PP plot.

### ***Composition***

A listing of the most speciose families and most dominant species in each of the plots demonstrates their compositional differences (Table 8). As might be expected for savanna habitat, the most speciose family in each of the plots is the Poaceae, with between 15 and 25 species. The next most speciose family varies across the formations. In the seasonally inundated termite savanna (FO1, FO2, and FT) the Cyperaceae is the second most speciose. In the cerrado and cerradão plots (FC1, FC2, and H1), the Myrtaceae, Euphorbiaceae, Rubiaceae, and Leguminosae were the next most speciose families. For the campo rupestre plot (GR), the Cyperaceae was the second most speciose, and for the inundated grassland plot (PP) the Sterculiaceae was the second most speciose.

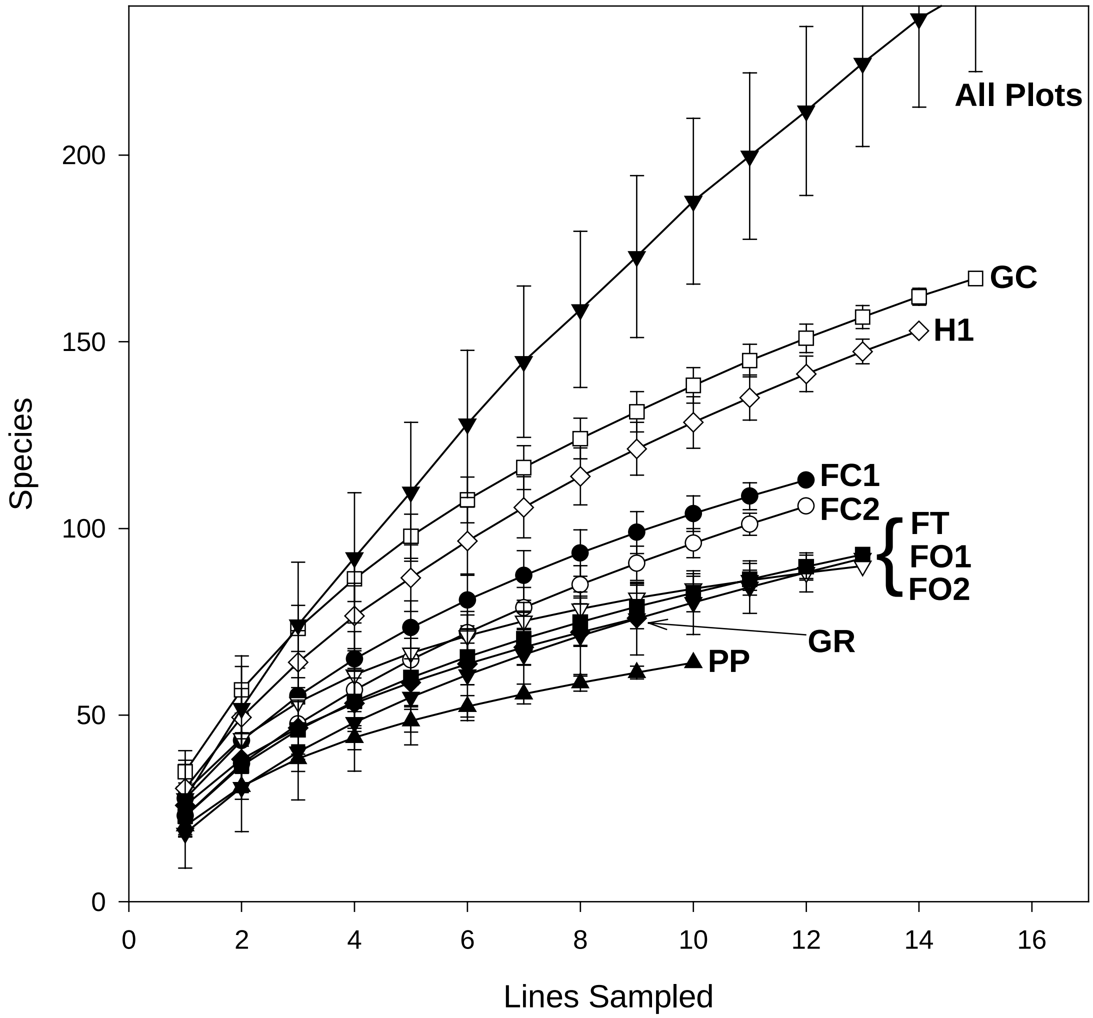

**Figure 6. The rate of species accumulation as a function of the number of 20 m lines sampled. Error bars show the standard deviation of 50 randomized runs.**

The dominant species were extremely variable among plots (Table 8). In terms of relative cover, a grass species was dominant in all of the plots, but the identity of that species was different for each plot except the FO1 and FT plots, where *Paspalum lineare* was dominant. The only plot where a tree or shrub species represented a large proportion of the total cover was in the cerradão plot, FC2, where a species of *Caraipa* had a relative cover of 19.9%. The top three species represented at least 30% of the total cover in each plot and the top 12 species represented at least 54% (GC) and as much as 89% (GR) of the total cover, indicating that many rare species are responsible for small amounts of the total cover.

### ***Similarity***

We found that the plots had low levels of species similarity (Table 9). The greatest value for Sorensen’s similarity index for presence/absence was 0.38. There was more overlap among the upland formations and among the seasonally inundated formations than there was between these groups. The FC2 (cerradão) plot showed moderate levels of overlap with the cerrado and campo sujo plots (FC1, GC, and H1). Slightly higher levels of overlap were recorded among the seasonally inundated termite savannas, FT, FO1 and FO2. There were much lower levels of species overlap between the upland plots and the termite savanna plots, and the pampa inundada plot (PP) had the least similarity with any of the other formations.

### ***Structure***

The savannas at Noel Kempff contain a diversity of life forms as well as species (Table 10). Graminoids are the dominant life form in all plots in terms of frequency. They also represent at least half of the total cover for all plots except GC, where graminoids represent 45.4% of the total cover. Forbs represent less than 10% of the individuals and cover in all plots except PP, where they account for 22.2% of the individuals, and 16.5% of the cover. Shrubs represented between 3.1% (GR) and 23.9% (GC) of the individuals and between 2.4% (GR) and 39.0% (GC) of the cover. Trees were rare in terms of the number of individuals in all plots, but they represented substantial amounts of cover in the cerradão plot (FC2, 26.8%) because of their size. Herbaceous rosettes were unimportant in all plots except GR, where *Vellozia flavicans* (Velloziaceae) represents 6.6% of the individuals and 10.8% of the cover. Lianas, palms, epiphytes, and herbaceous vines are poorly represented in all plots.

**Table 8. The most speciose families and the most dominant species for each plot. Species are ranked by relative cover (RC) and the relative frequency (RF) of the species with the greatest cover is also shown.**

| PLOT | TOP FAMILIES | SPECIES | TOP SPECIES | RC | RF |
|---|---|---|---|---|---|
| FC1 | Poaceae | 18 | *Andropogon virgatus* Desv. | 12.4 | 17.8 |
| | Euphorbiaceae | 7 | *Paspalum pectinatum* Nees ex Trin. | 10.6 | 11.4 |
| | Myrtaceae | 7 | *Elyonurus muticus* (Spreng.) Kuntze | 10.3 | 6.5 |
| | Leguminosae-Pap | 7 | *Paspalum stellatum* Humb. & Bonpl. ex Flugge | 9.8 | 20.9 |
| | Leguminosae-Caes | 7 | *Borreria* sp. 1 | 4.9 | 3.2 |
| | | | *Davilla grandiflora* A. St.-Hil. & Tul. | 3.8 | 2.0 |
| | | | *Trachypogon plumosus* (Humb. & Bonpl. ex Will.) Nees | 3.4 | 5.7 |
| | | | *Maytenus spinosa* (Griseb.) Lourt. & O' Donell | 3.3 | 0.2 |
| | | | *Lafoensia vandelliana* Cham. & Schltdl. subsp. vandelliana | 2.6 | 0.6 |
| | | | *Eriotheca gracilipes* (K. Schum.) Robyns | 2.4 | 0.1 |
| | | | *Eugenia parviflora* (L.) DC. | 2.4 | 3.6 |
| | | | *Bauhinia rufa* (Bong.) Steud. | 1.9 | 0.7 |
| | | | TOTAL | **67.8** | |
| FC2 | Poaceae | 16 | *Trachypogon plumosus* (Humb. & Bonpl. ex Will.) Nees | 22.6 | 42.1 |
| | Myrtaceae | 7 | *Caraipa aff. densifolia* Mart. | 19.9 | 2.2 |
| | Rubiaceae | 7 | Indet. sp. 11 | 11.8 | 9.3 |
| | Leguminosae-Pap | 6 | Indet. sp. 5 | 4.4 | 8.7 |
| | Erythroxylaceae | 5 | *Paspalum pectinatum* Nees ex Trin. | 3.0 | 4.8 |

| PLOT | TOP FAMILIES | SPECIES | TOP SPECIES | RC | RF |
|---|---|---|---|---|---|
| | | | *Sporobolus cubensis* Hitchc. | 2.8 | 3.4 |
| | | | *Thrasya petrosa* (Trin.) Chase | 2.6 | 3.6 |
| | | | *Miconia albicans* (Sw.) Triana | 2.5 | 1.8 |
| | | | *Ormosia* sp. 1 | 2.3 | 1.0 |
| | | | *Roupala montana* Aubl. | 2.1 | 0.8 |
| | | | *Eriotheca gracilipes* (K. Schum.) Robyns | 2.1 | 0.3 |
| | | | *Emmotum nitens* (Benth) Miers | 2.1 | 0.3 |
| | | | TOTAL | **78.2** | |
| FO1 | Poaceae | 24 | *Paspalum lineare* Trin. | 20.3 | 23.4 |
| | Cyperaceae | 6 | *Andropogon virgatus* Desv. | 19.6 | 15.5 |
| | Xyridaceae | 5 | *Axonopus pulcher* (Nees) Kuhlm. | 16.4 | 12.7 |
| | Apocynaceae | 4 | *Schizachyrium sanguineum* (Retz) Alston | 6.7 | 6.1 |
| | Myrtaceae | 4 | *Paspalum plicatulum* Michx. | 4.0 | 7.2 |
| | | | *Panicum olyroides* Kunth | 2.7 | 0.8 |
| | | | Poaceae indet. | 2.7 | 3.2 |
| | | | *Didymopanax distractiflorus* Harms | 2.5 | 0.3 |
| | | | Poaceae indet. | 2.2 | 0.6 |
| | | | *Hancornia speciosa* B.A. Gomes | 1.9 | 0.2 |
| | | | *Trachypogon plumosus* (Humb. & Bonpl. ex Will.) Nees | 1.9 | 4.4 |
| | | | *Bredemeyera altissima* (Poepp.) A. W. Benn. | 1.9 | 1.3 |
| | | | TOTAL | **82.8** | |
| FO2 | Poaceae | 19 | *Elyonurus muticus* (Spreng.) Kuntze | 21.9 | 12.1 |
| | Cyperaceae | 9 | *Schizachyrium sanguineum* (Retz) Alston | 16.1 | 22.6 |
| | Rubiaceae | 5 | *Andropogon selloanus* (Hack.) Hack. | 7.6 | 3.6 |
| | Lentibulariaceae | 3 | pasto10 | 6.9 | 7.4 |
| | Labiatae | 3 | *Ocotea aciphylla* (Nees) Mez | 4.3 | 0.1 |
| | Euphorbiaceae | 3 | *Leptocorypheum lanatum* (HBK) Nees | 3.5 | 2.5 |
| | Melastomataceae | 3 | *Casearia arborea* (Rich.) Urban | 3.0 | 1.4 |
| | Xyridaceae | 3 | *Axonopus fissifolius* (Raddi) Kuhlm. | 2.7 | 2.9 |
| | Sapindaceae | 3 | *Siparuna guianensis* Aubl. | 2.7 | 1.5 |
| | | | *Curatella americana* L. | 2.7 | 0.2 |
| | | | *Gymnopogon fastigiatus* Nees | 2.5 | 8.3 |
| | | | *Axonopus pulcher* (Nees) Kuhlm. | 1.8 | 2.6 |
| | | | TOTAL | **75.7** | |

| PLOT | TOP FAMILIES | SPECIES | TOP SPECIES | RC | RF |
|---|---|---|---|---|---|
| FT | Poaceae | 25 | *Paspalum lineare* Trin. | 21.5 | 13.2 |
| | Cyperaceae | 7 | *Mesosetum cayennense* A. St.Hl. | 14.6 | 13.2 |
| | Melastomataceae | 6 | *Elyonurus muticus* (Spreng.) Kuntze | 11.7 | 4.3 |
| | Rubiaceae | 4 | *Andropogon lateralis* Nees | 5.5 | 4.0 |
| | Asteraceae | 4 | *Leptocorypheum lanatum* (HBK) Nees | 5.2 | 1.5 |
| | Polygalaceae | 4 | *Paspalum gemniflorum* Steud. | 4.0 | 2.2 |
| | | | Cyperaceae Indet. 9 | 3.6 | 9.2 |
| | | | *Syngonanthus nitens* (Bong.) Ruhl. | 2.6 | 6.8 |
| | | | Paspalum sp2 | 2.5 | 2.4 |
| | | | Poaceae indet. | 2.3 | 2.8 |
| | | | *Rhynchospora hirta* (Nees) Boeck. | 1.6 | 4.5 |
| | | | *Rhynchospora confinis* (Nees) C. B. Clarke | 1.6 | 3.7 |
| | | | TOTAL | **76.7** | |
| GC | Poaceae | 17 | *Axonopus fissifolius* (Raddi) Kuhlm. | 16.0 | 31.3 |
| | Myrtaceae | 16 | *Thrasya petrosa* (Trin.) Chase | 9.7 | 10.2 |
| | Malpighiaceae | 10 | *Axonopus pulcher* (Nees) Kuhlm. | 6.6 | 5.8 |
| | Leguminosae-Pap | 8 | *Ilex inundata* Poepp. ex Reisseck | 3.9 | 2.0 |
| | Cyperaceae | 8 | *Miconia macrothyrsa* Benth. | 3.6 | 0.9 |
| | Rubiaceae | 8 | *Erythroxylum* aff. *macrophyllum* Cav. | 2.5 | 1.9 |
| | | | *Tapirira guianensis* Aubl. | 2.3 | 0.2 |
| | | | *Aiouea trinervis* Meisn. | 2.2 | 0.9 |
| | | | *Byrsonima orbygniana* Adr. Juss. | 2.1 | 0.3 |
| | | | *Virola sebifera* Aubl. | 2.0 | 1.4 |
| | | | *Rhynchospora exaltata* Kunth | 2.0 | 2.3 |
| | | | *Alibertia steinbachii* Standl. | 1.9 | 2.1 |
| | | | TOTAL | **54.8** | |
| GR | Poaceae | 21 | *Axonopus canescens* (Nees) Kuhlm. | 31.9 | 19.7 |
| | Cyperaceae | 7 | *Leptocorypheum lanatum* (HBK) Nees | 21.1 | 20.9 |
| | Leguminosae-Pap | 6 | *Vellozia flavicans* C.Mart. ex Schult. f. | 10.8 | 6.6 |
| | Euphorbiaceae | 6 | *Elyonurus muticus* (Spreng.) Kuntze | 9.8 | 6.2 |
| | Leguminosae-Caes | 5 | *Axonopus* sp. | 6.5 | 12.7 |
| | | | *Andropogon virgatus* Desv. | 2.3 | 5.6 |
| | | | *Schizachyrium microstachyum* | 1.9 | 2.5 |
| | | | Poaceae indet. | 1.3 | 2.0 |

| PLOT | TOP FAMILIES | SPECIES | TOP SPECIES | RC | RF |
|---|---|---|---|---|---|
| | | | *Axonopus pulcher* (Nees) Kuhlm. | 1.2 | 1.5 |
| | | | *Paspalum carinatum* HBK | 1.0 | 2.3 |
| | | | *Chamaecrista fagonioides* (Vogel) H. S. Irwin & Barneby | 0.9 | 0.8 |
| | | | *Mimosa* sp. 2 | 0.8 | 0.5 |
| | | | TOTAL | **89.3** | |
| H1 | Poaceae | 22 | *Paspalum pectinatum* Nees ex Trin. | 23.1 | 18.8 |
| | Myrtaceae | 9 | *Elyonurus muticus* (Spreng.) Kuntze | 17.7 | 19.7 |
| | Leguminosae-Pap | 9 | *Davilla grandiflora* A. St.-Hil. & Tul. | 5.8 | 2.6 |
| | Leguminosae-Caes | 7 | *Andropogon virgatus* Desv. | 4.4 | 8.1 |
| | Asteraceae | 6 | *Ouratea* sp. 1 | 3.2 | 2.4 |
| | Indet. | 6 | *Richardia* sp. 1 | 3.1 | 1.7 |
| | | | *Digitaria dioica* Killeen & Rúgolo | 2.6 | 3.4 |
| | | | *Axonopus pulcher* (Nees) Kuhlm. | 1.9 | 2.5 |
| | | | *Trachypogon plumosus* (Humb. & Bonpl. ex Will.) Nees | 1.5 | 2.4 |
| | | | *Axonopus* sp. 1 | 1.3 | 1.8 |
| | | | *Erythroxylum* sp. 4 | 1.2 | 0.8 |
| | | | *Duguetia furfuracea* (A. St. Hil.) Benth & Hook. F. | 1.2 | 0.8 |
| | | | TOTAL | **67.1** | |
| PP | Poaceae | 15 | Poaceaee indet. | 16.0 | 11.2 |
| | Sterculiaceae | 7 | Poaceaee indet. | 10.8 | 8.7 |
| | Labiatae | 4 | *Andropogon bicornis* L. | 10.7 | 5.5 |
| | Leguminosae-Pap | 4 | *Leersia hexandra* Sw. | 10.5 | 10.8 |
| | Asteraceae | 4 | *Mikania congesta* DC. | 7.8 | 13.5 |
| | | | *Pavonia angustifolia* Benth. | 4.5 | 5.3 |
| | | | *Panicum tricholaenoides* Steud. | 4.5 | 4.7 |
| | | | *Helicteres gardneriana* A. St. Hil. & Naudin | 3.6 | 2.3 |
| | | | *Hyptis recurvata* Poit. | 3.4 | 4.0 |
| | | | *Melochia pilosa* (Mill.) Fawc. & Rendle | 2.9 | 0.6 |
| | | | *Hyptis parkeri* Benth. | 2.7 | 2.0 |
| | | | *Bauhinia rufa* (Bong.) Steud. | 2.7 | 1.2 |
| | | | TOTAL | **80.2** | |

**Table 9. Plot similarity. The values below the diagonal are Sorensen's presence/absence index and the values above the diagonal are Sorensen's similarity index for abundances. All values ≥ 0.20 are marked in bold type.**

|  | **Plot** | **FC2** | **FC1** | **GC** | **H1** | **GR** | **FO1** | **FO2** | **FT** | **PP** |
|---|---|---|---|---|---|---|---|---|---|---|
| Cerradao | FC2 |  | 0.19 | 0.08 | 0.13 | 0.04 | 0.08 | 0.04 | 0.03 | 0.02 |
| Cerrado | FC1 | **0.26** |  | 0.08 | **0.36** | 0.16 | **0.25** | 0.07 | 0.08 | 0.01 |
| Cerrado | GC | **0.21** | 0.19 |  | 0.1 | 0.1 | 0.13 | 0.11 | 0.05 | 0.02 |
| Campo sujo | H1 | **0.23** | **0.23** | 0.18 |  | 0.18 | 0.19 | **0.2** | 0.09 | 0.03 |
| Campo rupestre | GR | 0.14 | 0.16 | 0.2 | 0.17 |  | 0.12 | 0.13 | 0.11 | 0.03 |
| Termite savanna | FO1 | 0.15 | 0.12 | 0.14 | 0.12 | 0.13 |  | 0.16 | **0.21** | 0.03 |
| Termite savanna | FO2 | 0.13 | 0.12 | 0.15 | 0.09 | 0.1 | **0.38** |  | 0.12 | 0.02 |
| Termite savanna | FT | 0.13 | 0.11 | 0.15 | 0.1 | 0.09 | **0.29** | **0.34** |  | 0.03 |
| Pampa inundada | PP | 0.01 | 0.05 | 0.05 | 0.03 | 0.04 | 0.05 | 0.06 | 0.08 |  |

**Table 10. The relative frequency (RF) and relative cover (RC) of 9 different life forms found in the study plots.**

|  | epiphyte |  | graminoid |  | herb |  | liana |  | palm |  | rosette |  | shrub |  | tree |  | vine |  |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Plot | RF | RC | RF | RC | RF | RC | RF | RC | RF | RC | RF | RC | RF | RC | RF | RC | RF | RC |
| FC2 | 0.0 | 0.0 | 79.0 | 50.9 | 4.1 | 1.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 13.3 | 20.4 | 2.9 | 26.8 | 0.6 | 0.4 |
| FC1 | 0.0 | 0.0 | 69.3 | 51.2 | 9.4 | 7.7 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 18.2 | 23.9 | 2.8 | 16.9 | 0.3 | 0.2 |
| GC | 0.0 | 0.0 | 71.2 | 45.4 | 1.6 | 0.7 | 0.0 | 0.0 | 0.3 | 0.6 | 0.3 | 0.5 | 23.9 | 39.0 | 1.9 | 12.9 | 0.8 | 0.8 |
| H1 | 0.0 | 0.0 | 67.3 | 57.9 | 9.0 | 6.5 | 1.7 | 3.2 | 0.2 | 0.5 | 0.0 | 0.0 | 17.4 | 26.9 | 0.9 | 3.0 | 2.9 | 1.5 |
| GR | 0.0 | 0.0 | 84.7 | 82.6 | 5.3 | 3.7 | 0.0 | 0.0 | 0.0 | 0.0 | 6.6 | 10.8 | 3.1 | 2.4 | 0.1 | 0.1 | 0.3 | 0.3 |
| FO1 | 0.0 | 0.0 | 90.5 | 82.7 | 1.5 | 0.4 | 1.0 | 1.1 | 0.1 | 0.1 | 0.2 | 0.3 | 5.4 | 9.4 | 0.7 | 5.7 | 0.6 | 0.2 |
| FO2 | 0.0 | 0.0 | 84.7 | 73.2 | 7.0 | 2.7 | 0.4 | 0.3 | 0.0 | 0.0 | 0.6 | 1.2 | 6.0 | 18.5 | 0.4 | 3.2 | 0.8 | 0.8 |
| FT | 1.4 | 0.5 | 86.5 | 86.7 | 5.8 | 2.0 | 0.1 | 0.0 | 0.0 | 0.0 | 0.1 | 0.1 | 5.5 | 7.9 | 0.2 | 2.3 | 0.5 | 0.5 |
| PP | 0.0 | 0.0 | 54.4 | 61.4 | 22.2 | 16.5 | 0.2 | 0.1 | 0.0 | 0.0 | 0.0 | 0.0 | 8.8 | 12.5 | 0.2 | 1.4 | 14.3 | 8.2 |
| Means | 0.1 | 0.0 | 77.7 | 63.8 | 6.5 | 4.1 | 0.4 | 0.5 | 0.1 | 0.2 | 0.9 | 0.9 | 11.3 | 20.2 | 1.1 | 8.3 | 1.8 | 1.4 |

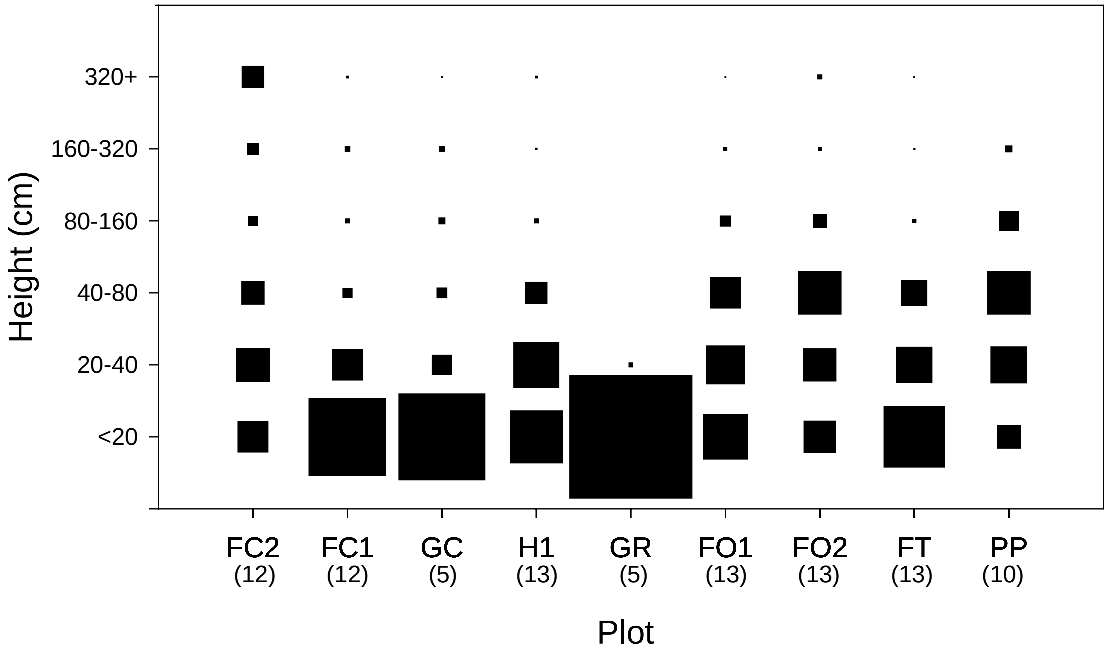

**Figure 7. The vertical structure of the plots. The size of the squares represents the proportion of intercept points in each of the height ranges. The number in parentheses below the plot code is the number of 20 m lines sampled in each plot.**

### *Soils*

The soils in all of the plots are acidic, have low fertility and many have high concentrations of aluminum (TABLE 11). The texture of the soils at all sites except FO1 and PP are sandy loams or loamy sands. These two sites have greater organic matter content and higher CEC than the other sites. We sampled soil from both a termite mound and from the surrounding low area to determine if soil conditions differed with microsite. We found that the greatest difference between these samples was in acidity, organic matter, and texture. CEC was lower in the low area than in the soil present in the termite mound.

**Table 11. Soil characteristics of the A horizon. For the FT plot, soils were collected from the low portion of the plot (FT(a)) and from a termite mound (FT(b)).**

| Plot | Depth (cm) | pH$_w$ | Elec. Cond. 1:5 uS/cm | Acidity cmol/kg | Total N (%) | P, Olsen mg/kg | K cmol/kg | Na cmol/kg | Ca cmol/kg | Mg cmol/kg | Total Exchangeable Bases cmol/kg | Cation Exchange Capacity cmol/kg | Al cmol/kg | Al/CEC (%) | Organic Matter (%) | Sand (%) | Silt (%) | Clay (%) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| FC2 | 0-8 | 4.5 | 21 | 1.8 | 0.09 | 2 | 0.1 | 0.04 | 0.2 | 0.1 | 0.4 | 2.2 | 1.3 | 59.1 | 1.4 | 61 | 24 | 15 |
| FC1 | 0-18 | 4.3 | 22 | 1.8 | 0.07 | 1 | 0.11 | 0.03 | 0.3 | 0.1 | 0.5 | 2.3 | 1.4 | 60.9 | 1.4 | 67 | 8 | 25 |
| GC | 0-22 | 4.9 | 12 | 0.3 | 0.03 | 1 | 0.04 | 0.04 | 0.2 | 0.1 | 0.4 | 0.7 |  | 0.0 | 0.3 | 68 | 17 | 15 |
| H1 | 0-18 | 4.9 | 18 | 1.6 | 0.07 | 0 | 0.05 | 0.04 | 0.2 | 0.1 | 0.4 | 2 | 1.1 | 55.0 | 0.9 | 69 | 3 | 28 |
| GR | 0-20 | 4.8 | 25 | 1.8 | 0.14 | 0 | 0.1 | 0.04 | 0.2 | 0.1 | 0.4 | 2.2 | 1.3 | 59.1 | 1.4 | 85 | 3 | 12 |
| FO1 | 0-18 | 4.3 | 23 | 4.4 | 0.19 | 0 | 0.09 | 0.04 | 0.2 | 0.1 | 0.4 | 4.8 | 3.5 | 72.9 | 2.0 | 11 | 47 | 42 |
| FO2 | 0-30 | 4.5 | 27 | 2.2 | 0.10 | 1 | 0.06 | 0.04 | 0.2 | 0.1 | 0.4 | 2.6 | 2 | 61.5 | 1 | 57 | 26 | 17 |
| FT (a) | 0-15 | 4.5 | 18 | 1.5 | 0.23 | 1 | 0.04 | 0.04 | 0.3 | 0.1 | 0.5 | 2 | 1.0 | 50.0 | 3.2 | 70 | 13 | 17 |
| FT (b) | 0-30 | 4.1 | 29 | 4.1 | 0.13 | 2 | 0.09 | 0.04 | 0.3 | 0.1 | 0.5 | 4.6 | 3.3 | 71.7 | 1.7 | 49 | 18 | 33 |
| PP | 0-22 | 4.8 | 24 | 0.9 | 0.36 | 1 | 0.19 | 0.11 | 0.3 | 0.1 | 0.7 | 1.6 | 0.4 | 25.0 | 3.9 | 30 | 55 | 15 |
| MEANS |  | 4.6 | 21.9 | 2.0 | 0.1 | 0.9 | 0.1 | 0.0 | 0.2 | 0.1 | 0.5 | 2.5 | 1.7 | 51.5 | 1.7 | 56.7 | 21.4 | 21.9 |

# DISCUSSION

We recorded a total of 662 vascular plant species among the 16368 individuals sampled in this study. Unfortunately, it is difficult to compare this value to other savannas, because a standard methodology for measuring the diversity of savannas has not been established. For tropical forests, the 1 ha plot sampled for all trees ≥ 10 cm dbh (Gentry 1988) and the 0.1 ha plot sampled for all woody stems ≥ 2.5cm dbh (Clinebell et al. 1995) have become standards that allow for direct comparison of one forest to another. No such standard exists for savannas. Our search of the literature shows that plot-based studies of cerrado diversity generally consider only the woody vegetation (de Oliveira-Filho et al. 1989) (Felfili and Dasilva 1993) and studies that do include the herbaceous flora are checklists or use phytosociological methods that preclude direct comparisons to our results. One comprehensive survey of the literature reviewed 145 species lists from Brazilian cerrado formations and estimated that between 3000 and 7000 angiosperm species inhabit the cerrado (Castro et al. 1999). Castro et al. considered 7000 species to most likely be a gross over-estimate, yet we encountered nearly 10 % of this total in our plots. This is remarkable given that we sampled a tiny fraction of the 2 million km$^2$ covered by cerrado vegetation (Ratter et al. 1997).

Though the lack of standardized methodology in savanna studies prevents us from making direct comparisons of the diversity of the savannas at Noel Kempff with those in other parts of the Amazon basin, we can compare the diversity of the different savanna formations found within our study area. In general, we found that the upland formations had greater richness than the seasonally inundated ones, though the campo rupestre plot at the Las Gamas site (GR) had richness comparable to several of the seasonally inundated sites.

The two richest sites are both from the Huanchaca plateau (GC and H1). At GC, the vegetation is dominated by plants < 20 cm tall, with a small proportion of individuals in each of the taller height classes. At the H1 site, there are a greater proportion of taller individuals, and the overall density of individuals is lower. Though these two sites have the highest diversity encountered in this region, they do not share a large proportion of their species. Sorensen's presence-absence similarity index for these plots is just 0.18 and only one species (*Axonopus pulcher*) is among the list of 12 species with greatest coverage for both plots.

Though the number of plots sampled is low, it is interesting that the two richest sites are found on top of the plateau, while upland formations below the plateau (FC1 and FC2) are less diverse. Soil conditions do not appear to be responsible for this difference in diversity. Soils at all four of these plots are similar, though the soil at GC has lower cation exchange capacity than the other plots and is the only one of these plots with low acid saturation. Vegetation history may therefore be more significant than edaphic differences in explaining the different levels of diversity.

Pollen analysis of sediment cores collected in two lakes in the lowland portion of Noel Kempff Park indicate that forest formations were not present until 1000 to 3000 yr BP and that savanna formations dominated the lowlands until the arrival of the forests (Mayle et al. 2000). This suggests that the present lowland savannas are relicts of more expansive savanna. Since the lowland savannas presently cover a small area compared to the savannas of the plateau, island biogeographic effects may be responsible for their reduced richness. On top of the plateau, carbon isotope analysis of soil organic matter suggests that forest formations have been persistent for several thousand years, while the savannas have been more wooded than they are at present (Panfil et al. Chapter 4 this dissertation). The soil carbon study cannot rule out the possibility that the savannas were entirely replaced by forest in the past, but the high diversity of the savanna formations on the plateau suggests that this is unlikely.

The pampa inundada plot at PP has the lowest species richness of all sites. The vertical structure of this plot is similar to that of other sites, but there are large differences in the relative frequency of herbaceous life forms. The relative frequency of graminoids is lower than in any other plot, and the relative frequency of free-standing herbs and herbaceous vines is higher than in any other plot. This is the plot that experiences the greatest amount of flooding, and is covered by 1-2 m of standing water during the rainy season each year. This flooding is likely a limiting factor for the survival of many species at this site, since the soil is not substantially different in quality than at the other sites and high acidity is not a factor. The species found at PP are largely unique to this site, as there is very little overlap in the species composition of this plot and any of the other plots, including the other seasonally inundated formations.

The greatest amount of overlap among plots was for the three seasonally inundated termite savanna plots (FO1, FO2, and FT). Sorensen’s index for these plots ranged from 0.29 to 0.38. The two FO plots are located less than 2 km apart, but the FT plot is approximately 100 km to the south, and these sites are separated by continuous tall forest. Despite the distance, the relatively large amount of species overlap between these sites suggests that the conditions found in these termite savannas are similar. It is striking that there is almost as much similarity between the FT plot and each of the FO plots (0.29 and 0.34) as there is between the two FO plots (0.38). Within site species turnover is nearly as great as between site turnover.

Despite similarities in the termite savanna plots, we found that the savanna formations were taxonomically distinct overall. We found that no single species was dominant at multiple plots, and that the same species had the greatest relative cover for only two of the plots (FO1 and FT). Though the Poaceae was the most speciose family in all plots, the other top families varied from plot to plot. Even plots located very close to one another geographically had low compositional similarity. This low level of compositional overlap indicates high $\beta$-diversity in the savannas of this region.

Our analysis of the savanna formations of Noel Kempff shows several results that are similar to our previous study of the forests (Panfil et al. Chapter 2, this dissertation). In that study, we found that upland forest formations were generally richer than lowland ones, though we did not find that the forests of the plateau were richer than those in the lowlands. Our sample of forest plots was larger than our sample of savanna plots, and we found high diversity and low diversity upland plots both on and off the plateau. We also found that the forests of the region had low levels of similarity between plots, and that the distance between plots was not a good predictor of similarity.

Since both the savannas and the forests of Noel Kempff Park have high $\beta$-diversity, it is clear that the conservation value of this park is its total regional diversity and not the diversity of any of its component ecosystems. This diversity of habitats is partly the result of geomorphology, with the inundation regime undoubtedly responsible for some species associations, but history is also likely to have been important in determining the modern array of species across the landscape. Soil quality does not vary considerably among sites, suggesting that edaphic differences are not responsible for the heterogeneity in species associations. Paleoecological studies also show that the past vegetation of this region has not been constrained by edaphic conditions, and that the vegetation formations of the region are dynamic. Past changes in vegetation are almost certainly responses to climate change, since human habitation of this region has been so sparse.

The mechanisms that link climate change to shifts in vegetation are poorly known. Fire is undoubtedly significant in determining the species composition and structure of the savanna formations (Panfil et al. Chapter 3, this dissertation, Coutinho 1982, Hoffmann 1996, Pivello and Norton 1996, Mistry 1998). The frequency of burns determines species composition, because fuel loads increase with decreased fire frequency, and because susceptibility to fire can depend on a plant’s size. At Noel Kempff, the frequency of burns is unknown for any of the savanna formations. Flood frequency and duration are also factors that link climate change with vegetation, and their influence is even less-well studied than fire.

The long-term ability of this park to conserve its great species richness will depend on the maintenance of habitat heterogeneity. Future climate change may favor one vegetation type over another, resulting in a loss of $\beta$-diversity and a consequent reduction in the total number of species. Like many tropical parks, the primary goal of management at Noel Kempff has been to limit human encroachment. In the future, management may also need to actively manage the ecosystems of this region. To make this possible, a detailed understanding of the mechanisms responsible for habitat heterogeneity is necessary.

# CHAPTER 4

# CARBON ISOTOPE ANALYSIS OF WHOLE SOIL AND HUMIN YIELDS DIFFERENT PALEOECOLOGICAL INTERPRETATIONS: RESULTS FROM AMAZONIAN BOLIVIA[3]

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[3] Panfil, S.N., G. Hodgins, T.J. Killeen, and C.J. Peterson to be submitted to *Quaternary Research*.

# ABSTRACT

We used soil carbon isotope analysis to investigate the history of conversion between forest and savanna at the edge of the Amazon basin in Bolivia. This technique is infrequently used, yet it provides an important alternative to pollen analysis for Amazonia, where pollen-preserving lakes and bogs are rare. A major difficulty with the technique is that soil is a complex mixture of carbon of different ages, making paleoecological interpretation difficult. We used a density and chemical fractionation protocol to improve the resolution of radiocarbon dating of our Bolivian soils. Our results show that the fractionation residue has a lower percentage of modern carbon than whole soil, indicating that our treatment preferentially removed young organic matter. We also found that the $\delta^{13}C$ of the residue is up to 8‰ more depleted than the whole soil. This suggests that young carbon can mask the isotopic signature of past vegetation. Other studies have not considered this phenomenon, and our results show that consideration of only the whole soil $\delta^{13}C$ may lead to incorrect interpretations of past vegetation.

For our site, we found that forest formations have persisted for several thousand years, and that the savanna has experienced at least one period with increased amounts of $C_3$ vegetation during this time. Our data also suggests that savanna is near its maximum geographic extent presently, and that the forest may currently be encroaching on the savanna.

# KEYWORDS

Amazon, accelerator mass spectrometry (AMS), carbon isotope analysis, cerrado, ecotone, forest/savanna boundary, paleoecology, soil organic matter

# INTRODUCTION

Stable carbon isotope analysis of soil organic matter (SOM) is a powerful tool for understanding the history of vegetation change in areas where $C_3$ and $C_4$ plants dominate distinct habitats. This method can be used in many tropical and subtropical locations where forest and grassland co-occur (Schwartz et al. 1986, Boutton et al. 1998). Most of the lowland margin of the Amazon basin and numerous isolated pockets of savanna in the interior of the basin are candidates for analysis with this technique. The method is especially valuable because it can be applied in areas where pollen analysis is not feasible because pollen-bearing sediments are absent. Carbon isotope analysis of soil does have some significant limitations, but new approaches, like soil fractionation and accelerator mass spectrometry (AMS) may greatly improve the accuracy and precision of the analysis. The careful application and interpretation of carbon isotope analysis of soil can greatly enhance our knowledge of past shifts in vegetation.

A second advantage of carbon isotope analysis over pollen analysis is that the method provides fine spatial resolution. Pollen analysis is typically performed in lakes, and the geographical extent represented in a pollen record is frequently unknown. Much tropical tree pollen is animal dispersed and not wind dispersed, but transport of pollen in water is likely to be important (Haberle and Maslin 1999). In large catchments, pollen may have been transported great distances, making spatial extrapolation of a pollen record difficult. Soil organic matter is unlikely to be transported long distances on flat terrain, though longer distance transport may be possible for slopes (Pessenda et al. 2001).

The principal disadvantages of soil carbon isotope analysis are poor taxonomic and temporal resolution. By itself, the technique can only discriminate between $C_3$ and $C_4$ species. However, taxonomic resolution can be improved by coupling the technique with phytolith analysis (Piperno and Becker 1996, Alexandre et al. 1999).

More serious concerns relate to chronology because the soil carbon cycle is complex. Carbon of different ages is mixed throughout the soil profile, so isolating carbon of a particular age by its depth is not possible. One approach to separate SOM of different ages is through physical and chemical fractionation techniques. These methods reduce the age range of carbon in each fraction. The humin fraction is tightly bound to mineral particles in the soil and cycles over longer timescales than more labile carbon in soil (Trumbore et al. 1989). Carbon in the humin fraction is still a mixture of ages, so high resolution chronologies cannot be developed from soil, but the age range of carbon in this fraction is greatly reduced when compared with whole soil.

Despite disadvantages of the technique, large differences between the $\delta^{13}C$ of standing vegetation and SOM have been shown at a number of sites and provide strong evidence that shifts between forest and savanna vegetation have occurred (Victoria et al. 1995, Desjardins et al. 1996, Martinelli et al. 1996, Pessenda et al. 1998, de Freitas et al. 2001). Unfortunately, a range of protocols has been used to process samples, and we believe that this makes comparison among studies difficult. A shortfall of several previous studies is that they have only analyzed whole soil (Victoria et al. 1995, Desjardins et al. 1996, Pessenda et al. 1998). Other studies have isolated the humin fraction of soil for dating, but they present the $\delta^{13}C$ for whole soil (Pessenda et al. 1996a, de Freitas et al. 2001). We found only one Amazonian study that explicitly referred to the $\delta^{13}C$ of the humin fraction (Pessenda et al. 1996b). In this study, the authors found that no significant difference existed between the $\delta^{13}C$ of the whole soil and the humin fraction.

In that study, we apply carbon isotope analysis of soil organic matter to an ecotone between moist tropical forest and cerrado-type savanna at a site in northeastern Bolivia. The goal of this work is to document the past change between these two vegetation types. To reduce the imprecision inherent in analyzing whole soil, we performed a fractionation technique to isolate the humin fraction. We present $\delta^{13}C$ and radiocarbon data for both the whole soil and the humin fraction and compare paleoecological interpretations that can be made for both types of data.

### ***Stable carbon isotope analysis of SOM***

The ratio of $^{13}C$ to $^{12}C$ in plant tissue is primarily a function of a plant's photosynthetic pathway, though small variations can be caused by local environmental conditions. Plants using the $C_3$ pathway discriminate against $^{13}C$ more strongly than $C_4$ plants and thus have tissue that is more depleted in $^{13}C$ than $C_4$ plants. Typical values, expressed as a per mil difference from the Pee Dee Belemnite standard ($\delta^{13}C$) are –27 ‰ for $C_3$ plants and –13 ‰ for $C_4$ plants (Boutton 1996).

Over time, the isotopic signature of SOM approximates that of the standing vegetation. In tropical savannas $C_4$ plants are dominant and savanna soils typically have higher levels of $^{13}C$ than forest soils, which are dominated by $C_3$ plants. For places where the vegetation has not changed, one would expect to see similar $\delta^{13}C$ values throughout the soil profile. For sites where there has been a conversion between forest and savanna, one would expect that surface samples have $\delta^{13}C$ values similar to that of the modern vegetation and deeper samples would have a value typical of the previous vegetation type.

## METHODS

### ***Location***

Our study site is the Huanchaca Plateau in Bolivia’s Noel Kempff Mercado National Park. This park spans the ecotone between moist Amazonian forest to the north and Chiquitano deciduous tropical forest to the south (Killeen and Schulenberg 1998, Panfil et al. Chapter 2, this dissertation). It is also the western-most limit of cerrado savanna vegetation (Eiten 1978). Cerrado formations separate islands of tall moist forest over much of the plateau (Figure 8). Detailed descriptions of the species composition of the forest and savanna habitats can be found in Panfil et al. (Chapters 2 and 3, this dissertation). The modern distribution of vegetation does not appear to be the result of direct human

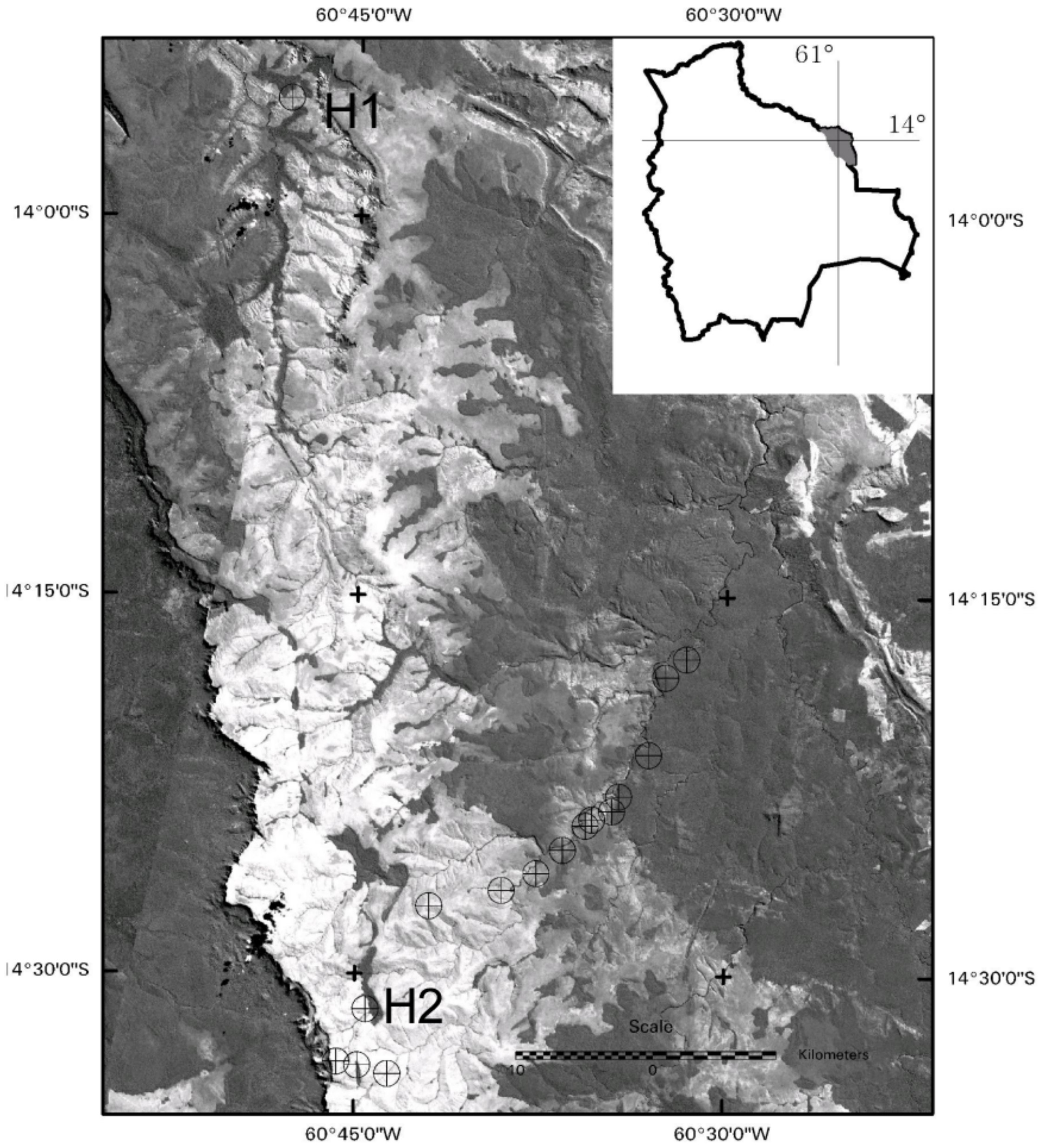

Figure 8. LandSat TM image of Noel Kempff Mercado National Park. The park's location in Bolivia is shown in the inset figure. The Huanchaca I and Huanchaca II study sites are marked, and the position of the Trans-Huanchaca transect is also marked with crosshairs at the points where soil samples were collected. Lighter portions of the image indicate savanna, and increased amounts of woody vegetation are increased by increased darkness. Forest is dark grey in this image.

influence. Human habitation in the region is sparse and no permanent settlements are known to have existed on top of the plateau. The remote location of the park means that climate, and not direct human activity, is likely to have driven shifts in vegetation.

The savannas in the north of the plateau have a greater density of woody stems than those in the south and this may indicate that the northern savannas are in the process of converting to forest (Panfil et al. Chapter 3, this dissertation). We chose one northern site and one southern site to collect soil samples for this study. At the northern site (Huanchaca I), the woody plants in the savanna form a nearly closed canopy in some places. Most shrubs and small trees are < 3 m tall, with occasional trees to 6 m. Charred bark indicates that fires occur, but the frequency of burn is unknown. At the southern site (Huanchaca II), woody plants are shorter, less dense and natural grass fires occur at 2-3 year intervals.

### *Climate*

The Noel Kempff region is characterized by a warm tropical climate with strongly seasonal precipitation. Long-term weather data do not exist for the park, so we infer meteorological conditions from stations located 160-200 km to the southwest and 150–200 km northwest of the park. Data from these stations show that mean annual temperature is 25-26º C with a mean annual minimum of 10º C, and frost is not known in the region (Roche and Rocha 1985). During the austral summer, the inter-tropical convergence zone (ITCZ) brings warm, moist

Amazonian air masses to the region. Total mean annual precipitation is approximately 1500 mm, with almost all falling between October and June (Killeen et al. *In press*). The northern parts of the park receive two to several hundred mm more of precipitation per year than those to the south (Roche and Rocha 1985). During the austral winter, the ITCZ shifts to the north and dry weather patterns replace the moist air masses.

### ***Sample collection***

At each site, we collected soil samples from three transects oriented perpendicularly to the edge of a mesic tall-forest island (Table 12). These transects range in length from 87 to 240 m and serve to document fine scale movement of the forest-savanna boundary. We also sampled soil from a 38.5 km transect that crosses the broad ecotone from open savanna at the western side of the Huanchaca Plateau to continuous forest on the eastern side (Figure 8). There are 15 pits distributed along this transect, with the distance between pits ranging from 0.6 km to 8.8 km.

For each of the pits, we collected >1 kg of soil at each of 5 depths: 0-1 cm, 1-6 cm, 10-15 cm, 35-50 cm, and 80-100 cm. We manually removed all visible roots in the field. Upon return to the laboratory, we dried the soils to constant weight and archived them for later processing.

**Table 12. The location, length, and number of pits sampled for each of the transects used in this study.**

| Transect | Site | Latitude | Longitude | Elevation (m) | Length (m) | Pits |
|---|---|---|---|---|---|---|
| 4 | Huanchaca I | 13°54.2' | 60°48.8' | 550 | 160 | 5 |
| 7 | Huanchaca I | 13°54.3' | 60°48.4' | 550 | 120 | 4 |
| 31 | Huanchaca I | 13°55.1' | 60°49.0' | 550 | 240 | 7 |
| 9 | Huanchaca II | 14°30.6' | 60°44.2' | 850 | 87 | 4 |
| 13 | Huanchaca II | 14°31.7' | 60°44.2' | 850 | 120 | 5 |
| 30 | Huanchaca II | 14°30.5' | 60°44.3' | 850 | 160 | 5 |
| Trans- | start | 14°33.5' | 60°45.7’ | 900 | 38.5 km | 15 |
| Huanchaca | end | 14°17.5’ | 60°32.0’ | 600 | | |

### *Sample preparation*

We analyzed soil samples either as minimally processed whole soils or as the residue that remained following a density and chemical fractionation (Figure 9). For the whole soil samples, we used a sieve to remove all particles >2 mm and then we ground the samples to a fine powder with a ball mill grinder before submitting the samples for isotopic analysis.

We selected 18 samples from Transect 30 and the Trans-Huanchaca transect for density and chemical fractionation using the protocol described by Trumbore and Zheng (Trumbore and Zheng 1996). We used sodium polytungstate (SPT; manufactured by SOMETU-USA, Sherman Oaks, California) mixed to a density of 2 g/cm$^3$ for the density separation. After sieving each sample,

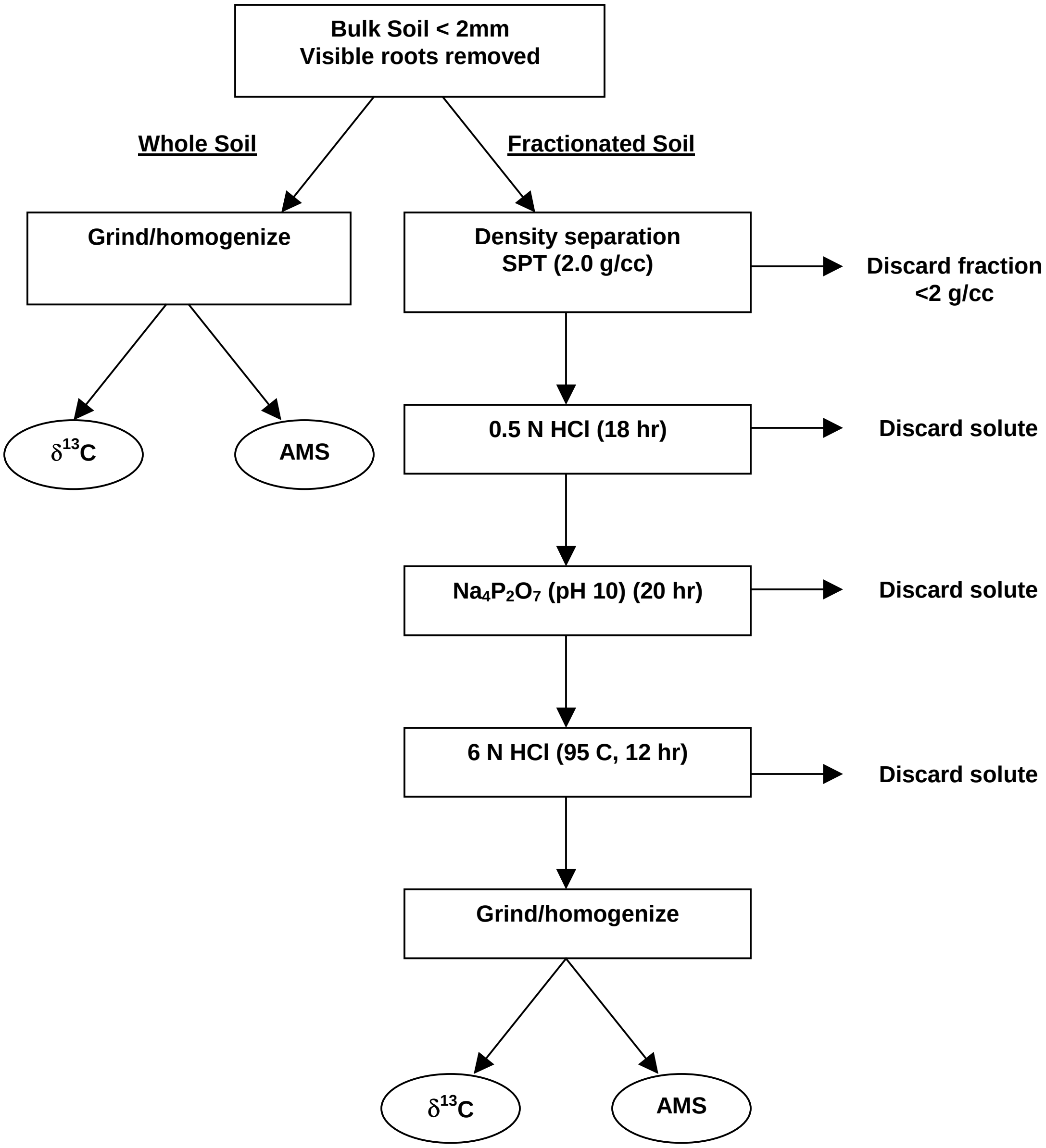

**Figure 9. Diagram of the protocol used to analyze soil. Samples were analyzed as whole soils (left side of diagram) or as the residue remaining following a density and chemical fractionation (right side of the diagram).**

we added 25 ml of SPT solution to 6 g of soil. We mixed the soil and SPT thoroughly on a motorized shaker, and then centrifuged the mixture until we obtained a clear separation. We discarded all floating material and repeated this separation up to five times until no more material floated. We then washed each sample 3 times with deionized water. Next we added 10 ml of 0.5 M HCl to each sample and slowly shook this mixture for 24 hours at room temperature. We discarded the solute and washed the samples twice with deionized water, then added 25 ml of 0.1N $Na_4P_2O_7$ (pH 10) and shook the samples slowly for 20 hrs at room temperature. We again discarded the solute and performed two more washes with water. For the final treatment, we added 12 ml of 6N HCl to each sample. We heated the samples to 95 C for 12 hr, then discarded the solute and washed the samples again with water. We then dried the samples and ground them to a fine powder in a ball mill for $\delta^{13}C$ and $^{14}C$ AMS analysis.

### ***Analytical methods***

We analyzed soil samples for $\delta^{13}C$ at the isotope laboratory of Augustana College, Sioux Falls, SD, USA. We corroborated $\delta^{13}C$ measurements at the Analytical Chemistry Laboratory of the Institute of Ecology at the University of Georgia, Athens, GA, USA and at the Stable Isotope Ratio Facility for Environmental Research at the University of Utah, Salt Lake City, UT, USA.

Radiocarbon dates were determined by accelerator mass spectrometry at the Center for Applied Isotope Studies at the University of Georgia. Soil and soil fractions ranging from 1.5 to 0.11 % carbon were combusted in evacuated sealed ampoules in the presence of excess CuO. Carbon dioxide was cryogenically purified from the resulting combustion products and catalytically converted to graphite using the method of Vogel *et al.*(Vogel et al. 1984).

Graphite $^{14}C/^{13}C$ ratios were measured using the CAIS 0.5 MeV accelerator mass spectrometer. The results are expressed in uncalibrated radiocarbon years BP (Before Present – AD 1950) using the $^{14}C$ half-life of 5568 years (or percent Modern Carbon). The data were corrected for isotopic fractionation using the measured $\delta^{13}C$ values. The errors are quoted as one standard deviation.

## RESULTS

### *Whole soil $\delta^{13}C$*

Whole soils collected from the 0-1 cm depth have $\delta^{13}C$ values consistent with the current vegetation (Figure 10 and 11). At forested sites, the 0-1 cm depth samples had $\delta^{13}C$ values ranging from –27.78 ‰ to –29.86 ‰ (n=17); these values are typical of $C_3$ vegetation. Samples collected from the top centimeter at the present forest/savanna boundary had values similar to those of the forest, with a range of –28.04 ‰ to –29.77 ‰ (n=4). This was expected, since trees form the boundary and tree leaf litter covers the soil surface. We found much greater variability in the isotopic value of surface soils in the savanna than we did in the forest or at the boundary. These values ranged from –15.51 ‰ at the savanna end of the Trans-Huanchaca transect to –29.52 ‰ at a point on Transect 31 at the Huanchaca I site (n=26). This range of values is reflective of the variation in density of woody plants at the sites. The savanna at Transect 31 is the most densely wooded of all the transects sampled.

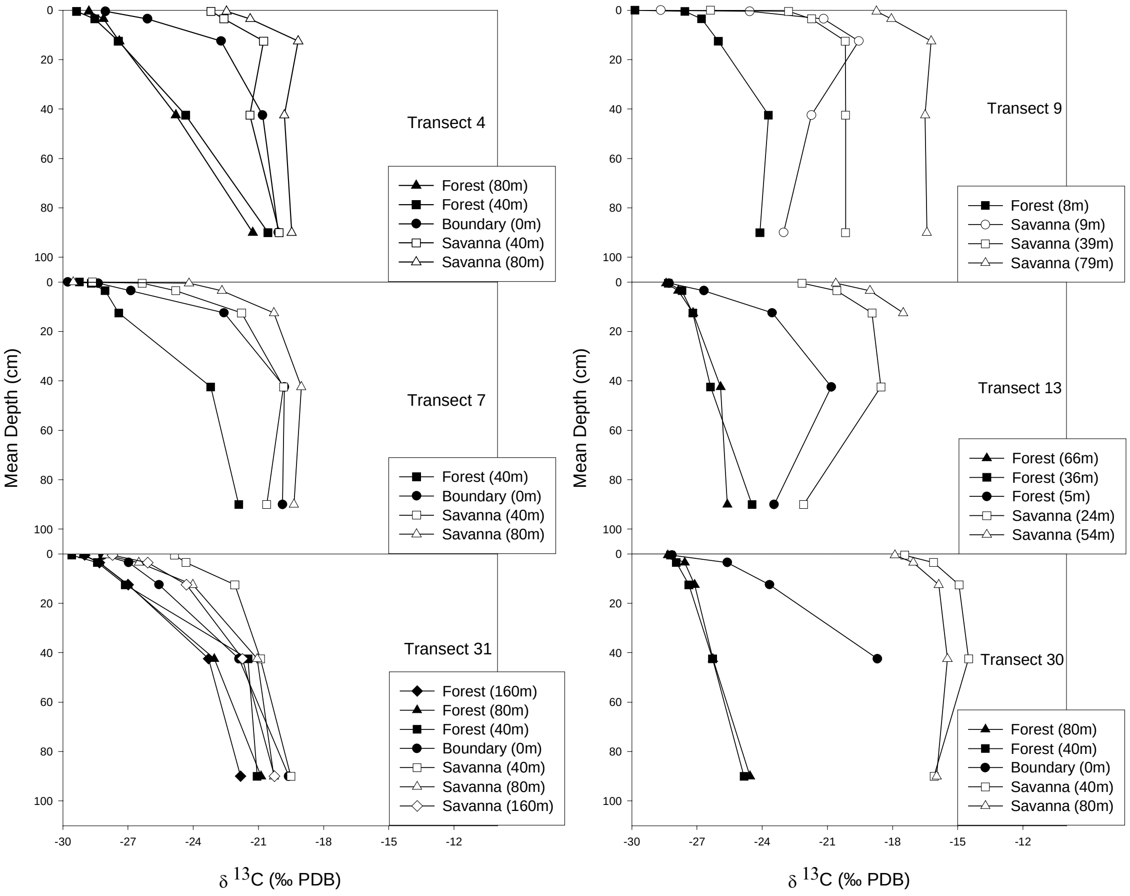

**Figure 10. Whole soil $\delta^{13}$C values for transects at the Huanchaca I and Huanchaca II sites in northeastern Bolivia. Each panel shows the profiles for pits along a single transect. The current vegetation found at each pit is listed in the legend, with the distance from the forest edge listed in parentheses. Depths indicated are mean depths based on the sampling protocol described in the methods. For two of the pits (54m into the savanna at transect 13, and at the Boundary of transect 30), we hit rock and were unable to collect soil from the deeper depths.**

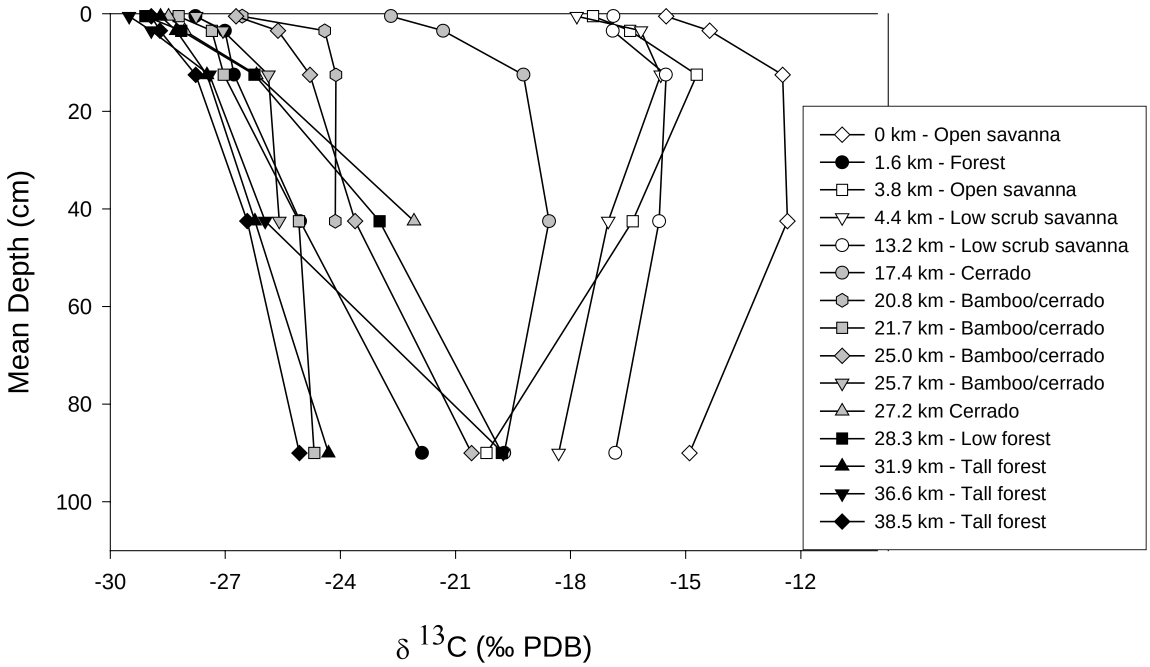

**Figure 11. Whole soil $\delta^{13}$C values for pits along the Trans-Huanchaca transect. At two of the pits (17.4 km and 27.2 km), we were unable to collect from the 90 cm mean depth because of rock.**

In all but 2 of the 45 pits sampled, we found that $\delta^{13}$C of the surface soil was more negative than that of the deepest sample. This difference between surface and deeper soils was significant for pits in the forest, at the boundary, and in the savanna (Figure 12). To determine if the amount of $\delta^{13}$C change over depth differed between vegetation type, we performed an analysis of variance and found that the amount of change with depth differed significantly ($p< 0.001$) between vegetation types. A post-hoc Bonferroni t-test indicates that the amount of shift with depth is less in the savanna than in either the boundary ($p = 0.003$)

or forest (p = 0.019), but that there is no difference between the boundary and forest (p = .226). For all pits, the greatest shift was found in the shallower portion of the soil profile; the $\delta^{13}C$ of the two deeper samples (35-50 cm and 80-100 cm) in each pit tended to be similar (Figures 10, 11).

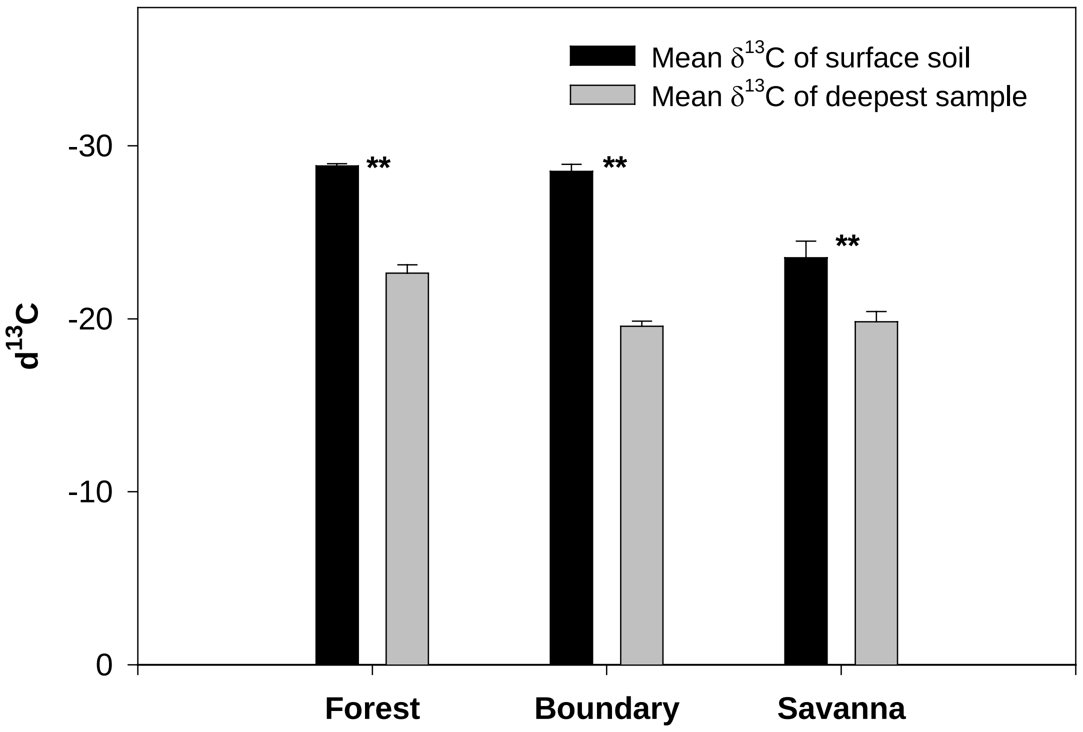

**Figure 12. Mean $\delta^{13}C$ values for the top and bottom sample of soil for pits in forest, at the boundary, and in savanna. The double asterisks (**) signify that for each type of vegetation, the top and bottom sample means are significantly different ($p < 0.005$).**

### *Humin $\delta^{13}C$*

The $\delta^{13}C$ values for the residue that remained after density and chemical fractionation of whole soil are substantially more depleted than the whole soil (Figure 13). In all cases, the isotope ratio of the residue is depleted relative to the

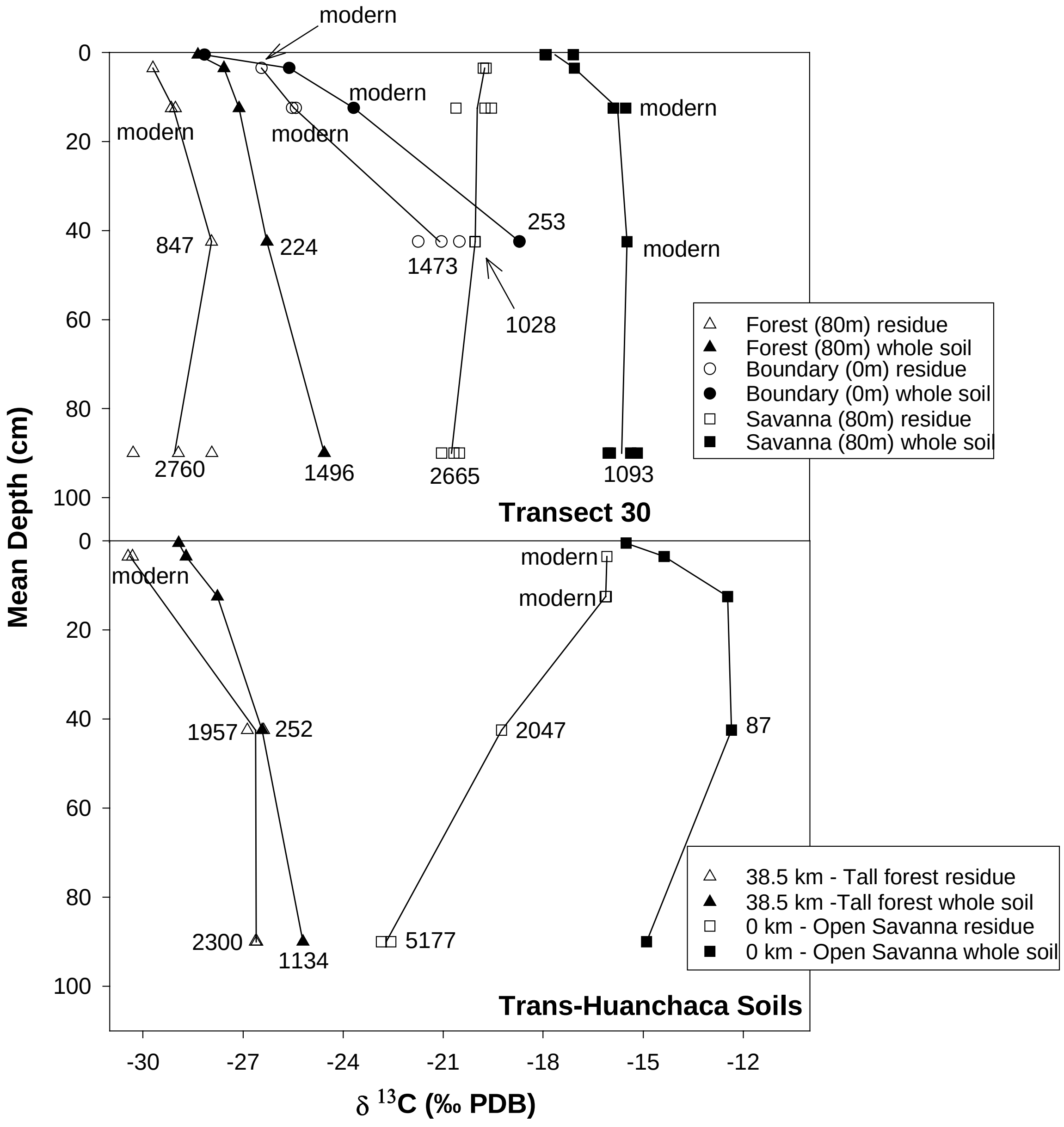

**Figure 13. $\delta^{13}$C profiles for the humin fraction and for whole soils from three pits on Transect 30 and from the endpoint pits of the Trans-Huanchaca transect. Replicate fractionation runs were performed on many of the samples and are marked by separate symbols. Lines connect the mean value of the replicates.**

bulk soil. Overall, the amount of depletion ranges from 0.8 ‰ to 8.1 ‰. Depletion is generally greater with depth, and is greater in the savanna profiles than in the forest or boundary profiles.

### *Radiocarbon dates*

Radiocarbon dates were modern for whole soil samples as deep as 35-50 cm, and for humin samples as deep as 10-15 cm (Table 13). For all profiles, radiocarbon dates increase with depth, and at any depth, the humin fraction is approximately 1000 to 2000 $^{14}$C yr older than the whole soil. We find $^{14}$C ages at a given depth to be consistent among sites.

## DISCUSSION

Our initial interpretation of the whole soil $\delta^{13}$C data (Figures 10, 11) was that modern vegetation contains a greater proportion of $C_3$ plants than was found at these sites in the past. This is because the whole soil stable isotope profiles show enrichment with depth for nearly all of the pits we sampled. However, two factors suggest that this interpretation is incorrect.

The first is a widely observed phenomenon in $C_3$ systems, whereby soil organic matter becomes slightly enriched in $^{13}$C during decomposition (Boutton and Yamasaki 1996). Decomposition is typically responsible for a shift in $\delta^{13}$C of up to 3 ‰ in $C_3$ ecosystems. Various hypotheses to explain this enrichment have been proposed, including a depletion of atmospheric levels of $^{13}$C due to the

**Table 13. A comparison of $\delta^{13}C$ and radiocarbon age for whole soil and residue at Transect 30 and the Trans-Huanchaca transect. Radiocarbon ages are corrected for $\delta^{13}C$ but not calibrated to calendar years. For samples with super-modern levels of 14C, the percent modern carbon (pMC) is shown. The errors reported are instrument error.**

| Modern Vegetation | Distance from Boundary (m) | Mean depth (cm) | Whole soil | | | Humin | | |
|---|---|---|---|---|---|---|---|---|
| | | | %C | $\delta^{13}C$ (‰) | $^{14}C$ yr BP | %C | $\delta^{13}C$ (‰) | $^{14}C$ yr BP |
| **Transect 30** | | | | | | | | |
| Forest | 80 | 12.5 | 1.44 | -27.1 | | 0.43 | -29.11 | (101.6 ± 0.39%) |
| | | 42.5 | 1.21 | -26.3 | 224 ± 46 | 0.25 | -27.78 | 847 ± 29 |
| | | 90 | 0.42 | -24.5 | 1496 ± 26 | 0.19 | -29.04 | 2760 ± 29 |
| Savanna | 80 | 3.5 | 1.21 | -17.05 | | 0.36 | -19.70 | (108.1 ± 0.42%) |
| | | 12.5 | 1 | -15.87 | | 0.31 | -19.54 | (105.7 ± 0.44%) |
| | | 42.5 | 0.74 | -15.47 | (104.5 ± 0.34%) | 0.16 | -20.03 | 1028 ± 27 |
| | | 90 | 0.43 | -15.3 | | 0.11 | -20.66 | 2665 ± 27 |
| Boundary | 0 | 3.5 | 1.78 | -25.6 | (111.2 ± 0.36%) | 0.36 | -26.43 | |
| | | 12.5 | 1.53 | -23.7 | (113.4 ± 0.77%) | 0.44 | -25.40 | (105.2 ± 0.38%) |
| | | 42.5 | 0.8 | -18.7 | 299±60 | 0.23 | -20.41 | 1473±31 |
| **Trans-Huanchaca** | **Position along transect (km)** | | | | | | | |
| Savanna | 0 | 3.5 | 1.33 | -14.37 | | 0.32 | -16.09 | (109.5 ± 0.40%) |
| | | 12.5 | 1.57 | -12.47 | | 0.32 | -16.11 | (103.4 ± 0.35%) |
| | | 42.5 | 0.61 | -12.35 | 87 | 0.11 | -19.25 | 2047 ± 29 |
| | | 90 | 0.22 | -14.41 | | 0.06 | -22.51 | 5177 ± 29 |
| Forest | 38.5 | 3.5 | 3.4 | -28.71 | | 0.83 | -30.45 | (112.0 ± 0.36%) |
| | | 42.5 | 0.5 | -26.43 | 252 ± 31 | 0.12 | -26.87 | 1957±29 |
| | | 90 | 0.31 | -25 | 1134 ± 26 | 0.11 | -26.59 | 2300 ± 25 |

combustion of fossil fuels and isotopic fractionation by microbes (Ehleringer et al. 2000). Nevertheless, many of our whole soil profiles show enrichment greater than 3 ‰, suggesting that conversion between forest and savanna vegetation has occurred.

More importantly, we found that the $\delta^{13}C$ of whole soil can be much different than that of the humin fraction. This leads to a different paleoecological interpretation than we initially made for the whole soil. The greatest difference between whole soil and humin $\delta^{13}C$ was for the two savanna profiles. In both cases, the older carbon present in the humin fraction had a $\delta^{13}C$ that indicates that $C_3$ plants were more common in the past than in modern vegetation.

We also found a difference between the $\delta^{13}C$ values of humin and whole soil at the boundary and in the two forest pits, but this difference was not as great as in the savanna. We do not have an explanation for the small differences that we did find, but the $\delta^{13}C$ value of the humin is typical of $C_3$ plants, indicating that $C_4$ carbon is not represented in this fraction.

These results suggest that the forest at both locations has been dominated by $C_3$ vegetation for the time period represented by the organic matter in the soil profile. This is at least 2300 years at the Trans-Huanchaca transect and 2760 years at transect 30. Since these dates represent mean residence times for the carbon in the humin fraction, and since the $\delta^{13}C$ value of the humin contains little or no $C_4$ carbon, forest is likely to have been present at these sites for much longer than the stated radiocarbon ages.

The boundary profile at transect 30 has a much greater $\delta^{13}C$ at 35-50 cm than at the surface, indicating that $C_4$ plants occupied that location in the past. This is true for both the whole soil and the humin fraction. The fact that the forest profile located 80 m from this pit shows no evidence of $C_4$ vegetation indicates that any previous contraction of the forest was limited in distance to less than 80

m. The timing of forest contraction is difficult to determine because the relative contribution of $C_3$ and $C_4$ carbon to the humin are unknown, and because multiple shifts between forest and savanna could have occurred at this location.

In summary, our results suggest that the forest has persisted at these locations for at least several thousand years. The savanna locations have previously had a greater amount of woody vegetation than they presently have. This indicates that recent conditions have been drier, and likely have favored more frequent burns than was true during the last several thousand years. Though the boundary profile indicates a recent encroachment of forest on the savanna, the savanna appears to be near its maximum extent for the last several thousand years.

With the exception of Pessenda et al. (1996), other studies of forest/savanna conversion in the Amazon basin do not compare the $\delta^{13}C$ of whole soil to the humin fraction. The authors of that study found humin to be isotopically similar to whole soil. In the present study we found large differences, indicating that new inputs of organic matter can mask the signature of past vegetation. We therefore urge caution in describing past vegetation based on $\delta^{13}C$ values of whole soil alone.

Since other studies analyze only whole soil, or do not present $\delta^{13}C$ data for the humin fraction, it is difficult to compare the conclusions we drew in our study with those for other sites. The Pessenda et al. (1996) paper is the only study whose methodology allows direct comparison, yet this study is based on soil collected at sites > 1000 km from Noel Kempff Park, and it is based on individual profiles at three forested sites. At one of their sites in northern Amazonia, these authors found a $\delta^{13}$C signature typical of forest throughout the soil profile. At two semi-deciduous forests in southern Brazil, the authors found an enrichment of up to 9 ‰ in deep soils (up to 180 cm) indicating that $C_4$ vegetation was more important at these sites in the past. This finding in southern Brazil is different than the results from our site, but given the great distances between sites, different findings are not surprising.

A more geographically appropriate comparison to our study is a pollen analysis done on cores collected from two lakes located 25-60 km west of the Huanchaca Plateau (Mayle et al. 2000). At the northern lake, grass pollen was dominant, and moist forest tree pollen was scarce through most of the Holocene. Approximately 3,000 yrs BP, this pattern was reversed, with pollen from moist forest taxa (Moraceae/Urticaceae) becoming common, and grass pollen becoming rare. The same pattern was found for a second lake located 100 km to the south, but with later timing. Forest development at the southern site occurred approximately 1000 yrs BP.

Soil data from the present study indicates that forest has existed at the Transect 30 and at the 38.5 km point on the Trans-Huanchaca transect for more than 2000 yrs. This is longer than forest has existed at the southern lake located in the lowlands west of the Huanchaca Plateau. Our soil record does not extend far enough into the past to determine if forest on the plateau existed before forest reached the northern lowland lake. The savanna on the plateau has a stronger $C_4$ signal than it did in the past. There is no analogous savanna signal in either of the lowland pollen cores. This suggests that vegetation change in this region has involved a complex mixture of conditions that have favored both forest and savanna. Though forests have persisted at some sites on top of the Huanchaca Plateau and in the lowlands to the west, savanna formations have been dynamic, with changes in the density of $C_3$ plants during the last several thousand years.

## CONCLUSION

Soil carbon isotope analysis across the ecotone between moist forest and cerrado savanna in northeastern Bolivia shows that this technique can document fine spatial-scale shifts in the forest/savanna boundary. Our analysis of $\delta^{13}C$ of the humin fraction of these soils suggests that analysis of whole soil can be misleading. At our sites, forest has been persistent for several thousand years, and may currently or recently be advancing on the savanna. Savanna vegetation appears to be near its maximal geographic extent for the last several millennia, and also has a smaller proportion of $C^3$ vegetation than it has had during this time.

# CHAPTER 5

# MODERN FOREST/SAVANNA BOUNDARY FLORISTICS AND DYNAMICS AT AN AMAZONIAN ECOTONE[4]

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[4] Panfil, S.N., T.J. Killeen, and C.J. Peterson. To be submitted to *Journal of Vegetation Science*.

# ABSTRACT

The boundary between forest and savanna on the Huanchaca Plateau in northeastern Bolivia is abrupt, with a sharp reduction in woody-plant basal area over a distance of less than 15 m. The species composition of the forest and savanna areas in the 40 m band along the ecotone shows differences in the most common species, but still moderately high levels of species overlap, indicating that the structural change between forest and savanna is more abrupt than the compositional change. Soil nutrient levels and texture do not differ significantly in the forest and savanna portions of the ecotone, suggesting that the vegetation differences are not due to edaphic conditions.

The density of woody stems in the savanna fluctuates greatly in response to naturally occurring fires in this area. Stem density nearly doubled in some portions of the savanna during a two year period with no fire, and many of the new stems were from forest species, indicating the possible colonization of the savanna by forest. However, naturally occurring burns or experimental controlled burns caused a reduction in stem density that offset any recent ingrowth. An analysis of the surviving stems indicates that larger stems have greater survival, so a reduction in fire frequency that allows trees in the savanna to reach a size large enough to resist fire may lead to forest expansion.

Key Words: Forest/savanna boundary, cerrado, ecotone, Amazon, fire

# INTRODUCTION

There is mounting evidence that the relative extent of vegetation types in the Amazon Basin is highly dynamic, expanding and contracting in response to changes in environmental conditions that occur on a variety of time scales. Fire (Cochrane and Schulze 1999), meandering rivers (Salo et al. 1986), and changing climate (Colinvaux and De Oliveira 2001) can all change local conditions and may lead to changes in both species composition and structure. Despite the growing appreciation that the Amazon contains heterogeneous and dynamic vegetation types, few studies have attempted to document the factors that govern the conversion of one vegetation type to another.

Over much of the lowland margin of the Amazon Basin, moist tropical forest intergrades with savanna. Paleoecological evidence at the perimeter of the basin shows that forest has been expanding during the Holocene (Panfil et al. Chapter 4, this dissertation, Mayle et al. 2000). It is unknown how much smaller the forested area of the Amazon was during the Pleistocene (Colinvaux et al. 2000), yet it is clear that the modern distribution of forest and savanna is not the same as it was in the past.

In this study, we examine the contemporary dynamics of vegetation across the ecotone from forest to savanna on the Huanchaca Plateau in Bolivia’s Noel Kempff Mercado National Park. This park spans the ecotone between moist tropical forest and dry forest and savanna formations. Pollen analysis and carbon isotope analysis of soil organic matter both show that the position of the forest/savanna boundary in the park has been dynamic throughout the Holocene

(Panfil et al. Chapter 4, this dissertation, Mayle et al. 2000). We use repeated inventories of vegetation sampling plots oriented perpendicular to the forest/savanna boundary to determine if there is evidence of modern forest or savanna expansion, and to examine the role of fire in regulating conversion between these vegetation types.

## METHODS

### ***Location***

Our study site is the Huanchaca Plateau in Bolivia’s Noel Kempff Mercado National Park. This park spans the ecotone between moist Amazonian forest to the north and Chiquitano deciduous tropical forest to the south (Killeen and Schulenberg 1998, Panfil et al. Chapter 2, this dissertation). It is also the western-most limit of cerrado savanna vegetation (Eiten 1978). Cerrado formations separate islands of tall moist forest over much of the plateau (Figure 8). Detailed descriptions of the species composition of the forest and savanna habitats can be found in Panfil et al. (Chapter 2, this dissertation). The distribution of vegetation does not appear to be the result of direct human influence as human habitation in the region is sparse and no permanent settlements are known to have existed on top of the plateau. The lack of human intervention suggests that climate is likely to have driven past shifts in vegetation.

We chose two study sites in order to represent a range of forest-savanna transitions. The savannas in the north of the plateau have a greater density of woody stems than those in the south and this may indicate that the northern savannas are in the process of converting to forest (Panfil et al. Chapter 3, this dissertation ). Fires have

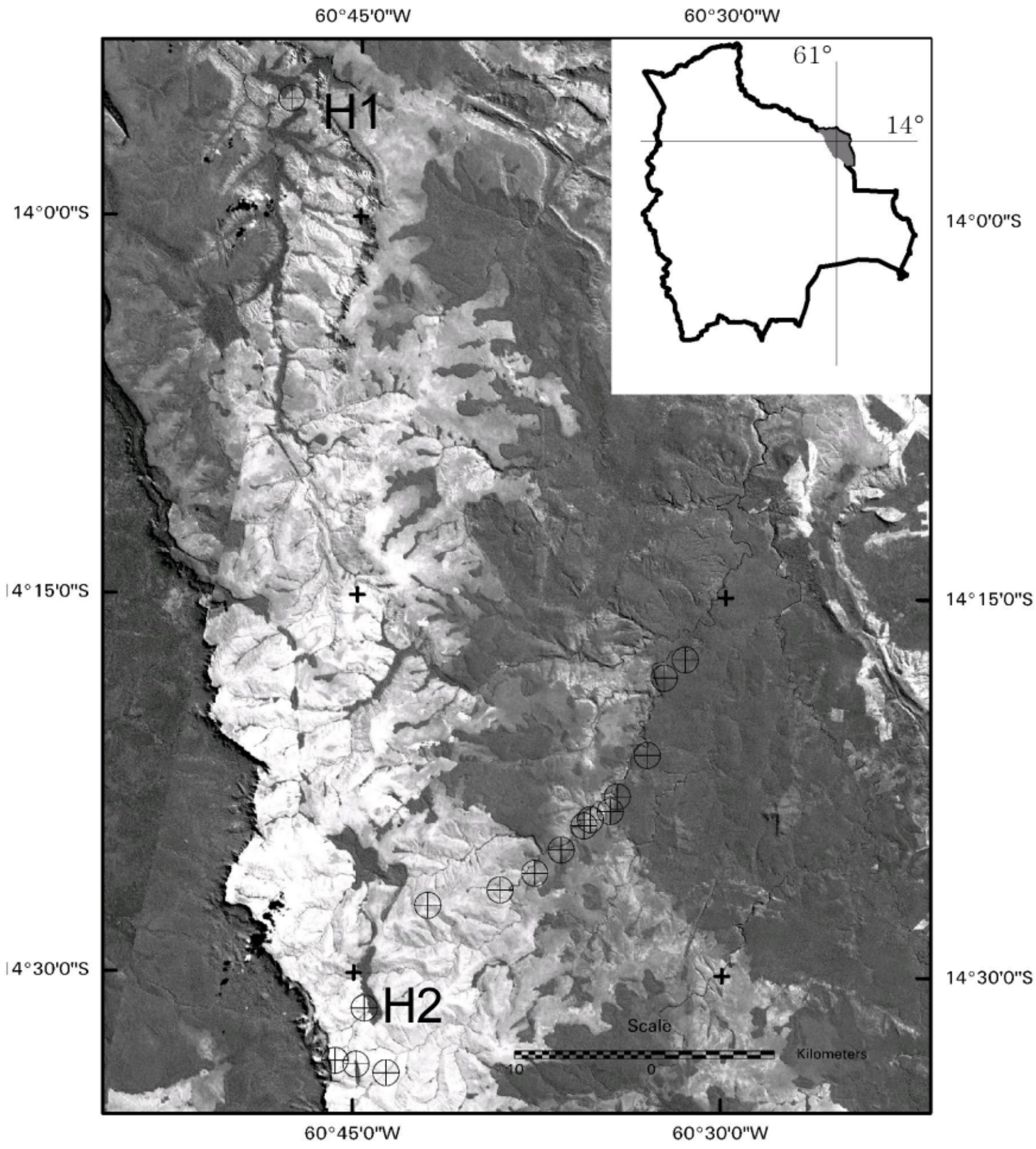

**Figure 14. LandSat TM image of Noel Kempff Mercado National Park. The park's location in Bolivia is shown in the inset figure. The Huanchaca I and Huanchaca II study sites are marked, and the position of the Trans-Huanchaca transect is also marked with crosshairs at the points where soil samples were collected. Lighter portions of the image indicate savanna, and increased amounts of woody vegetation are increased by increased darkness. Forest is dark grey in this image.**

occurred at the northern site in the past, as the trunks of savanna trees are charred, but no burns occurred at this site between 1996 and 1999. Two natural fires occurred at the southern site during this time.

### ***Climate***

The Noel Kempff region is characterized by a warm tropical climate with strongly seasonal precipitation. Long-term weather data do not exist for the park, so we infer meteorological conditions from stations located 160-200 km to the southwest and 150–200 km northwest of the park. Data from these stations show that mean annual temperature is 25-26º C with a mean annual minimum of 10º C, and frost is not known in the region (Roche and Rocha 1985). During the austral summer, the inter-tropical convergence zone (ITCZ) brings warm, moist Amazonian air masses to the region. Total mean annual precipitation is approximately 1500 mm, with almost all falling between October and June (Killeen et al. *In press*). The northern parts of the park receive two to several hundred mm more of precipitation per year than those to the south (Roche and Rocha 1985). During the austral winter, the ITCZ shifts to the north and dry weather patterns replace the moist air masses.

### ***Vegetation sampling***

All vegetation sampling was done in belt transect plots oriented perpendicular to the boundary between forest and savanna. Plots were long enough to span from visually homogeneous savanna to visually homogeneous forest. Depending on the study site, the plot length varied from 40 to 200 m (Table 14). Plot width varied; the first plot installed was 20 m wide, but later plots were narrower, ranging from 1 to 5 m in width. The narrower plot design allowed for multiple transects to be installed parallel to one another to sample the local variation in vegetation.

We sampled all species in each of the plots, recording the position, identity, height, and diameter at 1.4 m above the ground (dbh) of all freestanding woody plants ≥ 1.5 m tall. We did not include herbs or lianas in the inventories. We attached an aluminum tree tag with an identification number to each plant, using a loose loop of wire for plants < 5 cm dbh, and an aluminum nail for trees >5 cm dbh. When a new species was encountered, or when identification was in doubt, we made a botanical collection for later determination. Collections were identified by comparison to specimens at the herbarium of the Museo de Historia Natural Noel Kempff Mercado in Santa Cruz, Bolivia (SCZ), and at the New York Botanical Garden (NY). Specimens which could not be identified with this method were sent to plant family specialists for determination (Table 15). Voucher specimens from this study are deposited at SCZ.

**Table 14. Plot location, dimensions, and the chronology of sampling and burns. The calendar months of 1997, 1998, and 1999 each represent a column. An "I" in a column indicates that the plot was inventoried during that month. A "B" indicates that the plot burned during that month. B* is a plot that was experimentally burned in October of 1999. The other fires were naturally occuring.**

| | | | | | | 1997 | | | | | | | | | | | | 1998 | | | | | | | | | | | | 1999 | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Site | Plot | Latitude | Longitude | Dimensions (m) | Tran- sects | J | F | M | A | M | J | J | A | S | O | N | D | J | F | M | A | M | J | J | A | S | O | N | D | J | F | M | A | M | J | J | A | S | O | N | D |
| Huanchaca I | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| | a | 13:54.2 | 60:48.8 | 200 x 5 | 1 | I | | | | | | | | | | | | | | | | | | | | | | I | | | | | | | | | | | | I | |
| | b | 13:53.6 | 60:49.2 | 70 x 2 | 2 | I | | | | | | | | | | | | | | | | | | | | | | I | | | | | | | | | | | | I | |
| | b* | 13:53.6 | 60:49.2 | 70 x 2 | 3 | I | | | | | | | | | | | | | | | | | | | | | | I | | | | | | | | | | | B | I | |
| | c | 13:54:26 | 60:48:35 | 120 x 2 | 2 | | I | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | I | | | |
| | h | 13:55:14 | 60:49:03 | 100 x 1 | 1 | | | | | | | | | | | | | | | | | | | | | | | | I | | | | | | | | | | | I | |
| Huanchaca II | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| | d | 14:30:59 | 60:44:19 | 140 x 20 | 1 | | | | | | | | | B | | | | | I | | | | | | | | | | | | | | | | | | | | B | I | |
| | e | 14:31:68 | 60:44:21 | 50 x 2 | 8 | | | | | | | | | | | | | | I | | | | | | | | | | | | | | | I | | | | | B | I | |

**Table 15. Family specialists consulted for specimen identification. Institutional abbreviations are as in *Index Herbariorum*.**

| Family | Specialist | Institution |
|---|---|---|
| Annonaceae | P.J.M. Maas | U |
| Asteraceae | H. Robinson | US |
| Burseraceae | D. Daly | NY |
| Euphorbiaceae | G.L. Webster | DAV |
| Lamiaceae | Harley | K |
| Lauraceae | H. van der Werf | MO |
| Leguminosae | R. Barneby | NY |
| Malpighiaceae | W.R. Anderson | MICH |
| Melastomataceae | F. Almeda | CAS |
| Myrtaceae | B.K. Holst | SEL |
| Pteridophyta | A.R. Smith | UC |
| Rutaceae | J. Kallunki | NY |
| Rubiaceae | C.M. Taylor | MO |
| Sapotaceae | T.D. Pennington | K |

### *Soil analysis*

We collected soil samples from the top 10 cm of pits dug in the savanna, forest, and at the forest/savanna boundary at each plot. The samples were dried in the field and analyzed later at the Centro de Investigaciones para la Agricultura Tropical (CIAT) in Santa Cruz, Bolivia. Soil analysis methods are described in Cochrane and Barber (1993) but are summarized here. The pH and electro-conductivity of the soil were determined by water extraction at a soil-water ratio of 1:5 (Page et al. 1982, Van Reeuwijk 1987). Total nitrogen was determined by the Kjeldahl method (Varley 1966, Page et al. 1982, Van Reeuwijk

1987), and the organic matter content was measured using a modified Walkley-Black procedure (Metson 1956, Van Reeuwijk 1987). A modified version of the Olsen method was used to determine the soluble phosphorous content (Van Reeuwijk 1987). The exchangeable bases Ca, Mg, K, and Na were extracted with ammonium acetate at pH 7.0 and measured with atomic absorption (Begheyn 1981, 1982, Van Reeuwijk 1987). Exchangeable acidity and aluminum were determined by titration after extraction with potassium chloride (Mclean 1965). The hydrometer method was used for determining sand, silt, and clay percentages (Day 1965). Total exchangeable base content was calculated by summing the values for Ca, Mg, Na and K. Cation exchange capacity (CEC) was calculated by summing the values for total exchangeable bases and acidity.

## RESULTS

### ***Soils***

The soils in the forest, savanna, and at the boundary for all sites are acidic, sandy, and nutrient poor (Table 16). High acid saturation is common, as all samples except the boundary sample from Plot F and the savanna from Plot E had of ratio of Al to cation exchange capacity (CEC) $\geq 0.5$. A multivariate analysis of variance (Proc GLM, SAS v. 8.2) showed no significant difference among plots for the group of soil characteristics in Table 16 (Pillai’s Trace F=1.28, DF=24, p=0.35), though the individual ANOVA for pH indicated possible significant differences between habitats (F = 4.78, DF = 2, p = 0.0248).

### *Structure*

The forest/savanna boundary at most of our plots is abrupt, with savanna grasses giving way to closed canopy forest over a span as short as 1 m. Woody stems are larger in size and more dense in the forest, contributing to much greater basal area in the forest portion of each plot (Figures 15, 16). The transition is slightly broader at Plots C and H, with more basal area in the savanna than at the other plots. Basal area values in Figures 15 and 16 are calculated with extrapolations from 10 m long plot segments to the 1 ha scale for comparison. These measurements are subject to large amounts of fluctuation because the sampled areas are small, but they provide a rough comparison of the amount of woody vegetation in the forest and savanna at each plot.

**Table 16. The chemical and textural characteristics of the top 10 cm of soil in the study plots. Soils were sampled between September and December of 1999.**

| Plot | Habitat | pH | Ca | Mg | K | Na | CEC | Total N | P | Al/CEC | O.M. (%) | Sand | Silt | Clay |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| B | Savanna | 4.50 | 0.20 | 0.10 | 0.09 | 0.03 | 2.52 | 0.07 | 2.00 | 0.52 | 2 | 80 | 9 | 11 |
|  | Edge | 4.20 | 0.20 | 0.10 | 0.12 | 0.03 | 3.35 | 0.09 | 3.00 | 0.60 | 3 | 81 | 9 | 10 |
|  | Forest | 3.90 | 0.20 | 0.10 | 0.10 | 0.03 | 3.83 | 0.12 | 2.00 | 0.63 | 3 | 79 | 9 | 12 |
| C | Savanna | 4.30 | 0.20 | 0.10 | 0.09 | 0.03 | 1.72 | 0.08 | 2.00 | 0.52 | 2 | 81 | 7 | 12 |
|  | Edge | 4.30 | 0.20 | 0.10 | 0.14 | 0.03 | 3.17 | 0.09 | 1.00 | 0.50 | 2 | 84 | 3 | 13 |
|  | Forest | 4.10 | 0.10 | 0.10 | 0.15 | 0.04 | 2.49 | 0.1 | 3.00 | 0.68 | 2 | 77 | 11 | 12 |

| | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| D | Savanna | 4.40 | 0.20 | 0.10 | 0.23 | 0.05 | 2.68 | 0.12 | 6.00 | 0.52 | 3 | 78 | 11 | 11 |
| | Edge | 4.20 | 0.10 | 0.10 | 0.20 | 0.05 | 3.25 | 0.11 | 4.00 | 0.58 | 3 | 77 | 12 | 11 |
| | Forest | 4.30 | 0.20 | 0.20 | 0.21 | 0.07 | 4.08 | 0.21 | 4.00 | 0.56 | 4 | 65 | 14 | 21 |
| E | Savanna | 4.00 | 0.20 | 0.10 | 0.13 | 0.04 | 2.87 | 0.07 | 2.00 | 0.49 | 2 | 79 | 10 | 11 |
| | Edge | 3.80 | 0.20 | 0.10 | 0.22 | 0.05 | 3.97 | 0.19 | 6.00 | 0.73 | 4 | 75 | 11 | 14 |
| | Forest | 3.60 | 0.20 | 0.10 | 0.11 | 0.04 | 4.25 | 0.18 | 5.00 | 0.61 | 3 | 76 | 11 | 13 |
| F | Savanna | 4.60 | 0.20 | 0.10 | 0.09 | 0.03 | 1.72 | 0.05 | 2.00 | 0.58 | 2 | 84 | 4 | 12 |
| | Edge | 4.00 | 0.20 | 0.10 | 0.15 | 0.03 | 2.38 | 0.14 | 5.00 | 0.42 | 3 | 82 | 7 | 11 |
| | Forest | 3.40 | 0.20 | 0.10 | 0.10 | 0.03 | 4.53 | 0.2 | 8.00 | 0.64 | 5 | 82 | 7 | 11 |
| H | Savanna | 4.30 | 0.20 | 0.10 | 0.20 | 0.05 | 3.25 | 0.09 | 3.00 | 0.55 | 3 | 77 | 7 | 16 |
| | Edge | 4.10 | 0.20 | 0.10 | 0.13 | 0.03 | 3.06 | 0.09 | 1.00 | 0.56 | 3 | 78 | 8 | 14 |
| | Forest | 4.10 | 0.20 | 0.10 | 0.12 | 0.03 | 2.25 | 0.09 | 1.00 | 0.53 | 2 | 79 | 4 | 17 |

### ***Species Diversity***

We recorded a total of 271 species of freestanding woody plants in almost 0.60 ha of total plot area. To standardize comparisons, we examined the species composition of the area 20 m on either side of the forest edge at each of the plots. A total of 189 species was found in this area (Table 17). All individuals growing within 5 m of the forest/savanna edge were grouped, as were plants growing in the forest and savanna areas 5 to 20 m from the edge. The edge group represents less area than the forest and savanna groups in this analysis (10 m length compared to 15 m), yet it contains similar or greater numbers of species than the savanna in all plots. The forest contains more species than the savanna in all plots except H (Table 17). The compositional similarity between habitats was moderate, with Sorensen's presence/absence similarity index ranging from 0.27 to 0.63 for comparisons between the edge and either the forest or savanna group. Similarity between the forest and savanna is generally lower, but there is still moderate amounts of species overlap between these vegetation types (Table 17).

*Myrcia paivae* (Myrtaceae) was the most common species in the edge and forest habitats, representing 10.9 % of all stems in the edge, and 21.3 % of all stems in the forest (Table 18). *Chaetocarpus echinocarpus* (Euphorbiaceae) was the most common species in the savanna, representing 12. 3 % of all stems. Three species, *M. paivae*, *Sacoglottis mattogrossensis* (Humiriaceae) and an unidentified species of *Miconia* (Melastomataceae) were among the top fifteen species in each of the habitats.

### ***Vegetation Dynamics***

We found large net increases in the number of stems in the savanna and edge portions of 3 of the 4 plots which did not burn (Figure 17). In one 10 m segment of plot B, there was an increase of 300%, but the original number of stems in this plot segment was just 2. More meaningful increases were found in Plot A, where there was an increase of 50 % or more in the number of stems in much of the savanna portion of the plot. There was not a comparable increase of stems in the forest.

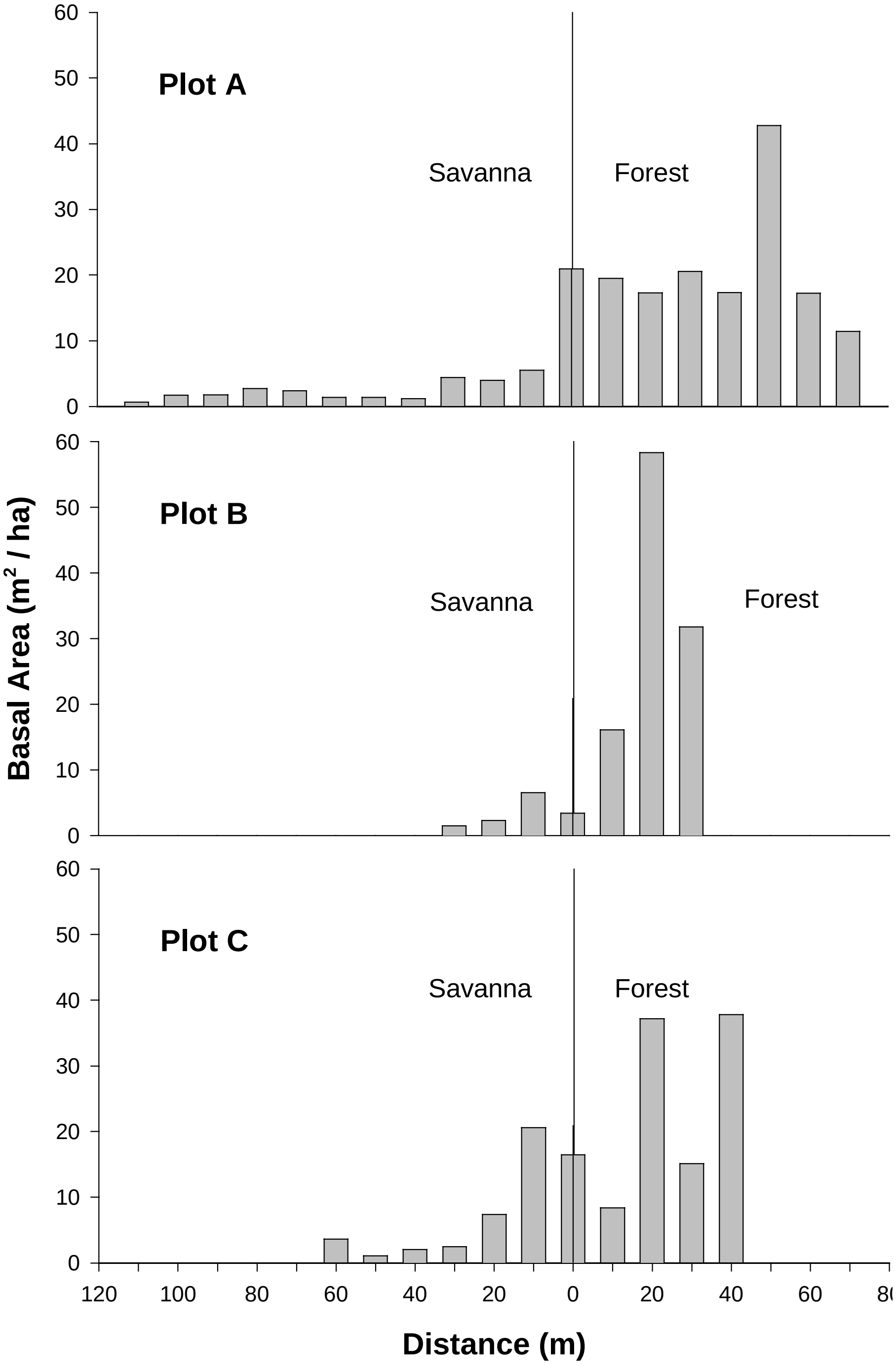

**Figure 15. Vegetation structure for Plots A, B, and C at the first inventory. The basal areas of all stems are summed for each 10 m long section of the sampling plots, and distances are reported relative the position of the forest edge. Basal area values have been extrapolated to per ha values for ease of comparison.**

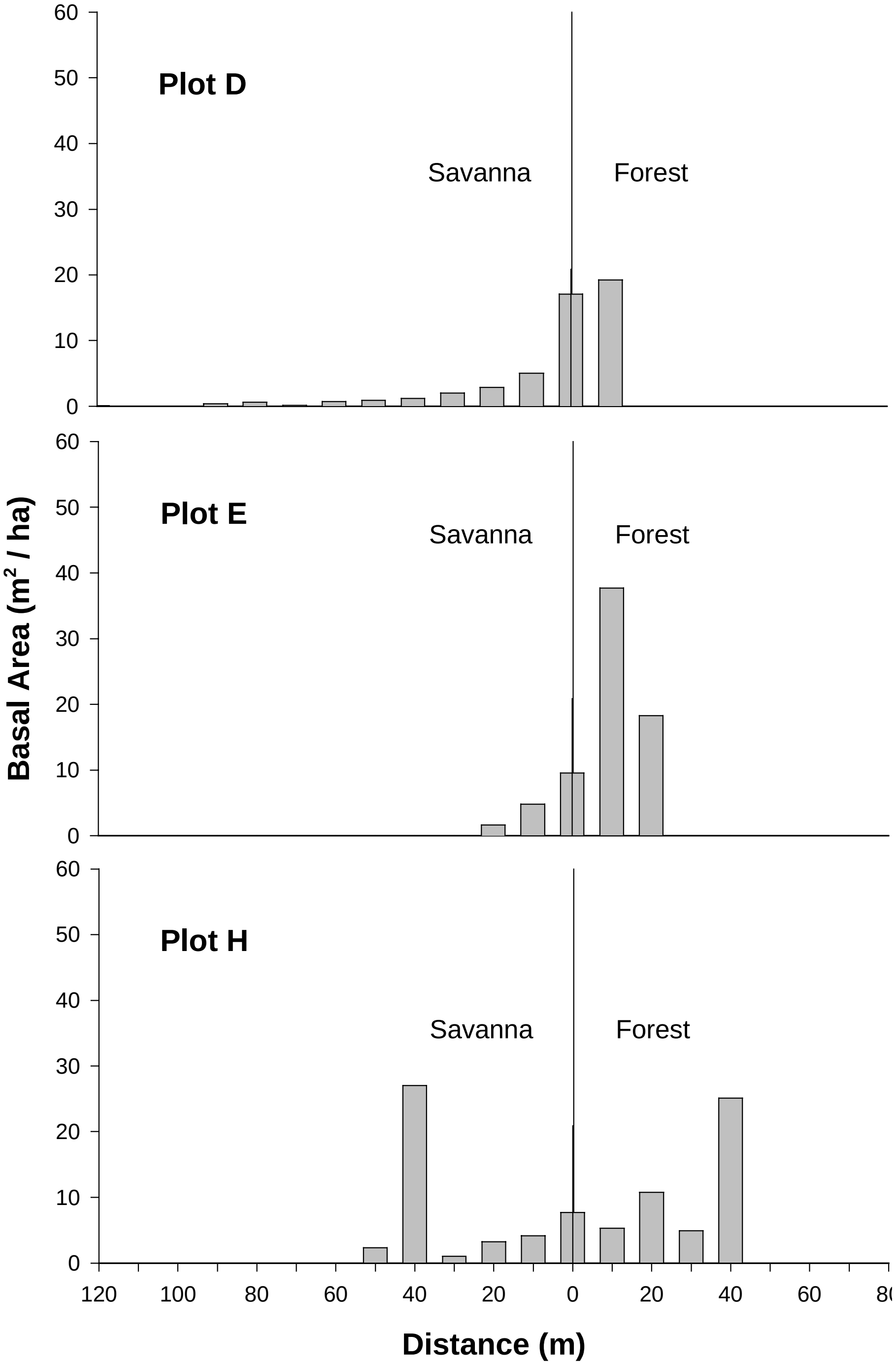

**Figure 16. Vegetation structure for Plots D, E, and H. Basal area is extrapolated to per ha values and distances are 10 m distance classes as in Figure 15.**

**Table 17. The species richness and compositional similarity of the forest and savanna at each plot during the first inventory. To allow comparison among all plots, these data only consider a portion of each plot: plants growing within 5 m (in either direction) of the forest edge are grouped in the "Edge" heading. The "Forest" and "Savanna" groups include all plants 5 m to 20 m from the edge in forest and savanna, respectively. The "Not Edge" is a combination of the forest and savanna groups. "Total S" is the total richness within 20 m of the edge. Sorensen's presence/absence similarity index is calculated for each pair of habitat types.**

| | | | Species | | | | | Sorensen's Index | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Plot Group | Area (ha) | Stems | Edge | Forest | Savanna | Not Edge | Total S | Edge/ Forest | Edge/ Savanna | Edge/ Not Edge | Forest/ Savanna |
| a | 0.02 | 209 | 16 | 29 | 24 | 41 | 48 | 0.31 | 0.40 | 0.35 | 0.42 |
| b | 0.04 | 349 | 30 | 51 | 31 | 69 | 78 | 0.42 | 0.43 | 0.46 | 0.29 |
| c | 0.016 | 246 | 21 | 37 | 27 | 59 | 66 | 0.31 | 0.46 | 0.43 | 0.16 |
| h | 0.004 | 71 | 9 | 6 | 12 | 16 | 23 | 0.27 | 0.29 | 0.32 | 0.22 |
| HI site | 0.08 | 875 | 50 | 76 | 55 | 102 | 109 | 0.51 | 0.63 | 0.59 | 0.43 |
| d | 0.08 | 492 | 42 | 45 | 20 | 60 | 77 | 0.46 | 0.42 | 0.55 | 0.15 |
| e | 0.064 | 684 | 52 | 60 | 40 | 88 | 104 | 0.46 | 0.52 | 0.56 | 0.24 |
| HII site | 0.14 | 1176 | 75 | 84 | 52 | 119 | 141 | 0.50 | 0.49 | 0.58 | 0.25 |
| All plots | 0.22 | 2051 | 103 | 123 | 88 | 168 | 189 | 0.57 | 0.58 | 0.63 | 0.41 |

**Table 18. The total number of new stems for some of the most common species in each habitat. For each plot, the top species is listed as ranked by the percentage of stems in all plots represented by the species.**

| Edge (945 total stems) | % | Forest (2523 total stems) | % | Savanna (2253 total stems) | % |
|---|---|---|---|---|---|
| *Myrcia paivae* | 10.9 | *Myrcia paivae* | 21.3 | *Chaetocarpus echinocarpus* | 12.3 |
| *Mabea angustifolia* | 7.6 | *Siparuna guianensis* | 9.2 | *Sacoglottis mattogrossensis* | 6.4 |
| *Chaetocarpus echinocarpus* | 5.9 | *Miconia dispar* | 3.0 | *Matayba guianensis* | 4.7 |
| *Miconia sp.* | 5.7 | *Family Indet* | 2.4 | *Chromolaena chaseae* | 4.4 |
| *Sacoglottis mattogrossensis* | 5.5 | *Nectandra cuspidata* | 2.3 | *Simarouba amara* | 4.2 |
| *Miconia tiliaefolia* | 4.6 | *Miconia sp* | 2.3 | *Roupala montana* | 4.2 |
| *Virola sebifera.* | 4.0 | *Protium spruceanum* | 2.2 | *Miconia sp.* | 3.9 |
| *Siparuna guianensis* | 3.6 | *Maytenus macrocarpa* | 2.1 | *Aiouea trinervis* | 3.4 |
| *Matayba guianensis* | 3.5 | *Mabea angustifolia* | 1.9 | *Myrcia paivae* | 3.2 |
| *Myrcia magnoliifolia* | 3.0 | *Guatteria sp.* | 1.8 | *Qualea multiflora* | 2.8 |
| *Casearia arborea* | 2.9 | *Sacoglottis mattogrossensis* | 1.7 | *Protium heptaphyllum* | 2.5 |
| *Guatteria sp.* | 2.5 | *Lacistema aggregatum* | 1.7 | *Miconia albicans* | 2.4 |
| *Nectandra cuspidata* | 2.5 | *Ecclinusa ramiflora.* | 1.6 | *Miconia puberula* | 2.4 |
| *Tibouchina stenocarpa* | 2.5 | *Protium pilosissimum.* | 1.5 | *Myrcia magnoliifolia* | 2.4 |
| *Chrysobalanaceae indet.* | 2.0 | *Hirtella gracilipes* | 1.4 | *Protium spruceanum* | 2.0 |

*Myrcia paivae* was the most common species among the ingrowth found in the forest (Table 19). It was also the most common ingrowth species at the edge in Plot C, and was tied for most common at the edge in Plot E. In the savanna portion of the plots, the most common ingrowth species differed at each plot, with *Simarouba amara* (Simaroubaceae), and unidentified species of *Chamaecrista* (Leguminosae), *Guatteria* (Annonaceae), and *Miconia* (Melastomataceae) each being most common in one of the plots.

**Table 19. The species that represent the greatest percentage of ingrowth in each study plot. The total number of new ingrowth is shown in parentheses below the plot letter.**

| | **Savanna** | | | | **Edge** | | | | **Forest** | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Plot** | **A** | **B** | **C** | **E** | **A** | **B** | **C** | **E** | **A** | **B** | **C** | **E** |
| (n) | (166) | (65) | (73) | (46) | (18) | (38) | (23) | (30) | (77) | (86) | (56) | (42) |
| **Species** | | | | | | | | | | | | |
| Simarouba amara | 28.9 | | | | | | | | | | | |
| Chamaecrista sect. Absus indet. | | 20.0 | | | | 15.8 | | | | | | |
| Guatteria sp. | | | 12.3 | | | | | | | | | |
| Miconia sp. | | | | 13.0 | | | | | | | | |
| Myrcia magnoliifolia | | | | | 16.7 | | | | | | | |
| Miconia tiliaefolia | | | | | | | | 13.3 | | | | |
| Nectandra cuspidata | | | | | | | | 13.3 | | | | |
| Myrcia paivae | | | | | | | 17.4 | 13.3 | 22.1 | 19.8 | 14.3 | 16.7 |

Fire caused large net decreases in the number of stems in the areas that burned (Figure 18). In each case, the fire was naturally extinguished when it reached the forest edge. The burns caused a loss of stems as high as 100 % in some segments of the plots. Plots B and E had each showed an increase in stem counts in the savanna before the burns occurred.

Overall, more plants in the burned areas survived the burns than not (survivors = 635, dead/top dead = 380). The fire was lethal to the above-ground portion of many stems, but most of the plants initially reported as dead resprouted within 2 months of the fire. Two months after the fire, only 71 of the 380 burned stems had failed to resprout. The plants that did not suffer the loss of stem due to the fire were larger than those whose stems burned. The mean height and diameter of unburned stems was 2.88 m and 3.1 cm, respectively, while the height and diameter of stems that were burned was 1.95 m and 1.0 cm.

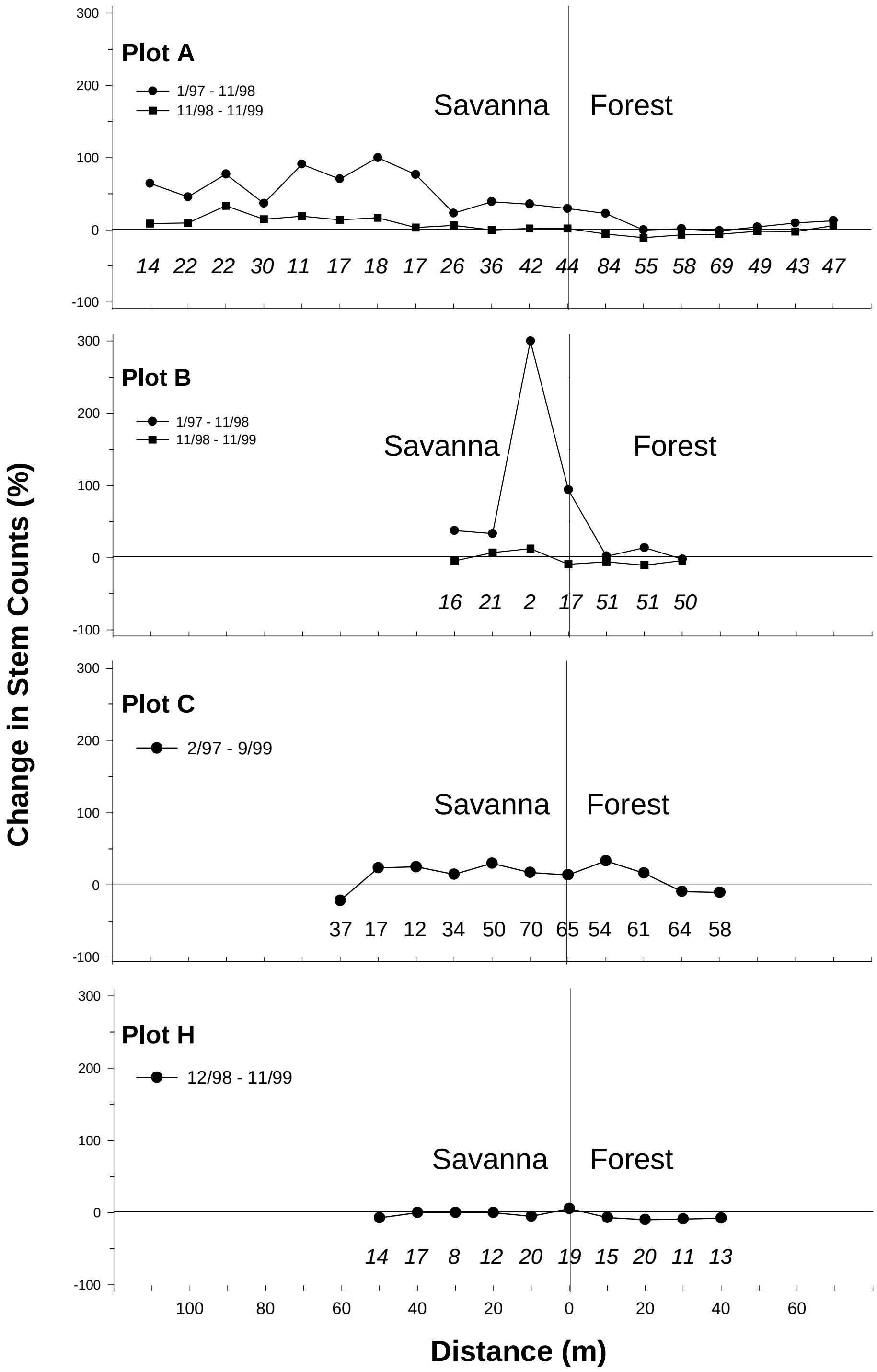

**Figure 17. The percent change in stem counts for each 10 m distance class in the unburned plots. Plots A and B were sampled a total of 3 times, and Plots C and H were sampled twice. Each line represents the change between inventories. The number of stems in each distance class at the first inventory is marked below the data points.**

# DISCUSSION

The ecotone between forest and savanna on the Huanchaca plateau is abrupt, but edaphic conditions do not appear to be responsible for determining the position of the forest/savanna boundary. Soil chemical and physical characteristics are very similar for samples collected in the forest, in the savanna, and at the edge. Forest soils may be slightly more acidic than those in the other locations, but this difference is of marginal statistical and biological significance. Further evidence that edaphic conditions do not limit forest/savanna boundary conversion comes from carbon isotope analysis of soils (Panfil et al. Chapter 4, this dissertation). A recalcitrant, slow-cycling pool of carbon in savanna soils at these sites contains a high proportion of carbon derived from $C_3$ plants, indicating that these savannas were occupied by forest or by densely wooded savanna in the past.

Despite little change in soil conditions, the structure of modern vegetation changes abruptly at the forest/savanna boundary. Basal area integrates stem diameter and density, and we found a sharp drop-off in basal area over distances of less than 15 m for most plots. Only in plot H is there an indistinct threshold between the forest and savanna in terms of basal area, and this can be explained by the small area sampled with this plot. This measure is subject to large amounts of error for small plot sizes.

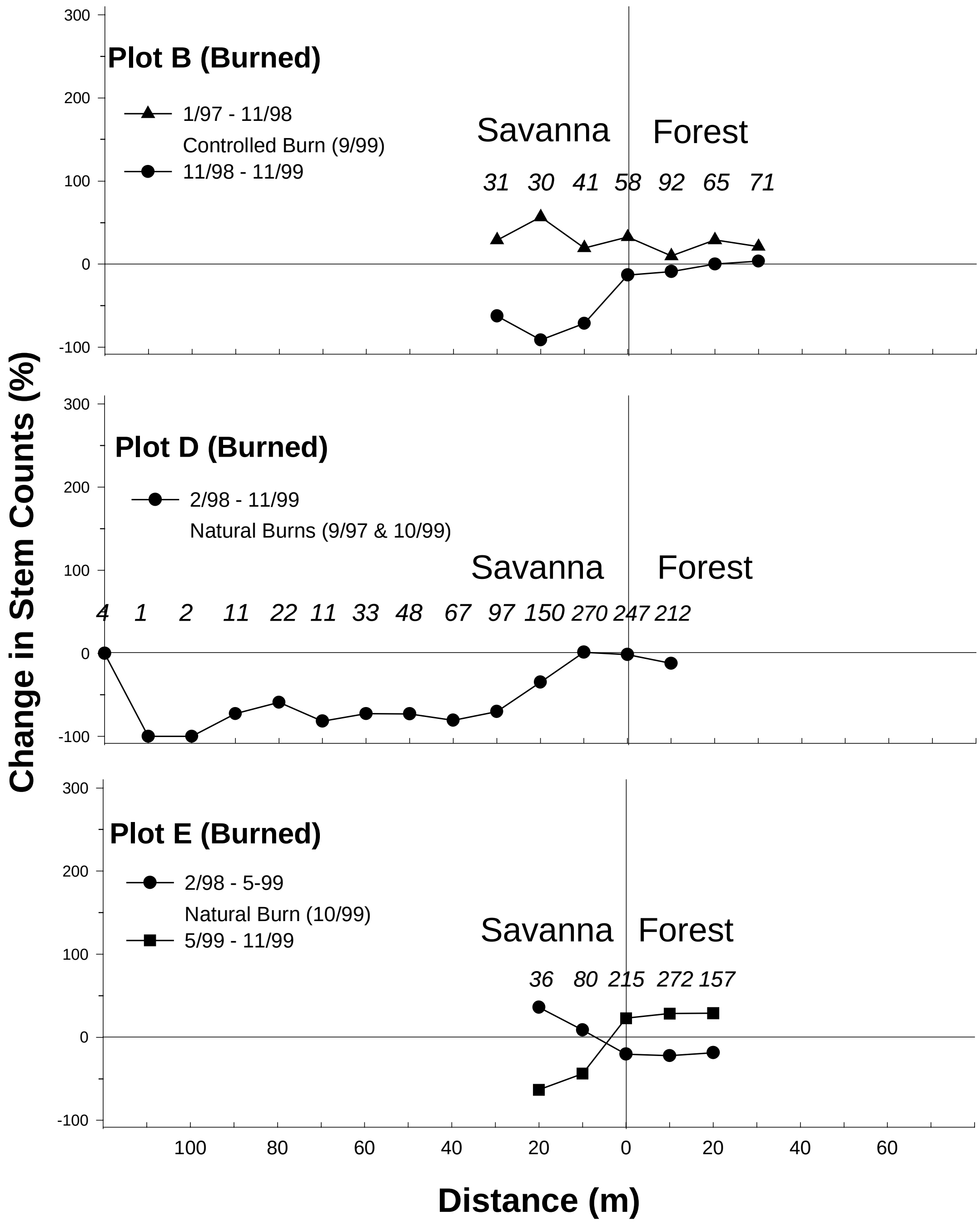

**Figure 18. Percent change in stem counts in plots that were burned. Plots B and E were sampled twice. The first two inventories spanned a period with no fire. The second sample interval spanned a burn.**

We did not find that the species composition of the ecotone changes as sharply as structure. We analyzed small-scale species turnover by comparing the first 15 m of forest and savanna vegetation with each other and with the 10 m that spans the boundary. At this scale, there was moderate compositional similarity between each of the vegetation types. On average, the savanna and forest portions of any plot shared roughly one quarter of their species. The similarity of the edge with forest and savanna was generally higher. We compared the composition of the edge to the pooled group of forest and savanna species to test the idea that the edge supports a distinct assemblage of species, and we found high levels of similarity, indicating that there is not a distinct edge flora at this scale.

Though we found relatively high overlap between forest and savanna in the areas immediately adjacent to the boundary, this is not true for larger spatial scales. Inventories of forest and savanna conducted in plots that were selected for internal homogeneity show little overlap between forest and savanna species composition ((Panfil et al. Chapters 2 and 3). These studies invite speculation about the relative richness of savanna and forest, but the different methodologies used to sample each habitat preclude direct comparison. In our ecotone plots, we found evidence that the community of freestanding woody plants greater than 1.5 tall is richer in the forest than in the savanna.

Both compositional and structural differences exist between the forest and savanna, yet edaphic conditions are not substantially different in these habitats. What factors allow these two vegetation types to coexist?

Our results show that ingrowth in the savanna can be very rapid in the absence of fire, with some portions of our plots doubling their stem densities in less than 2 years. The species that represent this new growth varied by plot, but some are forest species, suggesting that their establishment represents colonization of the savanna by forest. *Simarouba amara* (Simaroubaceae) was responsible for much of the ingrowth in plot A. This species can grow to be a large forest tree and is found throughout the Amazon (Killeen et al. 1993). An unidentified species of *Guatteria* (Annonaceae) was another important source of ingrowth, and we found large individuals of this species more than 75 m into the forest. Not all of the ingrowth was by forest species, however. Unidentified species of *Chamaecrista* (Leguminosae) and *Miconia* (Melastomataceae) were the main source of ingrowth in the savanna portion of two of the plots, and we found other individuals of these species only in the savanna or near the forest edge. In contrast to the savannas, we found that new stems in the forest of all plots were frequently of the species *Myrcia paivae* (Myrtaceae). This species represents more than 21 % of all stems in the forest portion of our plots, so its high representation in the new growth is not surprising.

The very high levels of ingrowth in the savanna would lead to rapid changes in the structure of the savanna if the mortality of the new stems was low. We found that fire greatly reduced stem densities in the savanna portion of each of the burned plots. Plots B and E had experienced rapid ingrowth in the savanna before fires removed all new growth and reduced the stem densities to less than what they had been at the start of the study. The majority of the plants were able to resprout from ground level, but above-ground mortality was high, substantially altering the structure of the savanna.

We found evidence of greater fire resistance by larger individuals, and there may be a size threshold which permits individuals to survive burns with no loss of stems. If this is true, it suggests that fire frequency is an important factor that regulates forest/savanna boundary dynamics. Episodes with low fire frequency would favor forest expansion, while episodes with frequent fires would favor savanna. A number of studies document this phenomenon in cerrado vegetation in Brazil (Mistry 1998). A large part of the Brazilian cerrado has been cleared for agriculture and much of what remains experiences a fire regime that is determined by human activities and not by climatic conditions (Ratter et al. 1997). Remote areas, like the Huanchaca Plateau, continue to experience a fire regime that is driven by lightning. Our results suggests that changes in the frequency of natural burns may be the proximate mechanism that drives conversion between forest and savanna vegetation.

# CHAPTER 6

# CONCLUSION

Both the forest and the savanna formations of Noel Kempff Mercado National Park in eastern Bolivia have great regional diversity despite moderate levels of local species richness. We recorded a total of 896 tree species in 29 one ha inventory plots in the forest formations of the region, and 662 vascular plant species in 9 line-intercept study plots in the savanna formations. These high species counts are the result of low levels of similarity in the species composition of individual plots. These results indicate that the landscape of Noel Kempff Park consists of highly heterogeneous habitats.

Carbon isotope analysis of soil organic matter corroborates an independent analysis of pollen collected from lake sediments in the region and indicates that the distribution of habitats in the landscape is dynamic. The isotope analysis shows that the forest formations have been stable, and continuously forested more than 2300 years. In contrast, the savanna formations have experienced vegetation change, and had a greater concentration of woody plants in the past. From the present study, it is not possible to determine if these savannas previously supported forest or simply had a higher density of woody vegetation than at present.

Inventories of the woody vegetation that presently exists along the ecotone between forest and savanna show that fire frequency may regulate the colonization of the forest by the savanna. In the absence of fire, woody plants rapidly establish in the savanna. The composition of this ingrowth includes species that are typical of both forest and savanna vegetation. Rates of ingrowth can by 50% or more per year. However, fires occur naturally in this region at the end of the dry season, and these burns can reduce the number of stems dramatically. These results suggest that in times of infrequent fires, forest trees may be able to establish in the savanna and reach sufficient size and density to reduce the flammability of the vegetation. In contrast, frequent fires limit the ability of trees to establish in the savanna, and help to maintain savanna vegetation.

The great species richness of this area is due to high habitat heterogeneity, and the conservation of species therefore depends on the maintenance of a diverse assemblage of habitats. These habitats are now known to be dynamic, so long-term conservation strategies must consider the processes of habitat conversion if they are to be successful.

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