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The Chiquitano Dry Forest, the Transition between Humid and Dry Forest in Eastern Lowland Bolivia

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ABSTRACT

The floristic similarities of 118 permanent plots established in Eastern Bolivia were compared using Detrended Correspondence Analysis (DCA) and Canonical Correspondence Analysis (CCA). The Chiquitano dry forest is characterized by a north to south floristic gradient that intergrades with the Amazon flora to the North and with the Gran Chaco flora to the south. However, the forest situated between these two biomes is composed of taxa which are neither Chacoan nor Amazonian, but are a local variant of the seasonal dry tropical forest that is found in other regions of the Neotropics. Species composition varied along both a latitudinal and longitudinal gradient reflecting the floristic differences in the humid forests of southwest Amazon on the Andean piedmont and those of south central Amazon on the Brazilian shield. The Chiquitano dry forest tree flora, as documented by these plot studies, was not particularly heterogeneous; although forests over calcareous rocks have a different floristic composition when compared with those found on soils derived from granitic rocks. The origin and of the floristic gradient is discussed in light of recent discoveries in paleoecology and future climate change.

INTRODUCTION

The forests of eastern lowland Bolivia are situated across a climatic transition zone between the humid evergreen forests of the Amazon and the deciduous thorn-scrub vegetation of the Gran Chaco. This transition has traditionally been divided into different forest types, or more recently as ecoregions, based on easily observable differences in forest structure, degree of deciduousness and floristic composition (Beck et al 1993). The most recent classifications (Ibisch and Merida

2003, Navarro and Maldonado 2003) recognize several different Amazonian forests types (inundated, pre-Andean, Beni–Santa Cruz), The Chiquitano forest, the Gran Chaco dry forest, and Serrano-Chaco forest. The region also contains numerous savanna habitats which are essentially western outliers of the Cerrado biome of central Brazil (Killeen and Nee, 1991; Mostacedo and Killeen, 1995; Killeen 1997; Ibisch et al. 2002) or are similar to the inundated savannas of the Gran Pantanal which borders this region to the south east.

The climatic transition is characterized by a north – south precipitation gradient with mean annual precipitation falling from 1500 to 500 mm (Figure 1). However, there is an anomalous non-latitudinal precipitation gradient associated with a topographical feature known as the Elbow of the Andes, where prevailing winds associated with the South American low level jet create a super humid precipitation zone where mean annual precipitation exceeds 6000 mm per year (Marengo et al 2003). The entire region is characterized by seasonality that also varies with the number of months with mean precipitation less than 100 mm increasing from three in the north to more than seven months at the Paraguayan border. No part of the Bolivian lowlands experience frost, although occasional southern cold fronts can lower temperatures to below 10°C during the austral winter.

Lowland Bolivia is also characterized by prominent differences in geomorphology and geological history: it is bordered on the West by the relatively young landscapes of the Andean piedmont and to the East by the ancient rocks of the Brazilian Shield. Between these two regions is the Chaco – Beni Plain, a flat plain composed of Quaternary sediments that has been deposited by the numerous rivers originating in the Andes. In the south, where the Amazon is separated from the watershed of the River Plate these alluvial sediments give way to older sedimentary rocks dating from the Cretaceous (Suarez-Soruco, 2000). Soils in the high precipitation zones are typically acidic, while to the South they tend to the alkaline (Navarro et al. 1998). The piedmont and adjacent plains are characterized by deep soils, which tend to be poorly drained and seasonally waterlogged in the north and well drained and sandy to the south. The landscape of the Brazilian

Shield is characterized by rolling hills with low superficial soil, most of which are derived from gneiss or other granitic rocks, although scattered throughout the area are circumscribed areas with metamorphic rock and on the southern edge of the Shield several small mountain ranges are composed of calcareous rocks (Litherland, 1984). The variety of landscapes and soils provide a considerable degree of edaphic variability which also influences the distribution of plant species. Ratter et al. (1978) documented that many species characteristic of deciduous dry forest are restricted to mesotrophic soils, while Killeen et al (2001) demonstrated that edaphic variability was one of the principal drivers of beta diversity in northeast Bolivia at the southern edge of the Amazon forest.

Recent paleoecological research has documented recent changes in the floristic composition of the forests of the region, with evidence of large-scale latitudinal shifts in the vegetation (Mayle, et al 2000; Burbridge et al. 2004). Humid species characteristic of the Amazon have expanded their ranges to the south, while many species that are today dominant in certain areas of eastern lowland Bolivia were absent from those very same localities just a few thousand years ago (Mayle et al. 2004).

The Chiquitano dry forest is a term used to describe a complex of forest communities that occur across this climatic transition (Killeen et al. 1998), representing what is probably the largest extant patch of what is now broadly recognized as the Neotropical seasonal dry tropical forest complex (Prado and Gibbs 1993; Prado, 2000; Pennington et al. 2004). The Chiquitano dry forest ranges from completely deciduous in the South to semideciduous in the North, while the degree of deciduousness in the intervening areas is highly variable depending on the amount of precipitation that falls within any given year at any given place. At the midpoint of what is considered to be its latitudinal extent, it is as a closed-canopy forest about 15 m tall with the largest tees reaching up to 35 meters in height and 120 cm in diameter (Killeen et al 1998). Many – if not all - species are fire adapted with thick corky bark; most species are relatively slow growing with very high wood

densities; the age of the largest trees (*Schinopsis brasilensis* Engl) are estimated to be more than 500 years old (Dauber et al 2001).

The derivation of the name comes from the geographic region of Bolivia that is more or less concomitant with this forest type. Known as Chuiquitania, it is also the land of the Chiquitano ethnic group which incorporates a number of related indigenous peoples of the Guaraní linguistic heritage (Gott 1993). The potential economic value of this forest is large because of the very high density wood that characterizes many of the most common species, particularly *Tabebuia impetiginosa* (C. Martius ex DC. in A. DC.) Standley, *Machaerium scleroxylon* Tul., *Astronium urundeuva* (Alemão) Engl. and *Schinopsis brasilensis* Engl. High transport costs and subsequent isolation from international markets has largely been responsible for conserving this forest ecosystem until the present decade. Unfortunately, areas adjacent to Chiquitania in Bolivia have experienced considerably greater rates of deforestation (Steininger, et al. 2001a, 2001b, Pacheco and Mertens 2004) and the future conservation of the Chiquitano dry forest is very much in doubt. The biggest threat comes from cattle ranching activities and mechanized agriculture, which are both technically feasible and economically attractive investments over the short-term.

In this article, we compare the composition of trees in 118 permanent 1-ha forest plots established at different localities in the eastern lowland and evaluate differences in the context of a high resolution vegetation map that documents the distribution of humid and deciduous forest, as well Chacoan scrubland, Cerrado savanna and Pantanal wetlands (Figure 2) Our goal is to document the floristic differences among the various forest types, in order to better characterize the Chiquitano dry forest and its biodiversity. In addition, we demonstrate that the geographic distribution varies among species and that species distributions are linked to both climate and edaphic factors. Information on the distribution of individual species is essential for understanding which species will be impacted by climate change and which species might be able to adapt to changing climatic conditions. Finally, we show how the consolidation of databases

from different projects and institutions can be used to enhance floristic analysis and conservation planning.

METHODS

The permanent plots incorporated in the study were established over 15 years by different institutions and individuals (Table 1 and Figure 1). Most of the plots are located within what is considered to be the Chiquitano dry forest, a seasonal forest that represents the transition between the humid Amazon and semi-arid Gran Chaco. However, the study also includes a few plots from adjacent regions including both lowland and montane localities, in order to document the transitional nature of this vegetation type and the geographic distribution of the species which characterize it.

The plots vary in design, typically being square (100 x 100m) or rectangular (20 x 500 m); all used the same minimum diameter of 10 cm at breast height (dbh) following other protocols described by Adler and Synott (1992). All sample plots adopted standard botanical practices to ensure the proper taxonomic identification of each species and the collection of a voucher specimens that was later identified by an experienced botanist with access to a modern herbarium.

The standardization of scientific names among plots and study sites was accomplished using the *TaxonScrubber* software application, which provides a semi-automated procedure for comparing and standardizing the orthographic variability that is common when combining data from different sources (Boyle 2004). The application splits concatenated information into separate fields in order to facilitate comparisons among databases with different field structures and provides a standard format for the analysis. It then checks the spelling of each name as well as the scientific authority with a standard list of validly published names and authorities based on the International Plant Names Index http://www.ipni.org/index.html) and the TROPICOS system at the Missouri Botanical Garden (http://mobot.mobot.org/W3T/Search/vast.html).

TaxonScrubber flags all names that match the standard list and provides pull-down menus to review all unmatched names; orthographic variants were corrected manually and all unmatched names are treated as unidentified morphospecies.

The similarity among plots was evaluated using both a Detrended Correspondence Analysis (DCA) and a Canonical Correspondence Analysis (CCA). A DCA partitions the variation among ordinate axes based entirely on florisitic similarity, while a CCA provides a gradient analysis where the ordinate axes are weighted by taxa whose distribution are correlated with a set of defined environmental parameter (Hill and Gauch, 1980; ter Braak, 1990; McCunem and Mefford, 1999). The CCA analysis was applied separately using four different sets of environmental parameters: climate, geographic location, major geological unit, and rock type. The climatic data was obtained from the interpolated values provided by the *WorldClim* data set (Hijmans et al 2004) and included mean annual precipitation (MAP), the mean precipitation of the driest quarter (MPDQ), the mean annual temperature (MAT, the temperature of the coldest quarter (MTCQ) and a measure of seasonal precipitation (coefficient of variation of precipitation - CVP). The major geological regions were defined as the Andean piedmont, Brazilian (Precambrian) shield and the Beni – Chaco alluvial plain. The geographic location included latitude and longitude as obtained by GPS instruments, while the rock types were obtained from the geological maps of Bolivia (Litherland, 1984; Suarez-Soruco, 2000)

The ordination of floristic similarity at the family and genus level used a matrix where the number of species for taxa within each plot was the data, while the analyses conducted at the species level were based on abundance values for individual species. In the latter case, all unidentified species were excluded from the analysis with the exception of generic determinations unique to a single plot or group of plots which were then treated as a species. The number of undetermined or partially determined species varied among plots, being greatest in those regions with high levels of species richness. The number of determined species ranged from a low of 50% in one plot established in the dry season in a poorly studied deciduous forest type Noel Kempff National

Park (*nklt1*) and 100% in a non-diverse plot in the relatively well studied region of the Gran

Chaco (*gtb-series*).

The ordination analyses were done in an iterative fashion, starting at the family level for all plots,

with subsequent analyses based on genera and species conducted on sequentially circumscribed

geographic areas. Plots with extreme differences in floristic composition that distorted the

analyses by heavily weighting one or more ordinate axes were eliminated from the analysis as they

were identified. The DCAs were conducted prior to the CCAs so as to identify the major floristic

groupings within the region. The CCAs were then conducted as a direct gradient analysis as test

of generally recognized hypotheses in biogeography and of the ecoregional classifications that

have been proposed for the region.

The vegetation map was made using orthorectified Landsat (TM and ETM) images obtained from

the Global Land Cover Facility at the University of Maryland ([http://glcf.umiacs.umd.edu/index.](http://glcf.umiacs.umd.edu/index.shtml)

[shtml](http://glcf.umiacs.umd.edu/index.shtml)). The map (Figure 2) is a mosaic of different studies conducted over several years and is the

result of a continuous effort to map and characterize vegetation and land cover in the Bolivian

lowlands. A variety of methodologies were used ranging including both supervised classifications

and unsupervised classifications. An electronic version of this map can be obtained from the

Museo Noel Kempff web site (http://www.museonoelkempff.org)

RESULTS

The DCA of plots based on species richness at the family level demonstrated the large floristic

differences between the montane and lowland forests. All of the lowland plots were tightly

grouped together with the first axis differentiating among the Andean plots due to the importance

of several families that were absent from lowland plots: Actinadaceae, Aquifoliaceae, Asteraceae,

Betulaceae, Caprifoliaceae, Clethraceae, Cunoniaceae, Myrtaceae, Podocarpaceae, Cyatheaceae,

Dicksoniaceae and Thymeleaceae (Figure 3). The second ordinate axis identified a gradient with

western Amazonian plots weighted negatively and central Amazonian plots positively; plots from Chiquitania and the Gran Chaco clustered around the intercept of the two axes.

A DCA conducted on the generic matrix after eliminating the montane "Yungas" plots (3 of the 4 plots situated in Amboró National Park *amb-series*), identified three additional plots that were radically different from the rest. Two of these plots were situated to the south of Santa Cruz (*pena, yerba*) and were separated due to the presence of *Vassobia* (Solanaceae), *Sambucus* (Caprifoliaceae), *Xylosma* (Flacourtiaceae), *Pfaffia* (Amaranthaceae), *Juglans* (Juglandaceae), *Diatenopteryx* (Sapindaceae), *Citronella* (Icacinaceae), *Aralia* (Araliaceae), and *Carica* (Caricaceae); the third plot situated in the Gran Chaco (*gt1s*) was identified as unique due to the dominance of two species: *Copernicia blanca* and *Geoffroea* sp. The results of these two DCA analyses correspond to the ecoregional classification that recognizes the Yungas Montane forests and the Tucumano-Boliviano forests

After eliminating the five montane plots and the idiosyncratic plot from the Gran Chaco from the data matrix, a DCA based on species richness at the generic level demonstrated floristic groupings that corresponds to the a priori classification of the plots into ecoregions (Amazon, Chiquitania, and Gran Chaco) and identified several plots that were intermediate in floristic composition. The DCA based on generic richness revealed little heterogeneity among plots within the Chiquitano dry forest, while showing a moderate amount of heterogeneity among plots from the Gran Chaco and a great deal of heterogeneity among Amazonian plots. This DCA analysis is not shown, because CCA analysis provides a better discrimination of plots and genera in regard to environmental variables (Figure 4a and 4b).

The CCA analysis of the generic data set showed that genera are distributed across gradients correlated with both latitude and longitude, as well as with mean annual precipitation and seasonality. The trends first identified by the DCA conducted at the family level were more clearly shown by the CCA conducted at the generic level. There was discrimination among plots

situated in the southwest Amazon on the alluvial plains and piedmont adjacent to the Andes (*plrc, chimc, chimj, ambrs*) when compared to those situated in the southern central Amazon on the Brazilian Shield (*nk-series*), while those plots situated on the extreme western edge of the Brazilian shield (*cho-series*) were intermediate to these other two groups. The gradient identified based on geographic location was slightly different when the CCA was conducted using a precipitation data set, reflecting the non-latitudinal nature of the precipitation gradient in the southwest Amazon. The floristic differences of the plots situated in the Gran Chaco were discriminated forming a gradient with the plots that were located in Chiquitania. The genera which weighted the first two ordinate axes of the CCA are shown in Table 2.

Next, the DCA and CCA were applied to a subset that included all of the plots from Chiquitania and specific plots from Amazon ecotone that had been identified as being the most similar to the Chiquitania plots (e.g., select plots from the *nkm* series) or which were geographically situated so as to indicate that they should be transitional in nature (e.g., *cho* series). Plots situated to the south in the Gran Chaco (*gto* series and *tucavaca*) were excluded so as to discriminate the gradients on the northern ecotone better (Figure 5). The DCA analyses confirmed the previous observed floristic differences between the south central and south west Amazon (*cho* series). The CCA analysis was used to identifying the transitional species present along both the latitudinal and longitudinal gradients. Table 3 shows those species that weight the axes that separate the two subregions of the southern Amazon and which are present in the transitional plots; these are essentially Amazonian species at the extreme Southern extent of their geographic distribution. There are also Chiquitano species present in these plots and a comparison of the floristic composition of the plots from the south central Amazon (*nkm series*) and all of the plots within the core area of Chiquitania, revealed 79 species that were present in both regions. This CCA ordination also revealed that although most plots within Chiquitania are more or less tightly clustered around the intersection of the ordinate axes, a subset of plots from southeast Chquitania (*suto* series) were offset from the rest on the second ordinate axis.

The next iteration was performed using the same plots situated in the center of the Chiquitano seasonal dry forest region, but excluded the transitional plots from the Amazon ecotone while including the plots situated in the Gran Chaco (*gtb* series). The DCA identified a transition from the Chiquitano to Gran Chaco on the first ordinate axis; however, unlike the northern ecotone where the floristically intermediate plots could be associated with a latitudinal gradient the *gtb* plots in the south were all situated at the same latitude. Two sets of plots (*suto* and *sand*) were grouped separately from the majority of the plots from Chiquitania and the Gran Chaco. The CCA analyses that provided the best separation of the various groups was provided using rock type for the environmental parameters (Figure 6). The plots from the chaco (*gtb* series) were segregated on the first ordinate axis which was correlated with alluvial sediments ($r^2 = 0.912$, $p < 0.05$) and the *suto/sand* series were separated by the second ordinate axis which was highly with calcarious rocks ($r^2 = 0.83$, $p < 0.01$); the species identified as being characteristic of the plots from calcareous rocks are provided in Table 4.

The next iteration was made on a dataset that excluded the plots from both Amazon (*nkp-, cho-*) and the Gran Chaco (*gtb-, tucavaca*), as well as the plots from calcareous rocks identified in the previous analyses (*suto-m sand-*). The DCA performed on this set of plots from what is considered to be the heart of the Chiquitano forest showed little heterogeneity and all of the plots were tightly clustered around the center of the first, second and third ordinate axes. The subsequent CCA analyses all showed some grouping which was best explained using latitude and longitude as the environmental matrix (Figure 7, Table 5). The taxa that are at the center of this last ordination procedure and which were not weighted with any ordinate axis, can be considered to be the "typical' or characteristic species of the Chiquitano dry forest (Table 5d).

<center>DICUSSION</center>

BIOGEOGRAPHY AND ENDEMISM

The results confirm the hypothesis that the Chiquitano dry forest is a transition zone between the humid tropics and semi-arid subtropics and the distribution of species is related to climatic variables which are highly correlated with latitude. The species found in the Chiquitano dry forest do not represent a mixture of Amazonian and Gran Chaco species, but are a distinct assemblage of species when compared to the forests situated either north or south of the region (Table 6), thus also supporting the hypothesis that the Chiquitano dry forest merits recognition as a unique ecoregion (Olsen and Dinerstein 1998; Ibisch et al 2003).

The degree of endemism in the region is not well known, with only a few documented plant species, such as *Acosmium cardenasii, Cereus tacuaralensis,* and *Swartzia jorori* (see Table 5 D). In this study there were 11 undescribed taxa that were given morphospecies names by the botanists who identified the voucher specimens in the following genera *Phyllanthus, Acacia, Bauhinia, Inga, Lonchocarpus, Machaerium, Casearia, Myrcianthes, Myrciaria, Neea,* and *Zanthoxylum.* All of these genera are large, complex and hard to identify, which lessens the probability that represent endemic species new to science.

The low level of endemism may simply be a taxonomic artifact that is the result of too-few collections and too-few taxonomists in Bolivia. However, a more likely explanation may lie in its recent geological past. Almost all of the species identified as characteristic as the core area of the Chiquitano dry forest (Table 5) are also part of the seasonal dry forest complex described by Prado and Gibbs (1992), Prado 2000, Pennington et al (2004). Mayle et al (2004) hypothesize that flora of this region is essentially young and the constituent species of this seasonal dry forest flora are relatively recent arrivals that migrated into the region from more northerly latitudes after the last glacial maximum. Regardless of its past, the Chiquitano dry forest is situated at the crossroads of any potential scenario that describes how the different disjunct regions with taxa characteristic of this newly defined biome, might have once been in contact. This includes the Caatinga, the southern andean piedmont, eastern Paraguay and the dry valleys of the central Andes.

ALPHA AND BETA DIVERSITY

Gentry (1995) using limited data from a few localities suggested that the dry forests in this region were some of the most floristically diverse in the New World, a conclusion that was supported by a study that identified a total of 107 tree species as part of a single site inventory (Killeen et al. 1998) and a compendium of 237 trees known from herbaria specimens (Jardim et al. 2002). However, this study of 56 1-ha plots identified only 155 tree species, which suggests that the tree flora of the region might only be moderately diverse. Nonetheless, since it is a relatively open forest type, the diversity of the herbaceous, shrub and liana life forms is large with up to 40% of all the species registered for the region (Killeen et al 1998, Ibisch et al. 2002).

Plots from the Chiquitano dry forest region were consistently grouped together based on tree composition when in comparison to both Gran Chaco and Amazon plots (see Figures 5 and 6), and spatial heterogeneity was only displayed when all transitional or edaphically unique areas were eliminated from the analysis. This apparent lack of beta diversity may be an artifact and the result of the data sets that were used for analyses. The Noel Kempff plots were part of a botanical and ecological inventory (Killeen et al 2002) where an effort was made to establish plots in contrasting vegetation types, which included inundated, dwarf, and liana-dominated habitats, as well as both semi-deciduous and evergreen forests. The Gran Chaco plots were systematically installed at predetermined intervals and identify a range of different plant communities that are related to edaphic conditions (R. Guillén, pers. comm.); for instance one of the most radically different plots in the entire dataset was located in a wetland dominated by the palm *Copernicia alba* L. In contrast, all of the Chiquitano dry forest plots were established by foresters who were interested in forest inventory and management (Dauber et al. 2003); thus they may represent a more homogeneous, closed-canopy, forest type on well-drained soils with high economic potential for hardwood species. In spite of the high overall similarity of the plots, the Chiquitano dry forest region has considerable edaphic variability that has not been sampled by this study, including sandstone mesetas, metamorphic and ultramaphic rocks, and extensive inundated forests (Litherland, 1984). Most of the plots from Chiquitania included in this study, with the notable exception of the

calcareous series, were situated on soils derived from granite or the very similar gneiss. The further exploration of the edaphic variability within the region will probably provide a much greater level of forest heterogeneity.

CLIMATE CHANGE

Mayle et al. (2000, 2004) and Burbridge et al. (2004) hypothesize that the species found within these seasonal dry forests are relatively recent arrivals having migrated into the region from the north as a response to millennial scale climate change. The identification of a floristic gradient that coincides with a latitidunal and climatic gradient supports that hypothesis. However, this study also shows that the gradient has two sub-axes over which migration into the region from the north might have occurred.

Currently, there is a great deal of interest in monitoring how climate change will impact biological diversity as species are forced to shift geographic ranges in response to global warming. Ecotonal and transitional environments are more likely to be impacted by climate change as many species are at the extreme limits of their ecological requirements or where competition from differently adapted species places their survival at a disadvantage. The eastern lowlands of Bolivia offer a unique and valuable laboratory to study the impact of climate change on biodiversity. Several groups of scientists are working in Eastern Bolivia with the objective to document how climate change may be impacting different aspects of ecosystem function across this climatic and ecological transition. The permanent plot network used for this study has been established largely for the purposes of biological inventory and forest management; however, it is an invaluable asset and should be integrated as core facility into linking studies focusing on climate change, geochemistry and ecosystem function with biodiversity and biodiversity conservation.

CONSERVATION

The Chiquitano dry forest is threatened by land-use change and forest degradation due to logging and fire. In a recent unpublished study conducted for the Vice Minsitry for the Environment, the

total original extent of the Chiquitano forest was estimated at 125,000 km² Of this original total, an estimated 18,600 km2 or 15% of the total had been deforested prior to 2001 and the annual rate of deforestation was documented at a mean annual rate of 108,000-ha for the decade spanning 1991 to 2001 (Killeen, pers. com.). Timber extraction may also threaten the long-term conservation of the forest. Current logging rates are still relatively low, but increased logging will quickly become unsustainable due to the very slow growth of the species in this forest. Most logging management plans contemplate a 25 year harvest cycle, but the current crop of trees being exploited are all much older than 100 years, with some probably approaching 500 years of age (Dauber et al 2002). Overexploitation of timber resources will spur deforestation, since natural forest communities will have little value in standing timber.

Both land-use change and logging promote fire, and in the fall of 2004 an estimated 1.5 million hectares was impacted by forest fires, most of which originated in forest being cleared for pasture, but which spread into adjacent intact forest. Fire is a well known ecological phenomenon in the Chiquitano forest, but anecdote from long-time residents indicates that fire frequencies are increasing from a decadal-scale phenomenon to a recurrent event that impacts large extensions of forest every few years, with large-scale fires having occurred in 2004, 2000, 1998, 1994, and 1987 (Killeen, pers. com).

Conservation efforts are being pursued by the Chiquitano Forest Conservation Foundation, a private non-profit organization funded by private industry in collaboration with Bolivian and international conservation organizations. Several protected areas have been established, but these tend to be zoned for multiple-use and contain within them logging concessions, land-claims and indigenous lands. Consequently, efforts by the Foundation focus on working with the various stakeholders who have the legal right to exploit forest resources. Key to this effort is an emphasis on working with municipal governments and local communities who under Bolivian laws have considerable leeway in monitoring natural resource use. In addition, research conducted by Bolivian Forest Research Institute is aimed at the definition of more sustainable management

practices. Likewise, the government and the private forest sector are working to open the timber market to new species so as to reduce the pressure on the few species that are currently harvested.

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Figure 1. Precipitation map of Bolivia showing the locations of the plot localities; plot codes as in Table 1.

Figure 2. Land Cover of Eastern Bolivia showing the position of the plot localities in relation to the major vegetation types in the region, which also correspond roughly to existing ecoregional classifications; land-use change (red) is current to 2002; plot codes as in Table 1.

Figure 3. DCA of 118 plots based on species richness of 99 families; he montane "yungas" forest plots (*amb series*) are separated on the first ordinate axis; pyramids are plots and plus signs are families. Families weighting the first axis are provided in the text; plot codes as in Table 1

Figure 4. CCA of 114 plots based on species richness of 379 genera constrained by geographic position (a) and precipitation (b); pyramids are plots and plus signs are genera. Table 2 provides the list of the genera that are weighted for Gran Chaco (*gtb series*), South Central Amazon (*nk series*) and the South West Amazon (*chim, amb, plrc*); plot codes as in Table 1

Figure 5. CCA of 72 plots and 277 species from the Chiquitano Forest and the most similar transitional plots in adjacent Amazonian humid forest; pyramids are plots and plus signs are species. Species with large axis loading factors are provided in Table 3; plot codes as in Table 1

Figure 6. CCA of 167 species from 67 plots in Chiquitania and Gran Chaco; the species identified by this ordination as associated with alluvial soils (*gtb*) or calcareous rocks (*suto*) are provided in Table 4; plot codes as in Table 1.

Figure 7. CCA of core plots from Chiquitania showing a spatial heterogeneity associated with proximity.

Table 1.Characteristics of the plots localities included in this study; see Figures 1 and 2.

Locality	Acronym	# of plots	Forest Type	Phenology	Ecoregion	Number of species
Afamosam[1]	afamo	1	Upland	Deciduous	Chiquitano	31
Amboro National Park[1,2]	ambcb ambra ambsr	4	Cloud	Evergreen	Yungas	39 – 70
	ambrs		Upland		Preandean Amazon,	
Bosque Chimanes[3,4]	chimc chimj	2	Upland Inundated	Evergreen	Preandean Amazon	47, 87
Chuquisaca[1]	peña herba	2	Upland Cloud	Evergreen Deciduous	Tucumano-Boliviano	40, 44
CIMAL Sandoval[5]	sand	3	Upland	Deciduous	Chiquitano	25 – 29
Estacion Tucavaca[1, 6]	tucav	1	Upland	Deciduous	Gran Chaco	29
CIMAL ex-Marabol[5]	mara	4	Upland	Deciduosu	Chiquitano	24 - 29
GTB Pipeline[1,7]	gtb 1 to 9	12	Upland	Deciduous	Gran Chaco	2- 24
INPA[5]	inpa 1 to 8	8	Upland	Deciduous	Chiquitano	29 – 42
La Chonta[5]	cho 1 to 12	12	Upland Inundated	Semi-Evergreen	Beni – Santa Cruz Amazon	46 – 64
Las Trancas[5]	ltr 1 to 18	18	Upland	Deciduous	Chiquitano	36 – 48
Noel Kempff Mercado National Park[1,4]	nk + misc codes	28	Upland Inundated	Evergreen Deciduous	Beni/Santa Cruz Amazon Cerrado	46- 123
Rio Colorado/Pilon Lajas[3,4]	plrc	1	Upland	Evergreen	Cloud Preandean Amazon	78
CIMAL San Miguel [5]	smig	12	Upland	Deciduous	Chiquitano	16 – 32
Santa Cruz Botanical Garden[1,2]	sczjb	1	Upland	Deciduous	Gran Chaco	31
Suto[5]	suto	8	Upland	Deciduous	Chiquitano	18 – 32

1. Museo Noel Kempff Mercado
2. New York Botanical Garden
3. Herbario Nacional de Bolivia
4. Missouri Botanical Garden
5. Instituto Boliviano de Investigaciones Forestales (IBIF)
6. Conservation International
7. Capitanía de Alto y Bajo Izozog

Table 2. Genera from 108 Lowland plots established across a transition from the Amazon to the Gran Chaco; genera are those with large loading factors for the eigen vectors associated with each ordinate axes of a CCA using latitude and longitude as the environmental parameters (see Figure 4a); Genera are arranged alphabetically according to plant family.

A. Genera with values in the First CCA AX1 < -1.5 (Gran Chaco plots).

Anacardiaceae	*Schinopsis*	Myrsinaceae	*Geissanthus*
Annonaceae	*Cremastosperma*	Nyctaginaceae	*Pisonia*
Arecaceae	*Trithrinax*	Polygonaceae	*Ruprechtia*
Bignoniaceae	*Tynanthus*	Rhamnaceae	*Ziziphus*
Cactaceae	*Browningia, Cereus, Echinopsis, Pereskia, Stetsonia*	Rutaceae	*Esenbeckia*
		Santalaceae	*Acanthosyris*
Capparaceae	*Capparis*	Sapindaceae	*Athyana*
Euphorbiaceae	*Phyllanthus*	Sapotaceae	*Sideroxylon*
Fabaceae	*Geoffroea, Mimozyganthus, Prosopis, Pterogyne*	Zygophyllaceae	*Bulnesia*
Meliaceae	*Cabralea*		

B. Genera with values in the first CCA > 1 (South Central Amazon Plots)

Anacardiaceae	*Tapirira*	Lecythidaceae	*Couratari, Eschweilera,*
Annonaceae	*Bocageopsis, Cardiopetalum, Ephedranthus, Onychopetalum*	Loganiaceae	*Strychnos,*
		Malpighiaceae	*Banisteriopsis, Byrsonima, Mascagnia*
Apocynaceae	*Apocynaceae*		
Arecaceae	*Bactris, Mauritia, Maximiliana*	Marcgraviaceae	*Norantea*
Asteraceae	*Mikania*	Melastomataceae	*Mouriri*
Bignoniaceae	*Callichlamys, Cydista, Jacaranda, Lundia, Mussatia, Paragonia*	Meliaceae	*Ruagea*
		Menispermaceae	*Anomospermum*
Bombacaceae	*Huberodendron, Crepidospermum, Dacryodes,*	Monimiaceae	*Siparuna*
		Moraceae	*Cecropia, Coussapoa, Maquira*
Celastraceae	*Elaeodendron*	Myristicaceae	*Myristicaceae, Osteophloeum*
Chrysobalanaceae	*Couepia, Licania, Parinari*	Myrsinaceae	*Myrsine*
Clusiaceae	*Kielmeyera, Vismia*	Myrtaceae	*Myrcia*
Combretaceae	*Buchenavia*	Olacaceae	*Chaunochiton, Dulacia, Schoepfia*
Connaraceae	*Connarus*	Polygalaceae	*Bredemeyera, Moutabea*
Convolvulaceae	*Dicranostyles*		
Dichapetalaceae	*Tapura*	Polygonaceae	*Symmeria*
Dilleniaceae	*Curatella, Doliocarpus*	Proteaceae	*Panopsis, Roupala*
Euphorbiaceae	*Alchornea, Alchorneopsis, Aparisthmium, Chaetocarpus, Conceveiba, Hyeronima, Maprounea, Maprounea ó Sebastiana, Pera*	Rhamnaceae	*Colubrina*
		Rosaceae	*Prunus*
		Rubiaceae	*Amaioua, Chomelia, Coussarea, Coutarea, Faramea, Ferdinandusa, Pagamea, Randia, Rubiaceae, Uncaria*
Fabaceae	*Ateleia, Derris, Diptychandra, Hymenolobium, Macrolobium, Mimosa, Pterodon, Stryphnodendron, Vataireopsis*		
		Rutaceae	*Dictyoloma*
Flacourtiaceae	*Banara*	Rutaceae	*Metrodorea*
Hippocrateaceae	*Anthodon, Cheiloclinium, Hippocratea, Prionostemma*	Sabiaceae	*Meliosma*
		Sapindaceae	*Matayba*
Humiriaceae	*Humiria, Sacoglottis*	Sapotaceae	*Ecclinusa, Sapotaceae*
Icacinaceae	*Citronella,*	Simaroubaceae	*Simarouba*
Lacistemataceae	*Lacistema*	Tiliaceae	*Mollia*
Lauraceae	*Aiouea, Caryodaphnopsis, Endlicheria*	Vochysiaceae	*Erisma*

C. Genera with values in the CCA AX2 < -1 (South West Amazon /Andean Piedmont Plots)

Acanthaceae	*Suessenguthia*
Annonaceae	*Annona, Cremastosperma, Ruizodendron*
Apocynaceae	*Peschiera*
Arecaceae	*Iriartea, Scheelea*
Bignoniaceae	*Tynanthus*
Bombacaceae	*Cavanillesia*
Burseraceae	*Tetragastris*
Caricaceae	*Jacaratia*
Clusiaceae	*Calophyllum, Rheedia, Symphonia*
Euphorbiaceae	*Croton, Hura, Margaritaria, Richeria, Sapium*
Fabaceae	*Albizia, Cyclolobium, Machaerium*
Flacourtiaceae	*Hasseltia*
Lauraceae	*Licaria, Nectandra, Ocotea*
Meliaceae	*Cabralea, Swietenia, Trichilia*
Moraceae	*Batocarpus, Clarisia, Coussapoa, Poulsenia*
Myristicaceae	*Otoba*
Myrsinaceae	*Geissanthus*
Myrsinaceae	*Stylogyne*
Papilionoideae	*Machaerium*
Polygonaceae	*Triplaris*
Rubiaceae	*GenipaIxora*
Sapindaceae	*Sapindus*
Sterculiaceae	*Guazuma*
Tiliaceae	*Heliocarpus*
Ulmaceae	*Ampelocera, Guazuma, Trema*
Verbenaceae	*Aegiphila*
Violaceae	*Leonia*

Table 3. Species from 72 plots established in the Chiquitano Region and the adjacent Amazon Ecotone; species are those with large loading factors for the eigen vectors associated with each ordinate axes of a CCA (see Figure 5); species are arranged according the magnitud of the loading factor.

A. Species with values from CCA AX1 > 1 and CCA AX2 > 2; identified as being characteristic in plots from the eastern part of northern Chiquitania (plots from the *nk*-series);.

Annonaceae	*Duguetia furfuracea* (A. St. Hil.) Benth. & Hook. f.
Bombacaceae	*Pseudobombax longiflorum* (Martius & Zuccarini) A. Robyns
Combretaceae	*Buchenavia grandis* Ducke
Burseraceae	*Crepidospermum goudotianum* (Tul.) Triana & Planchon
Fabaceae	*Acacia riparia* Kunth
Flacourtiaceae	*Banara guianensis* Aublet
Ochnaceae	*Ouratea castaneifolia* (DC.) Engl. in C. Martius
Rutaceae	*Metrodorea flavida* K. Krause
Nyctaginaceae	*Neea amplifolia* Donn. Sm.
Flacourtiaceae	*Casearia sylvestris* Sw.
Fabaceae	*Inga cylindrica* (Vell. Conc.) C. Martius
Tiliaceae	*Luehea grandiflora* C. Martius
Euphorbiaceae	*Sebastiania huallagensis* Croizat
Polygonaceae	*Coccoloba mollis* Casar.
Fabaceae	*Acacia multipinnata* Ducke
Euphorbiaceae	*Sapium laurifolium* (A. Rich.) Griseb.
Annonaceae	*Duguetia marcgraviana* C. Martius
Celastraceae	*Maytenus floribunda* Pittier
Dichapetalaceae	*Tapura amazonica* Poeppig in Poeppig & Endl.
Euphorbiaceae	*Chaetocarpus echinocarpus* (Baillon) Ducke
Fabaceae	*Inga thibaudiana* DC.
Fabaceae	*Ormosia coarctata* Jackson
Proteaceae	*Roupala montana* Aublet
Vochysiaceae	*Qualea cordata* (C. Martius) Spreng.
Fabaceae	*Machaerium jacarandifolium* Rusby
Fabaceae	*Inga cayennensis* Sagot ex Benth.
Humiriaceae	*Sacoglottis mattogrossensis* Malme
Bombacaceae	*Chorisia integrifolia* Ulbr.
Euphorbiaceae	*Margaritaria nobilis* L. f.
Bignoniaceae	*Macfadyena unguis-cati* (L.) A. Gentry
Araliaceae	*Didymopanax morototoni* (Aublet). & Planchon
Fabaceae	*Bauhinia rufa* (Bong.) Steudel
Arecaceae	*Attalea phalerata* Mart. ex Spreng.
Flacourtiaceae	*Casearia arborea* (Rich.) Urban
Rhamnaceae	*Rhamnidium elaeocarpum* Reissek

B. Species with values from CCA AX1 > 1 and CCA AX2 < 1; identified as being characteristic in plots from the western part of northern Chiquitania (plots from the *cho-series*);.

Myrtaceae	*Eugenia florida* DC.
Moraceae	*Batocarpus amazonicus* (Ducke) Fosb.
Acanthaceae	*Suessenguthia multisetosa* (Rugby) Wassh.
Caricaceae	*Jacaratia spinosa* (Aublet) A. DC.
Euphorbiaceae	*Sapium glandulosum* (L.) Moroni
Sapindaceae	*Cupania cinerea* Poeppig
Clusiaceae	*Rheedia brasiliensis* (C. Martius) C. MartiusPlanchon & Triana
Arecaceae	*Syagrus sancona* Karsten

Apocynaceae	*Peschiera australis* (Müll. Arg. in C. Martius) Miers
Moraceae	*Pseudolmedia laevis* (Ruiz Lopez & Pavon) J.F. Macbr.
Rutaceae	*Zanthoxylum sprucei* Engl.
Fabaceae	*Inga edulis* C. Martius
Bombacaceae	*Cavanillesia hylogeiton* Ulbr.
Arecaceae	*Copernicia alba* Morong ex Morong & Britton
Nyctaginaceae	*Neea hermaphrodita* S. Moore
Moraceae	*Pseudolmedia laevigata* Trecul
Bombacaceae	*Ceiba pentandra* (L.) Gaertner
Meliaceae	*Guarea guidonia* (L.) Sleumer
Moraceae	*Pourouma cecropiifolia* C. Martius
Fabaceae	*Ormosia nobilis* Tul.
Elaeocarpaceae	*Sloanea terniflora* (Sesse & Mocino ex DC.) Standley
Clusiaceae	*Calophyllum brasiliense* Cambess.
Fabaceae	*Inga marginata* Willd.
Lauraceae	*Ocotea guianensis* Aublet
Sapindaceae	*Sapindus saponaria* L.
Fabaceae	*Acacia bonariensis* Gillies ex Hook. & Arn.

Table 4. Species from 67 plots established in the Chiquitano Region and the adjacent Gran Chaco Ecotone; species are those with large loading factors for the eigen vectors associated with each ordinate axes of a CCA (see Figure 6);); species are arranged according the magnitud of the loading factor.

A. Species with values for the CCA AX1 > 1; identified as being important in plots from the northern sector of the Gran Chaco (*gtb-series*).

Fabaceae	*Prosopis nigra* (Griseb.) Hieron.
Fabaceae	*Mimozyganthus carinatus* (Griseb.) Burkart
Cactaceae	*Browningia caineana* (Cardenas) Cardenas
Fabaceae	*Prosopis nuda* Schinini
Capparaceae	*Capparis salicifolia* Griseb.
Nyctaginaceae	*Bougainvillea praecox* Griseb.
Santalaceae	*Acanthosyris falcata* Griseb.
Polygonaceae	*Ruprechtia triflora* Griseb.
Fabaceae	*Lonchocarpus nudiflorens* Burkart
Fabaceae	*Acacia praecox* Griseb.
Cactaceae	*Cereus dayamii* Speg.
Cactaceae	*Pereskia sacharosa* Griseb.
Fabaceae	*Geoffroea striata* (Willd.) Morong
Bignoniaceae	*Tabebuia nodosa* (Griseb.) Griseb.
Bombacaceae	*Pseudobombax heteromorphum* (Kuntze) Kuntze
Capparaceae	*Capparis tweediana* Eichler in C. Martius
Nyctaginaceae	*Neea hermaphrodita* S. Moore
Capparaceae	*Capparis speciosa* Griseb.
Fabaceae	*Caesalpinia paraguariensis* (Parodi) Burkart
Bombacaceae	*Ceiba insignis* (Kunth) KunthP. Gibbs & Semir
Opiliaceae	*Agonandra excelsa* Griseb.
Olacaceae	*Ximenia americana* L.
Ulmaceae	*Trema micrantha* (L.) Blume
Capparaceae	*Capparis retusa* Griseb.

B. Species with values for CCA AX2 > 0.5; identified as being characteristic in plots associated with calcareous rock (suto, sand)

Sapotaceae	*Pouteria nemorosa* Baehni
Rutaceae	*Esenbeckia almawillia* Kaastra
Rubiaceae	*Pogonopus tubulosus* (A. Rich.) Schumann
Flacourtiaceae	*Lunania parviflora* Spruce ex Benth.
Sterculiaceae	*Guazuma ulmifolia* Lam.
Sapotaceae	*Chrysophyllum gonocarpum* (C. Martius & Eichler) Engl.
Rutaceae	*Zanthoxylum coco* Gillies ex Hook. f. & Arn.
Vochysiaceae	*Vochysia haenkeana* C. Martius
Fabaceae	*Sweetia fruticosa* Spreng.
Combretaceae	*Terminalia oblonga* (Ruiz Lopez & Pavon) Steudel
Fabaceae	*Machaerium scleroxylon* Tul.
Capparaceae	*Capparis retusa* Griseb.
Anacardiaceae	*Spondias mombin* L.
Tiliaceae	*Lueheopsis duckeana* Burret

Table 5. Species from 43 plots from Chiquitania excluding ecotonal plots and those situated over calcareous rock (see Figure 7); species are arranged according the magnitud of the loading factor.

A.   Species with CCA AX1 < -0.75 and CCA AX2 < -0.75); identified as being important in the North West sector of Chiquitania (*inpa-series*).

Bignoniaceae	*Tabebuia roseoalba* (Ridley) Sandw.
Fabaceae	*Copaifera reticulata* Ducke
Fabaceae	*Machaerium saraense* Rudd
Polygonaceae	*Ruprechtia laxiflora* Meisn. in C. Martius
Fabaceae	*Machaerium pilosum* Benth.
Celastraceae	*Maytenus robustoides* Loes.
Bignoniaceae	*Tabebuia serratifolia* (M. Vahl) Nicholson
Tiliaceae	*Luehea candicans* C. Martius
Fabaceae	*Dalbergia riparia* (Mart.) Benth.
Nyctaginaceae	*Neea steinbachiana* Heimerl

B.   Species with CCA AX1 < 0.0 and CCA AX2 > 0.75; identified as being important the North Central sector of Chiquitania (*ltr-series*).

Vochysiaceae	*Qualea grandiflora* C. Martius
Fabaceae	*Caesalpinia paraguariensis* (Parodi) Burkart
Fabaceae	*Machaerium hirtum* (Vell. Conc.) Vell. Conc.
Lythraceae	*Physocalymma scaberrimum* Pohl
Violaceae	*Leonia glycycarpa* Ruiz Lopez & Pavon
Rutaceae	*Zanthoxylum hasslerianum* (Chodat) Pirani
Moraceae	*Cecropia concolor* Willd.
Bombacaceae	*Pseudobombax marginatum* (A. St. Hil., A. L. Juss. & Cambess.) A. Robyns
Sterculiaceae	*Guazuma ulmifolia* Lam.
Vochysiaceae	*Vochysia haekeana* C. Martius
Nyctaginaceae	*Bougainvillea modesta* Heimerl
Fabaceae	*Machaerium villosum* J. Vogel

C.   Species with CCA AX1 > 0.5 and CCA AX2 > 0.5 identified as being important in the South Central quadrant of Chiquitania (*mara-series*)

Capparaceae	*Capparis speciosa* Griseb.
Flacourtiaceae	*Casearia aculeata* Jacq.
Fabaceae	*Acacia loretensis* J.F. Macbr.
Fabaceae	*Bauhinia rufa* (Bong.) Steudel
Rutaceae	*Zanthoxylum monogynum* A. St. Hil.
Bombacaceae	*Ceiba insignis* (Kunth) KunthP. Gibbs & Semir
Ulmaceae	*Trema micrantha* (L.) Blume

D.   Species with CCA AX1 > 0.5 and CCA AX2 < 0.5; identified as being important the South East sector of Chiquitania (*smig-series*)..

Capparaceae	*Capparis speciosa* Griseb.
Anacardiaceae	*Schinopsis brasiliensis* Engl. in C. Martius
Flacourtiaceae	*Casearia aculeata* Jacq.
Fabaceae	*Acacia loretensis* J.F. Macbr.
Fabaceae	*Bauhinia rufa* (Bong.) Steudel
Rutaceae	*Zanthoxylum monogynum* A. St. Hil.
Bombacaceae	*Ceiba insignis* (Kunth) KunthP. Gibbs & Semir
Anacardiaceae	*Spondias mombin* L.
Bignoniaceae	*Tabebuia impetiginosa* (C. Martius ex DC. in A. DC.) Standley
Ulmaceae	*Trema micrantha* (L.) Blume

Fabaceae	*Acacia polyphylla* DC.
Fabaceae	*Caesalpinia pluviosa* DC.

D. Core species that were found in all sectors of the Chiquitano region; CCA AX1 > -0.5 and < 0.5 and CCA AX2 < 0.5 and > -0.5).

Achatocarpaceae	*Achatocarpus nigricans* Triana
Anacardiaceae	*Spondias mombin* L.
Bignoniaceae	*Tabebuia chrysantha* (Jacq.) Nicholson
Bignoniaceae	*Tabebuia impetiginosa* (C. Martius ex DC. in A. DC.) Standley
Bombacaceae	*Ceiba samauma* (C. Martius) Schumann
Bombacaceae	*Chorisia speciosa* A. St. Hil.
Boraginaceae	*Cordia alliodora* (Ruiz Lopez & Pavon) Cham.
Cactaceae	*Cereus tacuaralensis* Cardenas
Cochlospermaceae	*Cochlospermum orinocense* (Kunth) Steudel
Fabaceae	*Acacia polyphylla* DC.
Fabaceae	*Acosmium cardenasii* H.S. Irwin & Arroyo
Fabaceae	*Anadenanthera colubrina* (Vell. Conc.) Brenan
Fabaceae	*Caesalpinia pluviosa* DC.
Fabaceae	*Guibourtia chodatiana* (Hassler) Leonard
Fabaceae	*Lonchocarpus guillemineanus* (Tul.) Malme
Fabaceae	*Machaerium acutifolium* J. Vogel
Fabaceae	*Swartzia jorori* Harms
Fabaceae	*Sweetia fruticosa* Spreng.

Table 6. Floristic similarity of groups of plots in different ecoregions; the upper right quadrant are the number of shared species and the lower right quadrant is the Sorensen Index of similarity,

	Andes	Piedmont	Chore	Noel Kempff	NKM Dry Forest Types	Chiquitano	Chaco	Serrano
Andes		3	0	2	0	3	0	5
Piedmont	0.00		60	86	11	36	0	1
Chonta	-	0.07		53	17	33	2	2
Noel Kempff	0.00	0.04	0.03			79	8	11
NKM dry forest	-	0.01	0.03			44	6	6
Chiquitano	0.01	0.04	0.06	0.04	0.08		18	10
Chaco	-	-	0.00	0.00	0.01	0.03		6
Serrano	0.02	0.00	0.01	0.01	0.02	0.02	0.01	
Total	96	297	112	901	137	155	201	59
Number of plots	3	4	12	23	5	67	13	2

Andes: cloud forest > 1000 m (ambcb, ambra, ambfa)
Piedmont: preandean Amazon < 500 m (plrc, chmj, chms, ambrs)
Chonta   western edge of Brazilian shield (cho1 –12)
Noel Kempff: subset of nk- plots that exclude transitional
Noel Kempff Dry Forest: subset of nk- that were identified by ordination as transitional
Chiquitano   all plots from smig, mara, sand, ltr94, ltr95, inpa, afoma
Chaco: all plots from gtb, tucav
Serrano: southern Andes (pena, herbal)

1
2
3