The Effects of Past Climate Variability on Fire and Vegetation in the Cerrado Savanna
Ecosystem of the Huanchaca Mesetza, Noel Kempff Mercado National Park, NE Bolivia
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Abstract

Cerrado savannas have the greatest fire activity of all major global land-cover types
and play a significant role in the global carbon cycle. During the 21st century,
temperatures are predicted to increase by ~3°C coupled with a precipitation decrease of
~20%. Although these conditions could potentially intensify drought stress, it is unknown
how that might alter vegetation composition and fire regimes. To assess how Neotropical
savannas responded to past climate changes, a 14,500-year high-resolution sedimentary
record from Huanchaca Mesetza, a palm swamp located in the cerrado savanna in
northeastern Bolivia, was analyzed for phytoliths, stable isotopes and charcoal. A non-
analogue, cold-adapted vegetation community dominated the Late Glacial-Early
Holocene period (14.5-9 ka), that included trees and C3 Pooidae and C4 Panicoideae
grasses. The Late Glacial vegetation was fire sensitive and fire activity during this period
was low, likely responding to fuel availability and limitation. Although similar vegetation
characterized the Early Holocene, the warming conditions associated with the onset of
the Holocene led to an initial increase in fire activity. Huanchaca Mesetta became
increasingly fire-dependent during the Middle Holocene with the expansion of C₄ fire
adapted grasses. However, as warm, dry conditions, characterized by increased length
and severity of the dry season, continued, fuel availability decreased. The establishment
of the modern palm swamp vegetation occurred at 5,000 cal yr BP. Edaphic factors are
the first order control on vegetation on the rocky quartzite mesetta. Where soils are
sufficiently thick, climate is the second order control of vegetation on the mesetta. The
presence of the modern palm swamp is attributed to two factors: 1) increased
precipitation that increased water table levels, and 2) decreased frequency and duration of
surazos leading to increased temperature minima. Natural (soil, climate, fire) drivers
rather than anthropogenic drivers control the vegetation and fire activity at Huanchaca
Mesetta. Thus the cerrado savanna ecosystem of the Huanchaca Plateau has exhibited
ecosystem resilience to major climatic changes in both temperature and precipitation
since the Late Glacial period.

1. Introduction

The cerrado savanna of central South America is the largest, richest, and likely most
threatened savanna in the world (Da Silva Meneses and Bates, 2002). The cerrado is the
second largest biome in South America covering 1.86 million km² and is home to over
10,000 plant species (Myers et al. 2000). The tropical forest-savanna ecotones within the
cerrado biome are of considerable interest to biologists because of their high habitat
heterogeneity (beta diversity), importance in rainforest speciation (Smith et al. 1997) and
sensitivity to climate change (IPCC, 2014). According to current estimates however, only
20% of the cerrado remains undisturbed and only 1.2% of the area is preserved in
protected areas (Mittermeier et al. 2000). Additionally, cerrado savannas have a
significant role in the modern global carbon cycle because of high CO₂ loss associated
with frequent natural fire activity (Malhi et al., 2002). Currently savanna fires are
considered the largest source of natural pyrogenic emissions, with the most fire activity
of all major global land cover types (Pereira, 2003). In the last few decades, deforestation
for agriculture and increased drought have resulted in increased burning in savannas,
contributing to approximately 12% of the annual increase in atmospheric carbon (van der
Werf et al., 2010).

The cerrado biome comprises forest, savanna, and campestre (open field) formations
(Abreu et al., 2012; Mistry, 1998). Cerrado sensu stricto is characterized as a woody
savanna formation composed of dense, thin, and rocky outcrops with cerrado
physiognomies that are distinguishable based on their densities, heights, and scattered
tree-shrub covers with roughly 50% trees and 50% grass (Abreu et al., 2012). The
principal determinants of the growth and development of the cerrado vegetation types are
largely related to edaphic factors (Colgan et al., 2012). For example, the distribution of
major cerrado vegetation types are closely related to the geomorphology of the
Precambrian Brazilian shield in South America (Killeen, 1998a). The development of the
variety of cerrado vegetation communities is largely the result of heterogeneous nature of
the edaphic features (Killeen, 1998a) including the depth of the water table, drainage, the
effective depth of the soil profile, the presence of concretions (Haridasan, 2000), soil
texture and the percentage of exposed rock (Junior and Haridasan, 2005).
In addition to edaphic constraints, climate also has a prominent role in determining cerrado savanna vegetation structure and fire activity (Ribeiro and Walter, 2008). The cerrado biome is dominated by a warm, wet-dry climate associated with the seasonal migration of the Intertropical Convergence Zone (ITCZ) (Latrubesse et al., 2012; Da Silva Meneses and Bates, 2002; Vuille et al., 2012). On synoptic climatological timescales, temperature and precipitation are the most important effects of climate on fire (e.g. months to seasons to years) (Mistry, 1998). These factors govern net primary productivity (NPP) and the abundance of available fuels (Brown and Power, 2013; Marlon et al., 2013). Warmer temperatures are typically associated with increased burning through vegetation productivity and the occurrence of fire-promoting climatic conditions. However, the role of temperature can be mediated by precipitation (Brown and Power, 2013). Fire responds differently to increases in precipitation depending on whether fuel is initially abundant or limited in the ecosystem (Marlon et al., 2013; Mistry, 1998). In arid and semi-arid environments, such as the cerrado, increases in precipitation tend to increase fire, whereas increased precipitation in humid environments can reduce fire (Marlon et al., 2008, 2013).

The seasonality of the precipitation coupled with abundant wet-season lightning ignitions (Ramos-Neto and Pivello, 2000) is linked to high fire frequency in the cerrado (Miranda et al., 2009). Wet season lightning fires typically start in open vegetation (wet fields or grassy savannas) with significantly higher incidence of fire in more open savanna vegetation (Ramos-Neto and Pivello, 2000). High biomass production during the wet season results in abundant dry fuels favoring frequent fires throughout the year (Ramos-Neto and Pivello, 2000). Data show a positive correlation with fine fuel build-up
and both fire temperature and fire intensity (energy output) (Fidelis et al., 2010). Thus, increased wet season fuel accumulation in the cerrado increases fire intensity. Based on an ecosystems adaptation to fire it can be classified as independent, fire-sensitive, and fire-dependent (Hardey et al., 2005). In fire-independent ecosystems such as tundra and deserts, fire is rare, either because of unsuitable climate conditions or lack of biomass to burn. Fire-sensitive ecosystems such as tropical rainforests, are damaged by fire, which disrupts ecological processes that have not evolved with fire (Hardey et al., 2005). Fire-dependent systems such as the well-drained grasslands of the cerrado biome, have evolved in the presence of periodic or episodic fires and depend on fire to maintain their ecological processes (Hardey et al., 2005). Fire-dependent vegetation is fire-adapted, flammable and fire-maintained (Miranda et al., 2009; Pivello, 2011).

The study of fire and vegetation change in the cerrado is increasingly important as population, agricultural activity, and global warming create pressing management challenges to preserve these biodiverse ecosystems (Mistry, 1998). The long-term role of humans on vegetation and fire regimes of the cerrado remains unclear. During the Late Holocene (3000 cal yr BP) there is increasing evidence for the increase in Mauritia flexuosa and fire activity in Bolivia, Colombia, Venezuela and Brazil that has been attributed to both natural and anthropogenic drivers (Behling and Hooghiemstra, 1999; Berrio et al., 2007; Kahn and de Castro, 1985; Kahn, 1987, 1988; Montoya and Rull, 2011; Rull, 2009; Da Silva Meneses et al., 2013).

To investigate the drivers of vegetation and fire in the cerrado a long-term perspective is needed. The past few decades have experienced increased global temperatures, increased atmospheric CO2, and unprecedented levels of deforestation
(Malhi et al., 2002). These recent changes heavily influence modern ecological studies, thus limiting the understanding of the role of natural variability in these systems. Long-term paleoecological studies can provide baseline information on processes shaping forest-savanna fire-vegetation dynamics from centennial-to-millennial timescales (Mayle and Whitney 2012). These long-term studies can inform whether recent shifts in ecotones are the result of a minor short-term oscillation around a relatively stable ecotone or a longer-term (e.g. millennial scale) unidirectional ecotonal shift forced by climate change (Mayle et al. 2000; Mayle and Whitney 2012). Additionally, long-term paleoecological records help form realistic conservation goals and identify fire management strategies for the maintenance or restoration of a desired biological state (Willis et al., 2007).

In this study, the long-term paleoecological perspective provides a context for understanding the role of centennial to millennial climate variability in the evolution of fire and vegetation in cerrado savanna ecosystems. The purpose of this research is to explore long-term environmental change of cerrado savanna palm swamps in Bolivia from the Late Glacial (ca. 15,000 cal yr BP) to present. Paleoecological proxies including lithology, magnetic susceptibility, loss on ignition, charcoal, stable isotope, and phytolith data are used to investigate long-term ecosystem processes in the cerrado savanna. There are three primary hypotheses investigated in this study:

1. Edaphic conditions are the dominant control on the presence of savanna versus forest vegetation on the Huanchaca Mesetta.

2. Climate is the dominant control on savanna structure and floristic composition.
(3) The Late Holocene rise in *Mauritia flexuosa* was driven by climate rather than a change in human land-use.

1.1 Study Site

Noel Kempff Mercado National Park (NKMNP), a 15,230 km² biological reserve in northeastern Bolivia, is located on the Precambrian Shield near the southwestern margin of the Amazon Basin, adjacent to the Brazilian States of Rondônia and Mato Grosso (Burbridge et al., 2004). It is a UNESCO World Heritage Site, in recognition of its globally important biodiversity and largely undisturbed ecosystems, including *terra firme* (non-flooded) evergreen rainforest, riparian and seasonally-flooded humid evergreen forest, seasonally flooded savanna, wetlands, upland *cerrado* savannas, and semi-deciduous dry forests (Mayle et al., 2007). NKMNP occupies an ecotone between Amazon rainforest to the north and dry forests and savannas to the south, containing 22 plant communities (Figure 1) (Burn et al., 2010). Huanchaca Mesetta palm swamp (14°32'10.66"S, 60° 43'55.92"W, elevation: 1070 m a.s.l.) is located within NKMNP on the Huanchaca Mesetta – an 800-900 m elevation table mountain. The palm swamp is approximately 200 by 50 meters, comprised entirely of a mono-specific stand of the palm *Mauritia flexuosa*.

1.2 Climate

The climate of NKMNP is characterized by a tropical wet and dry climate (Da Silva Meneses and Bates, 2002). The mean annual precipitation at NKMNP derived from nearby weather stations (Concepción, Magdalena, San Ignacio) is ca. 1400-1500 mm per
year, with mean annual temperatures between 25° and 26° C (Hanağarth, 1993; Montes de Oca, 1982; Roche and Rocha, 1985). There is a three to five month dry season during the Southern Hemisphere winter (May to September-October), when the mean monthly precipitation is less than 30 mm (Killeen, 1990). Precipitation falls mainly during the austral summer (December to March), originating from a combination of deep-cell convective activity in the Amazon Basin from the South American Summer Monsoon (SASM) and the Intertropical Convergence Zone (ITCZ) (Vuille et al., 2012). The SASM transports Atlantic moisture into the basin and corresponds to the southern extension of the ITCZ. The ITCZ is driven by seasonal variation in insolation; thus, maximum southern hemisphere insolation and precipitation occur in the austral summer (Bush and Silman, 2004; Vuille et al., 2012). During winter (June, July, August), cold, dry polar advections from Patagonia, locally known as surazos, can cause short-term cold temperatures to frequently decrease down to 10°C for several days at a time (Latrubesse et al., 2012; Mayle and Whitney, 2012). These abrupt decreases in temperature may potentially influence the distribution of temperature-limited species on the Huanchaca Mesetta.

1.3 Geomorphology

The Huanchaca Mesetta table mountain is near the western limit of the Brazilian Shield and dominates the eastern half of NKMNP. It is composed of Precambrian sandstone and quartzite (Litherland and Power, 1989). The top of the mesetta is flat, with a gently rolling surface and at elevations ranging from 500-900 m above sea level (a.s.l.) (Da Silva Meneses and Bates, 2002). The substrate of the mesetta is rocky, and soils are
thin and low in organic material (Litherland and Power 1989). Continuity of the
 crystalline or sedimentary blocks of the mesetta is broken by an extensive network of
 peripheral or inter-mesetta depressions formed from a combination of erosion, dolerite
dike intrusions and faulting on the mesetta (Litherland and Power, 1989; Da Silva
Meneses and Bates, 2002). These depressions act as catchments for sediment and water,
resulting in sediment accumulation, which supports more complex vegetation
communities. High species diversity exhibited on the Huanchaca Mesetta, compared
with other savanna regions of South America, is attributed to the long history of isolation
of this edaphically-controlled table-mountain savanna (Mayle et al. 2007).

1.4 Vegetation

The cerrado savanna on Huanchaca Mesetta is dominated by a continuous grass
cover with sparsely scattered small trees and shrubs that grows on the thin, well-drained,
nutrient-poor soils (Killeen, 1998b). Woody species include Byrsonima coccolobifolia,
Caryocar brasiliensis, Erythroxyllum suberosum, Vochysia haenkeana, and Callisthene
fasciculata. Trees and shrubs include Qualea multiflora, Emmotum nitens, Myrcia
amazonica, Pouteria ramiflora, Diptychandra aurantiaca, Kielmeyera coriacea, Ouratea
spectabilis, and Alibertia edulis. Sub-shrubs include Eugenia puncifolia, Senna velutina,
and herbaceous species include Chamaecrista desvauxii and Borreria sp. Grass families
include the Rapataceae (C₃) (Cephalostemon microglochin), Orchidaceae (Cleistes
paranaensis) (CAM, C₄), Iridaceae (Sisyrinchium spp.) (C₄), Xyridaceae (Xyris spp.)
(C₄), and Eriocaulaceae (Eriocauleon spp., Paepalanthus spp., Syngonanthus spp.) (C₄)
(Killeen, 1998b). In the inter-fluvial depressions organic rich soil is sufficiently deep to
support humid evergreen forests islands which are typically dominated by mono-specific
stands of *Mauritia flexuosa* (Mayle and Whitney, 2012; Da Silva Meneses and Bates,
2002). *M. flexuosa* is a monocaulous, a bored palm, averaging 20–30 meters tall which
is typically associated with a low, dense understory (da Silva and Bates, 2002; Furley and
Ratter, 1988; Kahn, 1988;). *M. flexuosa* is confined to lower elevations (< ca. 1000m
elevation) in warm/wet climates (Rull and Montoya, 2014). *M. flexuosa* swamps favor
inter-fluvial depressions that remain flooded during the dry season, when the surrounding
terrains dry out (Huber, 1995a, 1995b; Kahn and de Granville, 1992). The abundance of
*M. flexuosa* in permanently flooded, poorly drained soils is the result of pneumatophores
(aerial roots) which enable its growth in anaerobic conditions (Kahn, 1988; Rull and
Montoya, 2014). Seasonal water deficits saturate the soil profile in the wet season and
desiccate soil during the dry season resulting in a dominance of herbaceous versus woody
plants surrounding the inter-fluvial depressions (Killeen, 1998b). The seasonal dryness
leads to drought, plant water stress, and frequent fire activity resulting in the development
of xeromorphic and sclerophyllous plant characteristics on the open mesetta (Killeen,
1998b). The spatial distribution of evergreen forest versus drought-tolerant savanna
vegetation is additionally constrained by edaphic conditions limiting the expansion of
forest vegetation because of the heavily weathered sandstone soils dominant outside the
inter-fluvial depressions (Killeen and Schulenberg, 1998). Limited soil development
precludes rainforest from developing on the large, rocky expanses of the mesetta (Killeen
and Schulenberg, 1998). The essentially treeless campo *cerrado* that grows around
Huanchaca Mesetta palm swamp is edaphically constrained and has likely grown on this
mesetta for millions of years (Mayle and Whitney, 2012). Thus, the vegetation of the
Huanchaca Mesetta is influenced by both climatic and non-climatic controls including seasonal hydrologic conditions, edaphic soil constraints and frequent fire activity (Killeen and Schulenberg, 1998).

2 Materials & Methods

2.1 Sediment core

A 5.48 meter-long sediment core from Huanchaca Mesetta palm swamp was collected in 1995 using a Livingstone modified square-rod piston corer from the center of the swamp. The uppermost 15 cm, containing a dense root mat, was discarded because of the presence of fibrous roots and potential for sediment mixing. Huanchaca Mesetta sediment cores were transported to the Utah Museum of Natural History for analysis. They were photographed and described using a Munsell soil color chart. Visual descriptions, including sediment type, structure, texture, and organic content were undertaken to assist interpretation of the palaeoenvironmental data.

2.2 Chronology

The chronological framework for Huanchaca Mesetta was based on eight radiocarbon dates from non-calcareous bulk sediment and wood macrofossils analyzed at the University of Georgia Center for Applied Isotope Studies (Table 1). The uncalibrated radiometric ages are given in radiocarbon years before 1950 AD (years ‘before present’, yr BP). The errors are quoted at one standard deviation and reflect both statistical and experimental errors. Radiocarbon ages were calibrated using CALIB 7.0 and the IntCal13 calibration dataset (McCormac et al., 2004). IntCal13 was selected in place of
the SHcal13 calibration curve because of the latitudinal location (14°S) of Huanchaca Meseta and the proximal hydrologic connection with the origin of the South American Monsoon in the northern hemisphere. The seasonal migration of the Intertropical
Convergence Zone (ITCZ) is thought to introduce a northern hemisphere $^{14}$C signal to the low latitude southern hemisphere (McCormac et al., 2004). This study area is located in the low latitudes (14°S) and within the range of the ITCZ migration; thus, the IntCal13 calibration curve was selected for the radiocarbon calibrations. Following calibration, the mean age value of the largest probability at 2 sigma was used to create the smoothing spline age model using classical age-depth modeling, in the package CLAM (Blaauw, 2010) within the open-source statistical software R (Figure 2).

2.3 Loss on Ignition

The variability in the organic and carbonate content of sediments is used, in conjunction with magnetic susceptibility, to identify periods of variability in sediment composition and organic content throughout the Holocene. Organic and carbonate sediment composition was determined by Loss-on-Ignition, conducted at contiguous 1 cm increments throughout the cores. For each sample, 1 cm$^3$ of sediment was dried in an oven at 100°C for 24 hours. The samples underwent a series of 2-hour burns in a muffle furnace at 550°C and 1000°C to determine the relative percentage of the sample composed of organics and carbonates. Concentration was determined by weight following Dean (1974) standard methodology.
2.4 Magnetic Susceptibility

Magnetic susceptibility (MS) was measured to identify mineralogical variation in the sediments (Nowaczyk, 2001). The MS of sediments is reflective of the relative concentration of ferromagnetic (high positive MS), paramagnetic (low positive MS), and diamagnetic (weak negative MS) minerals or materials. Typically, sediment derived from freshly eroded rock has a relatively high MS, whereas sediments that are dominated by organic debris, evaporites, or sediments that have undergone significant diagenetic alteration typically have a low or even negative MS (Reynolds, 2000). Shifts in the magnetic signature of the sediment can be diagnostic of a disturbance event (Gedye et al. 2000). Sediment cores were scanned horizontally, end to end through the ring sensor. MS was conducted at 1 cm intervals using a Barington ring sensor equipped with a 75 mm aperture.

2.5 Charcoal

Sediment samples were analyzed for charcoal pieces greater than 125 μm using a modified macroscopic sieving method (Whitlock and Larsen 2001) to reconstruct the history of local and extra-local fires. Charcoal was analyzed in contiguous 0.5 cm intervals for the entire length of the sediment core at 1 cm volume. Samples were treated with 5% potassium hydroxide in a hot water bath for 15 minutes. The residue was gently sieved through a 125 μm sieve. Macroscopic charcoal (particles >125 μm in minimum diameter) was counted in a gridded petri dish at 40× on a dissecting microscope. Non-arboreal charcoal was characterized by two morphotypes: (1) cellular 'graminoid' (thin
rectangular pieces; one cell layer thick with pores and visible vessels and cell wall
separations) and (2) fibrous (collections or bundles of this filamentous charcoal clumped
together). Arboreal charcoal was characterized by three morphotypes: (1) dark (opaque,
 thick, solid, geometric in shape, some luster, and straight edges), (2) lattice (cross-
hatched forming rectangular ladder-like structure with spaces between) and (3) branched
dendroidal, generally cylindrical with successively smaller jutting arms) (Jensen et al.,
2007; Mueller et al., 2014; Tweiten et al., 2009). Charcoal pieces were grouped into non-
arboreal and arboreal categories based on their morphology, which enabled the
characterization of fuel sources in the charcoal record (Mueller et al., 2014).

Charcoal counts were converted to charcoal concentration (number of charcoal
particles cm$^{-3}$) and charcoal accumulation rates by dividing by the deposition time (yr cm$^{-1}$
using CHAR statistical software (Higuera et al., 2009). In CHAR, charcoal data was
decomposed to identify distinct charcoal peaks based on a standard set of threshold
criteria. Low frequency variation is considered background charcoal which reflect
changes in the rate of total charcoal production, secondary charcoal transport and
sediment mixing (Higuera et al., 2007). If the charcoal data exceed that background
threshold, it is considered a peak and interpreted here as a fire episode. Background was
calculated using a 700-yr moving average.

2.6 Stable Isotopes

Stable carbon isotopes were analyzed as an additional proxy for changes in vegetation
structure and composition. Carbon isotopic composition of terrestrial organic matter is
determined primarily by the photosynthetic pathway of vegetation (Malamud-Roam et
al., 2006). Previous research on δ^{13}C values of the Huanchaca Mesetta have been used to
determine the relative proportions of C_{4} savanna grasses versus C_{3} woody vegetation
(Killeen et al., 2003; Mayle, Langstroth, Fisher, & Meir, 2007).

Sediment δ^{15}N integrates a variety of nutrient cycling processes including the loss of
inorganic N to the atmosphere through denitrification (McLaughlan et al., 2013;
Robinson, 1991). Denitrification and the subsequent enrichment of δ^{15}N requires
abundant available carbon, available nitrate, and anaerobic conditions (Seitzinger et al.,
2006). Thus, wet, anoxic soils tend to have enriched values of δ^{15}N. Environmental
conditions that alter from wet (anaerobic) to dry (aerobic) conditions also enrich δ^{15}N
values (Codron et al., 2005). During dry periods, denitrification is shut off because of an
increase in available oxygen in sediments, thus δ^{15}N values decrease. If dry soils become
hydrated, there is a preferential loss of ^{14}N, enriching δ^{15}N values (Codron et al., 2005).

Stable isotope analysis was conducted at 3-cm resolution for total carbon (C) and
nitrogen (N) throughout the length of the sediment core. One cm^{3} of bulk sediment was
dried, powdered, and treated with 0.5 molar hydrochloric acid to remove carbonates. A
range of 1-25mg of the dried carbonate-free sediment was weighed into tin capsules
depending on organic matter content. The samples were analyzed on a Finnigan Delta
dual inlet elemental analyzer at the Sirfer Lab at the University of Utah. ^{13}C/^{12}C and
^{15}N/^{14}N ratios are presented in delta (δ) notation, in per mil (^{δ}_{(oo)} relative to the PDB and
N_{2} air standards) (Codron et al. 2005).

2.7 Phytoliths
Phytoliths preserve well in sediment records and are especially useful in areas with intermittent dry periods. Phytoliths were used as a proxy to reconstruct past vegetation composition and are especially useful in the lower taxonomic identification of grasses (Piperno and Pearsall, 1998). Grass phytoliths can provide important paleoecological information. Tropical C₄ grasses, adapted to open environments with high seasonality of rainfall, typically expand at the expense of C₃ grasses and other tropical forest species during drier intervals (Hartley and Slater, 1960; Hartley, 1958a, 1958b; Piperno, 1997). C₄ Panicoideae grasses are generally adapted to warm moist conditions, whereas C₄ Chloride grasses are adapted to warm, dry conditions (Hartley and Slater, 1960). C₃ subfamilies, including the Pooidae, are adapted to cool and moist conditions, are currently confined to temperate climates with lower temperatures (Hartley, 1961, 1973; Iriarte, 2006). The presence of C₃ Pooidae grasses from phytolith data from southeastern Pampa grasslands in Uruguay have been interpreted to indicate a shorter dry season with overall conditions that were cooler than during the Holocene (Iriarte, 2006). Phytolith samples were taken every 4 cm. The extraction and slide preparation of phytoliths were conducted at the University of Exeter, UK, following standard procedures described by Piperno (2005). Slides were scanned and counted at the University of Utah Paleoenecology Lab using a Leica EMED compound light microscope (400-1000x). The number of phytoliths counted varied from 101-320 per slide. The modern palm swamp is a monospecific stand of *Mauritia flexuosa* that produces globular echinate phytoliths but does not produce hat-shaped phytoliths characteristic of other Areceae (Piperno, 2005). Although other palms produce globular echinate phytoliths, the current monospecific stand supports the identification of globular echinate phytoliths as belonging to this palm.
Given the abundance of *Mauritia flexuosa* during the Middle and Late Holocene, phytolith percentages from globular echinate phytoliths were calculated using a separate sum. Percentages of non-*Mauritia* phytoliths were calculated on the basis of the total sum of phytoliths. Phytolith identification was made by comparison with modern plant reference collections curated at the University of Exeter Archaeobotany Lab. The classification of Poaceae implemented a three-partite morphological classification related to grass taxonomy (Panicoideae-Chloridoideae-Pooideae) (Twiss et al., 1969) and further developed in both North America (Fredlund and Tieszen, 1994) and the Neotropics (Bertoli de Pomar, 1971; Iriarte and Paz, 2009; Iriarte, 2003; Piperno and Pearsall, 1998; Piperno, 2005; Sendulsky and Labouriau, 1966; Söndahl and Labouriau, 1970; Teixeira da Silva and Labouriau, 1970; Zucol, 1999, 2000, 1996, 1998). The phytolith percentage diagrams were plotted using Tilia and Tilia Graphing software (Grinn, 1987).

3 Results

Four distinct vegetation types were identified based on constrained cluster analysis (CCA) of phytolith assemblages. These four zones are: the Late Glacial (14,500-11,500 cal yr B.P.), the Early Holocene (11,500-9,000 cal yr B.P.), the Middle Holocene (8,000-3,500 cal yr B.P.), and the Late Holocene (3,500 cal yr B.P. to present).

3.1 Zone 1: 14,500-11,500 cal yr B.P. Late glacial

The Late Glacial vegetation on Huanchaca Meseta was dominated by arboreal taxa, grasses and Asteraceae (Opaque Perforated platelets) phytoliths (Figure 3). The phytolith
assemblage likely contains both in-situ vegetation production and wind-blow vegetation from the surrounding rocky savanna. Both C₄ Panicoideae and C₃ Pooideae grass phytoliths were present during the Late Glacial. The presence of C₃ Pooideae grasses is interpreted as cooler Late Glacial conditions compared to present. The Late Glacial vegetation community at Huanchaca Mesetta lacks a modern analogue plant community in NKMNP. The presence of both of C₁ Pooideae and C₄ Panicoideae grasses suggest some degree of landscape heterogeneity. A consistent layer of very dark sandy silt dominated the lithology of Huanchaca Mesetta during the Late Glacial. The magnetic susceptibility and bulk density values were low and exhibit minimum variability compared to the rest of the record (Figure 4). Coupled with LOI organic values below 10%, the sediment lithology was summarized as a low-energy depositional environment with relatively low nutrient input. Organic matter deposited during the Late Glacial had δ¹³C values of -16% (Figure 5), indicating a contribution of C₄ grasses to organic matter composition. The proportion of C₁ to C₄ grass contribution was calculated by using values of C₁ and C₄ grasses and a simple two-pool mixing model as described by Perdue and Koprivnjak (2007) with end member values of -27% for C₁ and -12% for C₄ plants (Figure 7). The contribution of C₄ vegetation was ca. 80%, higher than any other time in the Huanchaca record. Modern δ¹³C values in the basin range from -18 to -22‰. The location of these C₄ drought adapted grasses was likely the surrounding plateau. Organic carbon concentrations gradually increased from 1% to 4% during the Late Glacial, indicating relatively low amounts of organic matter in the system compared to those of today. The C:N ratio ranged from 20 to 30, indicating a terrestrial organic matter source. N concentrations were low from 0.1 to 0.2% and the δ¹⁵N values were ca. 5‰ indicating
minimal denitrification during the Late Glacial. The $\delta^{13}C$, % C$_4$ contribution, and high
C:N values coupled with the phytolith data dominated by trees and grasses, suggest a
predominantly terrestrial signal, characterized by an open savanna grassland during the
Late Glacial. The $\delta^{15}N$ values suggest that sediments within the swamp were drier than
present creating aerobic conditions and low denitrification rates.

Charcoal accumulation levels were low during the Late Glacial (14,500-12,000 cal yr
B.P.). Fire return interval (FRI) was 2 fire episodes per 1000 years (Figure 6). Based on
the 0.5 cm sampling resolution of this record, fire “episodes” were interpreted as periods
of increased fire activity rather than isolated fire “event”. The charcoal signature was
consistent with frequent, low intensity fires that likely occurred in the open, grass
dominated mesetra surrounding the basin. Low charcoal accumulation levels coupled
with low magnitude charcoal peaks, suggest that the non-analogue vegetation structure of
C$_3$ Pooidae, C$_4$ Panicoideae, and arboreal phytoliths likely created a fuel structure that
lacked sufficient density or fuel connectivity to produce abundant arboreal or grass
charcoal. Low charcoal accumulation coupled with low fire frequency suggest that the
Late Glacial environment was likely fire-sensitive within the basin.

3.2 Zone 2: 11,500-9,000 cal yr B.P., Early Holocene

Decreased C$_4$ Panicoideae grasses and consistent C$_3$ Pooidae grasses, arboreal, and
Asteraceae (Opaque perforated platelets) phytoliths dominated the assemblage. The
presence of C$_3$ grasses, and the absence of M. flexuosa, the dominant component of the
modern basin vegetation, suggest temperatures cooler than present. The lithology,
magnetic susceptibility, bulk density, and LOI values indicate minimal shift during the
vegetation transition. Organic geochemistry reflected a change in organic matter source,
with $\delta^{13}C$ values becoming more negative, indicating an increase in the contribution of $C_3$
vegetation ca. 11,000 cal yr B.P. The $\delta^{13}C$ contribution of $C_4$ grasses decreased
dramatically from 60 to 20% during this period. These data correspond to a decrease in
$C_4$ Panicoideae grass phytoliths and an increase in arboreal phytoliths. Low levels of
terrestrial organic input into the system were indicated by low carbon concentrations and
C:N values ranging between 25 and 30. N cycling changed during this zone, with $\delta^{15}N$
values exhibiting greater amplitude and higher frequency variability. The $\delta^{15}N$ values
ranged between 4 and 8‰ indicating increased variability in cembrification rates
associated with increasing wet (anaerobic) to dry (aerobic) conditions. The N
concentrations were low, between 0.05 and 0.01%, indicating minimal nitrogen
availability in the system.

Charcoal accumulation at Huanchaca Mesetta increased ca. 11,200 cal yr B.P. coupled
with an increase in the fire frequency to 5 episodes (periods of increased burning) per
1000 years. The peak magnitude values indicated two substantial fire episodes (periods of
increased burning) ca. 10,200 and 9,100 cal yr B.P. The lack of significant change in the
lithology suggests that taphonomic conditions were consistent during this interval. The
increase in grass phytoliths during this period coupled with the increase in charcoal
accumulation and fire episodes suggest that the Early Holocene vegetation community
was becoming increasingly more fire dependent and vegetation was likely adapting to the
increase in fire frequency associated with the period.
3.3 Zone 3: 8,000-3,750 cal yr B.P., Middle Holocene

Significant vegetation changes occur through the Middle Holocene. From 8,000 to 5,800 cal yr B.P., C₄ Panicoideae (warm/wet) grasses were at the lowest values in the record. C₃ Pooidaeae (cold/wet) grasses diminished after ca. 7,000 cal yr B.P. and remain absent for the remainder of the record. Arboreal phytoliths reached the highest levels in the record at 8,000 cal yr B.P., followed by a slight decline to 3,500 cal yr B.P. δ¹³C values ranged between -24 and -22‰ from 7,000 cal yr B.P. to 5,100 cal yr B.P. These values corresponded to a diminished C₄ contribution to organic matter (approximately 18%). Decreased C₄ grass phytoliths from 8,000 to 5,000 cal yr B.P. was interpreted as a decrease in vegetation density in the open mesetts surrounding the basin caused by drying conditions on the mesetts. After 5,000 cal yr B.P., C₄ Panicoideae grasses and C₃ Chloride (warm/dry) grasses gradually increased in the surrounding watershed, coupled increased δ¹³C values to -19‰. *Mauritia flexuosa* phytoliths first appeared at 5,000 cal yr B.P., and gradually increased to modern levels by 3,750 cal yr B.P. The δ¹³C values decreased, potentially associated with the development of the C₃ *M. flexuosa* community. A dark-brown clay-sand mixture from 8,000 to 3,750 cal yr B.P. dominated the lithology that transitioned to black detrital peat ca. 3,750 cal yr B.P. associated with the establishment of *M. flexuosa*. After 4,000 cal yr B.P. LOI, magnetic susceptibility, and C:N values increased, indicating increased organic material. Nitrogen cycling continued to fluctuate throughout this period. δ¹⁵N values exhibited the greatest frequency and amplitude of variability from 8,000 to 3,750 cal yr B.P. ranging from 2 to 12‰ indicating repeated and extensive dry periods on the mesetts.
Increased charcoal accumulation ca. 8,000 cal yr B.P. was followed by an abrupt decrease to the lowest values during the record from ca. 7,900 to ca. 3,800 cal yr B.P. Peak frequency reached the highest levels of 6 fire episodes (periods of increased burning) per 1000 yrs during the Middle Holocene. These data corresponded to the highest levels of $\delta^{15}$N values indicating extended dry periods that likely promoted frequent fires on the mesetta. The first evidence of grass charcoal appeared ca. 6,500 cal yr B.P. suggesting a change in the fire ecology on the mesetta. From 5,000 to 3,750 cal yr B.P., grass charcoal increased. This is coincident with the establishment of *M. flexuosa* palm swamp and increased C$_4$ grasses in the surrounding watershed. After 3,900 cal yr B.P., charcoal accumulation and fire frequency increased. Significant increases in grass charcoal reflected a change in the fuel composition in the watershed. Phytolith, isotope and charcoal data suggest that after 3,900 cal yr B.P., the *M. flexuosa* within the basin became increasingly fire-sensitive and the occurrence of a fire within the palm stand would have had consequences for the vegetation not adapted to fire. The fire adapted C$_4$ grass dominated watershed continued to be fire-dependent.

3.4 Zone 4: 2,800 cal yr B.P.- Present: Late Holocene

During the Late Holocene arboreal taxa was replaced by a pure stand of *M. flexuosa*. C$_4$ Panicoideae (warm, wet) grasses continued to dominate the surrounding watershed. *Mauritia flexuosa* values reached the highest levels during the Holocene from 2,000-1,200 cal yr B.P. The hat shaped phytoliths indicate very low concentrations of other
palms during this time. There was a gradual decrease in *M. flexuosa* towards present
coupled with the highest levels of C₄ Panicoideae grasses ca. 200 cal yr B.P. and a
decrease in C₄ Chloridoideae (warm, dry) grasses in the surrounding watershed. The
lithology consisted of black detrital peat ca. 2450–2050 cal yr B.P. associated with high
LOI (ca. 22%) and magnetic susceptibility values (ca. 1000). After 2,500 cal yr B.P. the
%C, %N, and δ¹⁵N increased suggesting moist, anoxic conditions that enabled moderate
denitrification from the swamp. These lithologic and isotopic data represented the
establishment of modern palm swamp characterized by increased autochthonous organic
accumulation. The δ¹³C values reached modern levels by 2,800 cal yr B.P. although,
values exhibit increased variability, fluctuating between -19 and -24‰ co-varying with
the C₄ grass contribution between 10-20%. After ca. 800 cal yr B.P. δ¹³C values were ca.
-18‰ and the % C₄ contribution was ca. 50%. These data corresponded to the highest
levels of C₄ Panicoideae grass phytoliths in the record. The dark detrital peat lithology
was interrupted by two coarse sand layers ca. 1550 cal yr B.P. and ca. 300-200 cal yr
B.P., followed by a shift back to black detrital peat ca. 200 cal yr B.P. to present. These
sand layers were characterized by a decrease in LOI from ca. 22 to 2, C:N ratios from ca.
25 to 0, and δ¹⁵N from ca. 5 to 0‰ coupled with increased magnetic susceptibility and
bulk density values suggesting clastic flood events associated with sandy sediments low
in organic material. From 300 cal yr B.P. %C values increased from ca. 1% to >20%
reached the highest values in the record. The %N values increased from ca. 0.1 to the peak
Holocene values of 1.2 [faint at present. The dramatic increases in both %C and %N were
likely the result of in situ carbon cycling and nitrogen fixation.

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Charcoal accumulation at Huanchaca Mesetta remained low 2,800 to 1,800 cal yr B.P. with a FRI of 5 episodes (periods of increased burning) per 1000 yrs from 2,800 to 1,800 cal yr B.P. Grass charcoal reached the highest continuous levels ca. 2,800 to 2,000 corresponding to high levels of fire adapted C₄ grass phytoliths. Increased grass charcoal coupled with low peak magnitude values and high fire frequency indicated that the vegetation surrounding the palm swamp was fire dependent and fire adapted. However within the moist M. flexuosa palm stand, the vegetation remained fire sensitive. Charcoal accumulation increased ca. 1,400 to 1,200 cal yr B.P. and 700 cal yr B.P., and reached peak Holocene values ca. 500-400 cal yr B.P. Increased charcoal was coupled with the lowest FRI values in the record. Peak magnitude increased significantly around 1,200 cal yr B.P. and the largest peak magnitude values ca. 200 cal yr B.P. These charcoal values were cropped for plotting and visualization purposes. Raw counts exceed 1,200 thus the values are also provided as log transformed (Figure 7). Peak frequency increased after ca. 400 cal yr B.P. to ca. 4 fire episodes (periods of increased burning) per 1000 yrs towards present. There was a decrease in grass charcoal indicating increased woody biomass burned. The increased charcoal accumulation coupled with low FRI and more woody charcoal was interpreted as fire episodes that infrequently penetrated the fire sensitive palm stand and burned the M. flexuosa woody biomass. The charcoal, phytolith, and isotope data collectively suggest that the vegetation surrounding the palm swamp was fire dependent and fire adapted while the vegetation within the palm swamp was fire sensitive.

4 Discussion
4.1 First Order Control: Edaphic Constraints

Modern vegetation distribution of cerrado savannas are largely related to edaphic factors (Colgan et al., 2012; Killeen, 1998a). Since the Late Glacial, the vegetation, soil geochemistry and fire history indicate edaphic constraints were the first order of control on vegetation on Huanchaca Mesetta. Despite significant climate variability since the Late Glacial, the open savanna surrounding the basin was continuously dominated by fire adapted C4 grasses. Within the basin, soil was sufficiently thick to support more complex vegetation communities that exhibited greater response to climate variability through time. On the highly weathered quartzite plateau however, vegetation was limited to drought and fire tolerant C4 grasses as indicated by the continued presence of C4 Panicoideae grass phytoliths that co-varied with the δ13C values.

The first hypothesis, that edaphic conditions are the dominant control of vegetation on the plateau, was supported. Irrespective of changes in temperature, precipitation, and fire activity, savanna vegetation has been present on the mesetta for the past 14,500 years. Edaphic conditions on the open rocky plateau have limited vegetation to C4 drought adapted grasses. Arboreal and palm vegetation was limited to the interfluvial depression basins where soil was sufficiently deep to support more complex vegetation communities.

4.2 Second Order Control: Climatological Drivers

4.2.1 Late Glacial Surazo Winds and Mauritia flexuosa
Non-analogue Late Glacial vegetation communities are documented from low
elevation sites including Laguna Chaplin (14° 28'S, 61° 04'W approximately 40 km west)
and Laguna Bella Vista (13°, 37'S, 61°, 33W, 140 km northwest). The absence of
*Anadenanthera*, a key indicator in deciduous and semi-deciduous dry forests was
interpreted as reduced precipitation (e.g. longer and/or more severe dry season), increased
aridity and lowered atmospheric CO₂ concentrations. These conditions favored C₄
grasses, sedges and drought adapted savanna and dry forest tree species (Burbridge et al.,
2004). Similarly, the non-analogue Late Glacial vegetation community at Huanchaca
Meseta is notable for the absence of *M. flexuosa*. *Mauritia flexuosa* can tolerate a broad
precipitation gradient ranging from 1500 mm to 3500 mm annually in areas with annual
temperature averages above 21°C, roughly coinciding with the 1000 masl contour line
(Rull and Montoya, 2014). *M. flexuosa* is dependent on local hydrology including water
table depth and flooded conditions (Kahn, 1987). The presence of *M. flexuosa* in the
lowland records at Laguna Chaplin and Laguna Bella Vista (ca. 200 masl) during the
Late Glacial (Burbridge et al., 2004), indicate conditions were sufficiently warm and with
a locally wet habitat below the mesetta to support the palms despite an estimated 20%
decrease in precipitation (Mayle et al., 2004; Punyasena, 2008). Temperature was thus,
likely a limiting factor for the establishment of *M. flexuosa* on the mesetta. However,
temperature reconstructions of Late Glacial conditions from Laguna La Gaiba, (ca. 500
km SE of Huanchaca Mesetta), indicate temperatures reached modern conditions (ca. 25
to 26.5°C) around 15,900 cal yr B.P. and have remained relatively stable to present
(Whitney et al., 2011). However, previous studies have suggested the increased
frequency of *surcus* winds (Bush and Silman, 2004). An ice cap located on the
Patagonian Andes generated an anomalously high pressure center in northwestern Patagonia resulting in increased *surazo* cold fronts blowing cold, dry, southerly winds northward penetrating the NKMNP region (Iriondo and Garcia, 1993; Latrubesse and Ramonell, 1994). The *surazos* may have been no more intense than those of present, but likely occurred more often and lasted more of the year (Bush and Silman, 2004). Increased frequency of *surazos* would have had little effect on the absolute temperature minima but the mean monthly and annual temperature minima may have been ca. 5°C lower (Bush & Silman, 2004). Based on a lapse rate of 6.4°C/km (Glickman, 2000), the 400 m difference between the lowland sites (Laguna Chaplin and Laguna Bella Vista, ca. 250 m a.s.l.) and Huanchaca Mesetta (ca. 650-800 m a.s.l.) could have resulted in up to ca. 2.6°C difference in average annual temperatures. Despite near modern annual temperatures ca.15,900 cal yr B.P., the elevational lapse rate coupled with lower mean monthly and annual temperature minima accompanying more frequent *surazos*, likely resulted in climatic conditions below the thermal optimum of 21°C for *M. flexuosa* (Rull and Montoya, 2014). Thus, during the Late Glacial, increased frequency of *surazos* likely resulted in increased biological stress on the vegetation community at Huanchaca Mesetta resulting in vegetation dominated by trees and grasses opposed to *M. flexuosa*.

4.2.2 Holocene Precipitation and Fuel Moisture and Fuel Availability

During the Middle Holocene the presence of dry forest taxa and increased charcoal accumulation at Laguna Chaplin and Laguna Bella Vista indicate a combination of seasonally flooded savannas and semi-deciduous dry forests (Mayle et al., 2004). At Laguna Oricore (13°20'44.02"S, 63°31'31.86"W, 335 km NW), peaks in drought tolerant
tree taxa, coupled with maximum charcoal concentrations indicate drier and regionally
more open vegetation (Carson et al., 2014). Laguna Granja (13°15'44" S, 63°, 42' 37'" W)
350 km NW was also characterized by open savanna vegetation. These data suggest lower
mean annual precipitation (<150 cm) and a longer dry season (>5 months with <100 cm)
during the Middle Holocene (Burbridge et al., 2004; Mayle et al., 2000). Additionally,
water levels at Lake Titicaca were ca. 100 m below present (Figure 7) attributed to
precipitation levels ca. 40% below present (Baker et al., 2001; Cross et al., 2000;
D’Agostino et al., 2002). The spatial extent of the Middle Holocene dry period suggests a
common mechanism affecting Amazonian moisture and precipitation. During this period,
weakened SASM convective activity was attributed to an orbitally-driven minimum in
January insolation at 15-10°S (Berger and Loutre, 1991). Reduced insolation would have
restricted the southerly penetration of the ITCZ and deep cell convective activity over the
Amazon Basin, thus decreasing the length of the summer rainy season resulting in longer,
more severe dry seasons (Berger and Loutre, 1991).

The discrepancy in increased fire activity in the lowlands sites and decreased fire
activity on the mesetta is attributed to fuel connectivity. In the lowland sites of Laguna
Bella Vista, Laguna Chapin, and Laguna Oricore, dry forest-savanna vegetation provided
sufficient fuel and increased fire activity during the Middle Holocene. At Huanchaca
Mesetta decreased available moisture limited vegetation growth and fuel availability,
particularly in the edaphically constrained rocky mesetta surrounding the basin. The lack
of fine C4 grass connective fuels resulted in decreased burning on the mesetta.

In the Late Holocene (3,550 cal yr B.P. to present) the pollen assemblages of Laguna
Bella Vista, Laguna Chaplin and Laguna Oricore, indicate an expansion of humid
evergreen closed-canopy rainforest vegetation coupled with significant decreases in charcoal concentrations (Burbridge et al., 2004; Burn et al., 2010; Carson et al., 2014). Additionally, Lake Titicaca reach modern water levels during this time (Rowe et al., 2003) indicating wetter regional conditions with less severe dry seasons. The rainforest–savanna ecotone is currently at its most southerly extent over at least the last 50,000 years (Mayle et al. 2000; Mayle and Whitney, 2012; Burbridge et al. et al., 2004). The progressive succession through the Holocene in the lowlands of NKMNP from savanna/semi-deciduous forest to semi-deciduous/evergreen forest to evergreen rainforest is part of a long-term uni-directional trend of climate-driven rainforest expansion associated with the regional increase in precipitation associated with a stronger [Southern American Summer Monsoon] (Mayle et al., 2004). The basin wide increase in mean annual precipitation and reduction in the length/severity of the dry season is attributed to increasing summer insolation at 10-15°S driven by the Milankovitch precessional forcing (Mayle and Whitney, 2012). The wet conditions of the Late Holocene created ideal waterlogged conditions for the establishment of the *M. flexuosa* palm swamp in the drainage basin.

The asynchrony of charcoal records between the low elevation sites and Huanchaca Mesetta is attributed to fuel flammability. Increased precipitation led to different effects on fire frequency, with decreases in the lowlands and increases on Huanchaca Mesetta. Increased precipitation in the low elevation closed canopy rainforests decreased fuel flammability along with fire activity. Whereas increased precipitation resulted in the build up of fire-adapted C₄ grasses on the surrounding plateau. Lightning-caused fire is common in *cerrado* savannas today and highest in more open savanna ecosystems, such
as the Huanchaca Mesetta (Ramos-Neto and Pivello, 2000). Increased precipitation would have been accompanied by increased incidence of lightning-caused fire, fueled by the abundance of fire adapted grass fuels in the surrounding watershed.

The second hypothesis, that climate was the dominant control on savanna vegetation structure and floristic composition was supported by the vegetation and fire data. Since the Late Glacial, climate change has coincided with both the vegetation composition and fire regimes on the plateau. The asynchrony in response to regional climate forcing at Huanchaca Mesetta and the low elevation sites emphasize the need to obtain more paleorecords across an elevational gradient to determine the effects of climate variability across heterogeneous ecosystems.

4.3 Human versus Natural Drivers on the Evolution of Mauritia Flexuosa

The development of *M. flexuosa* swamps and increases in charcoal accumulation have been seen in numerous paleoecological records from savanna ecosystems in Colombia (Behling and Hooghiemstra, 1998, 1999; Berrio et al., 2002b, 2007), Venezuela (Montoya et al., 2011b; Rull and Montoya, 2014; Rull, 1999, 2009) and Brazil (Da Silva Meneses et al., 2013). Previously two hypotheses have been proposed to account for the Late Holocene development of these *M. flexuosa* palm swamps. The first hypothesis suggests that the increase in *M. flexuosa* and charcoal accumulation is attributed to increased precipitation and wet season lightning fires driven by strengthened SASM activity (Kahn and de Castro, 1985; Kahn and de Granville, 1992; Kahn, 1987). The second hypothesis suggests that the simultaneous rise in *M. flexuosa* and charcoal was linked to intentional planting or semi-domestication of *M. flexuosa* for human use (Behling and Hooghiemstra, 1998, 1999; Montoya et al., 2011a; Rull and Montoya,
2014). Currently there is insufficient archaeological evidence from any of these savanna sites to support a robust anthropogenic signal (Rull and Montoya, 2014). Previous paleoecological studies in the lowlands demonstrate humans were the dominant driver of local-scale forest-savanna ecotonal change in those areas (e.g. Bolivian Llanos de Moxos) dominated by complex earth-moving pre-Columbian cultures (Carson et al., 2014; Whitney et al., 2014). These studies suggest that even in areas with extensive geometric earthworks, inhabitants likely exploited naturally open savanna landscapes that they maintained around their settlement, rather than practicing labor-intensive deforestation of dense rainforest (Carson et al., 2014). Evidence for human occupation of the lowlands has been found with ceramics from soil pits in an interfluve ca. 25 km northwest of Laguna Chaplin and abundant ceramics and charcoal dating to ca. 470 cal yr B.P. recovered from anthosols (terra preta) throughout La Chonta ca. 50 km west of NKMNP (Burbridge et al., 2004). Implementing a new methodology to concentrate and isolate cultigen pollen (Whitney et al., 2012), the re-analysis of pollen data from Laguna Bella Vista and Laguna Chaplin revealed Zea mays pollen was present around 1700 to 940 cal yr B.P., approximately 2000 years after the initial increase in M. flexuosa at these sites (B. Whitney personal communication, July 22, 2014). Although humans were present in NKMNP, there is no evidence that they drove regionally significant ecotonal changes in forest-savanna boundaries. The patterns of forest-savanna shifts exhibited at these sites are consistent with climate forcing (Burbridge et al., 2004). The absence of archaeological data on Huanchaca Mesetta dominated by nutrient poor, rocky soil, that would have been infertile for the practice of agriculture coupled with the limited access to the mesetta would have made human habitation unlikely. Although the M. flexuosa
swamps may have been used for hunting and gathering purposes, these data do not suggest humans were the driving mechanism behind the initial establishment or proliferation of *M. flexuosa* in the interfluvial depressions of the Mesetta.

The comparison of the Huanchaca Mesetta record to previous studies coupled with the absence of archaeological remains on the mesetta support the third hypothesis, that expansion of *M. flexuosa* at this site was largely controlled by natural drivers (edaphic, climate, lightning caused fires) opposed to anthropogenic drivers. In contrast to the conclusions from other studies, this record provides no evidence for an anthropogenically-driven fire regime, deforestation, soil erosion, or cultivation on the mesetta. These data suggest that natural drivers control the continued presence of savanna vegetation and fire activity on the Huanchaca Mesetta for the past 14,500 years.

5.0 Implications for Savanna Ecology and Conservation

The presence of savanna vegetation for the past 14,500 years at Huanchaca Mesetta has significant implications for understanding modern savanna ecology and for the implementation of conservation strategies in the 21st century. Previous research on the evolution and development of savanna ecosystems has attributed much of the development of savannas to anthropogenic origins driven by the intentional use of fire (Arroyo-Kalin, 2012; Behling and Hooghiemstra, 1999; Behling, 2002; Berrio et al., 2002a; Hooghiemstra et al., 1998; Ramos-Neto and Pivello, 2000; Rull and Montoya, 2014). The results from this study demonstrate that the continued presence of the savanna
ecosystem at Huanchaca Mesetta is attributable to edaphic and climatic controls. The
presence of fire in this system for the past 14,500 years indicates that naturally occurring,
lightning-caused fire is an integral part of the ecology of the savanna ecosystem. Despite
changes in floristic composition and tree density within the drainage basin, the savanna
ecosystem has been resilient to major climatic changes in both temperature and
precipitation since the Late Glacial period. These data suggest that savanna ecosystems
will continue to be resilient to future climate change associated with global warming.
The long history of ecosystem stability in the face of dramatic climate variability attests
to the fact that the Huanchaca Mesetta savanna is one of the most floristically diverse
savannas anywhere in the Neotropics (Da Silva Meneses and Bates, 2002). The continued
protection of the Huanchaca Mesetta savanna as a UNESCO world heritage site, coupled
with the savannas natural resilience to climatic change exhibited over at least the past
14,500 years, indicates that despite significant global warming projected for the 21st
century (IPCC, 2014), the future is optimistic for the conservation and preservation of
biological diversity in the Huanchaca Mesetta savanna ecosystem.

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References


Montes de Oca, I.: Geografía y recursos naturales de Bolivia, La Paz, Boliv., 1982.


# Tables and Figures

Table 1 AMS Radiocarbon Dates from Huanchaca Mesetta

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<tr>
<th>Lab Number</th>
<th>Material</th>
<th>Depth (cm)</th>
<th>¹⁴C age (yr BP)</th>
<th>δ¹³C Ratio</th>
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