Effects of past climate variability on fire and vegetation in the *cerrãdo* savanna of the Huanchaca Mesetta, NE Bolivia

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Abstract

Cerrãdo 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 projected to increase by ~3 ºC 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 Mesetta, a palm swamp located in the *cerrãdo* savanna in northeastern Bolivia, was analyzed with phytoliths, stable isotopes and charcoal. A non-analogue, cold-adapted vegetation community dominated the Lateglacial-early Holocene period (14,500-9000 ka), that included trees and C_3 Pooideae and C_4 Panicoideae grasses. The Lateglacial 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 C_4 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 5000 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* (cold wind incursions from Patagonia) 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 *cerrãdo* savanna ecosystem of the Huanchaca Plateau has exhibited ecosystem resilience to major climatic changes in both temperature and precipitation since the Lateglacial period.

1. Introduction

The *cerrãdo* savanna of central South America is the largest, richest, and likely most threatened savanna in the world (DaSilva Meneses and Bates, 2002) The *cerrãdo* is the second largest biome in South America covering 1.86 million km^2 and is home to over 10,000 plant species (Myers et al., 2000). The tropical forest-savanna ecotones within the *cerrãdo* biome are of considerable interest to biologists because of their high habitat heterogeneity (*beta* diversity), importance in rainforest speciation (Russell-Smith et al., 1997) and sensitivity to climate change (IPCC, 2014). According to current estimates however, only 20% of the *cerrãdo* remains undisturbed and only 1.2% of the area is preserved in protected areas (Mittermeier et al., 1999). Additionally, *cerrãdo* savannas have a significant role in the modern global carbon cycle because of high CO_2 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 *cerrãdo* biome comprises forest, savanna, and campestre (open field) formations (Abreu et al., 2012; Mistry, 1998). *Cerrãdo* sensu stricto is characterized as a woody savanna formation composed of dense, thin, and rocky outcrops with *cerrãdo* 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 *cerrãdo* vegetation types are largely related to edaphic factors (Colgan et al., 2012). For example the distribution of major *cerrãdo* vegetation types are closely related to the geomorphology of the Precambrian Brazilian shield in South America (Killeen, 1998a). The development of the variety of *cerrãdo* 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 *cerrãdo* savanna vegetation structure and fire activity (Ribeiro and Walter, 2008). The *cerrãdo* biome is dominated by a warm, wet-dry climate associated with the seasonal migration of the Intertropical Convergence Zone (ITCZ) (DaSilva Meneses and Bates, 2002; Latrubesse et al., 2012; 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 *cerrãdo*, 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 *cerrãdo* (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 *cerrãdo* increases fire intensity. Based on an ecosystems adaptation to fire it can be classified as independent, fire-sensitive, and fire-dependent (Hardesty 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 (Hardesty et al., 2005). Fire-dependent systems such as the well-drained grasslands of the *cerrãdo* biome, have evolved in the presence of periodic or episodic fires and depend on fire to maintain their ecological processes (Hardesty 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 *cerrãdo* 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 *cerrãdo* remains unclear. During the late Holocene (3000 cal yr BP) there is increasing evidence for the increase in *Mauritia flexuosa (M. 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., 2002a; DaSilva Meneses et al., 2013; Kahn and de Castro, 1985; Kahn, 1987, 1988; Montoya and Rull, 2011; Rull, 2009).

To investigate the drivers of vegetation and fire in the *cerrãdo* a long-term perspective is needed. The past few decades have experienced increased global temperatures, increased atmospheric CO_2, 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 *cerrãdo* savanna ecosystems. The purpose of this research is to explore long-term environmental change of *cerrãdo* savanna palm swamps in Bolivia from the Lateglacial (ca. 15,000 cal yr BP) to present. Paleoecological proxies including lithology, magnetic susceptibility, loss on ignition (LOI), charcoal, stable isotope, and phytolith data are used to investigate long-term ecosystem processes in the *cerrãdo* 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 *M. 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 km^2 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 *cerrãdo* 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 (14º32'10.66"S, 60º 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 *M. flexuosa*.

1.2 Climate

The climate of NKMNP is characterized by a tropical wet and dry climate (DaSilva Meneses and Bates, 2002). The mean annual precipitation at NKMNP derived form nearby weather stations (Concepción, Magdalena, San Ignacio) is ca. 1400-1500 mm per year, with mean annual temperatures between 25 and 26 ºC (Hanagarth, 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 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 ºC 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.) (DaSilva 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 (DaSilva Meneses and Bates, 2002; Litherland and Power, 1989). 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 *cerrãdo* 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, Erythroxylum suberosum, Vochysia haenkeana,* and *Callisthene fasciculate.* Trees and shrubs include *Qualea multiflora, Emmotum nitens, Myrcia amazonica, Pouteria ramiflora, Diptychandra aurantiaca, Kielmeyera coriacea, Ouratea spectabilis,* and *Alibertia edulis.* Small-shrubs include *Eugenia puncifolia, Senna velutina,* and herbaceous species include *Chamaecrista desvauxii,* and *Borreria sp.* Monocot families include the Rapateaceae (C_3) (*Cephalostemon microglochin),* Orchidaceae *(Cleistes paranaensis)* (CAM*,* C_3), Iridaceae *(Sisyrinchium* spp.) (C_4), Xyridaceae *(Xyris* spp.) (C_4), and Eriocaulaceae *(Eriocaulon* spp., *Paepalanthus* spp*., Syngonanthus* spp.) (C_4) (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 *M. flexuosa* (DaSilva Meneses and Bates, 2002; Mayle and Whitney, 2012). *M. flexuosa* is a monocaulous, aborescent 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. 1000 m 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 *cerrãdo* 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 m-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 accelerator mass spectrometry (AMS) 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). Radiocarbon ages were calibrated using CALIB 7.0 and the IntCal13 calibration dataset (Reimer et al., 2013). IntCal13 was selected in place of the SHcal13 calibration curve because of the latitudinal location (14°S) of Huanchaca Mesetta and the proximal hydrologic connection with the origin of the South American Monsoon in the northern hemisphere. The seasonal migration of the 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 calibrated years before present (cal yr BP) of the largest probability at 2 sigma standard deviation was used to reflect both statistical and experimental errors) (grey bars in Figure 2). These mean ages were 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.

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 (LOI), 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 standard methodology (Dean Jr, 1974).

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 et al., 2001). 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^3 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 influx (number of charcoal particles cm^{-3}) and charcoal influx rates by dividing by the deposition time (yr cm^{-1}) using CHAR Anlaysis 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 $\delta^{13}C$ values of the Huanchaca Mesetta have been used to determine the relative proportions of C_4 savanna grasses versus C_3 woody and herbaceous vegetation (Killeen et al., 2003; Mayle, Langstroth, Fisher, & Meir, 2007).

Sediment $\delta^{15}N$ integrates a variety of nutrient cycling processes including the loss of inorganic N to the atmosphere through denitrification (McLauchlan et al., 2013; Robinson, 1991). Denitrification and the subsequent enrichment of $\delta^{15}N$ requires abundant available carbon, available nitrate, and anaerobic conditions (Seitzinger et al., 2006). Thus, wet, anoxic soils tend to have enriched values of $\delta^{15}N$. Environmental conditions that alter from wet (anaerobic) to dry (aerobic) conditions also enrich $\delta^{15}N$ values (Codron et al., 2005). During dry periods, denitrification is shut off because of an increase in available oxygen in sediments, thus $\delta^{15}N$ values decrease. If dry soils become hydrated, there is a preferential loss of ^{14}N, enriching $\delta^{15}N$ 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 1-25 mg 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 ($^{0}/_{00)}$ 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 C_4 grasses, adapted to open environments with high seasonality of rainfall, typically expand at the expense of C_3 grasses and other tropical forest species during drier intervals (Hartley and Slater, 1960; Hartley, 1958a, 1958b; Piperno, 1997). C_4 Panicoideae grasses are generally adapted to warm moist conditions, whereas C_4 Chloride grasses are adapted to warm, dry conditions (Hartley and Slater, 1960). C_3 subfamilies, including the Pooideae, are adapted to cool and moist conditions, are currently confined to temperate climates with lower temperatures (Hartley, 1961, 1973; Iriarte, 2006). The presence of C_3 Pooideae 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 along the sediment core. 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 Power Paleoecology 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 *M. flexuosa* that produces globular echinate phytoliths but does not produce hat-shaped phytoliths characteristic of other Arecaceae (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 *M. flexuosa* during the middle and late Holocene, phytolith percentages from globular echinate phytoliths were calculated separately. Percentages of non-*Mauritia* phytoliths were calculated on the basis of the total sum of phytoliths excluding *M. flexuosa.* 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 (Grimm, 1987). CONISS was used to calculate phytolith zones (Grimm, 1987). CONISS is based on cluster analysis, with the constrain that clusters are formed by hierarchical agglomeration of stratigraphically-adjacent samples to minimize dispersion within the clusters (Bennett, 1996; Grimm, 1987). The divisions were chosen using a broken-stick model to determine the number of statistically significant zones at the lowest dispersion within the clusters (Bennett, 1996).

3 Results

Four distinct zones were identified including: Zone 1: the Lateglacial (14,500-11,800 cal yr BP), Zone 2: the early Holocene (11,800-9000 cal yr BP), Zone 3: the middle Holocene (8000-3500 cal yr BP), and Zone 4 and Zone 5: the late Holocene (3500 cal yr BP to present).

3.1 Zone 1: 14,500-11,800 cal yr BP Lateglacial

The Lateglacial vegetation on Huanchaca Mesetta 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-blown vegetation from the surrounding rocky savanna. Both C_4 Panicoideae and C_3 Pooideae grass phytoliths were present during the Lateglacial. The presence of C_3 Pooideae grasses is interpreted as cooler Lateglacial conditions compared to present. The Lateglacial vegetation community at Huanchaca Mesetta lacks a modern analogue plant community in NKMNP. The presence of both of C_3 Pooideae and C_4 Panicoideae grasses suggest some degree of landscape heterogeneity. A consistent layer of very dark sandy silt dominated the lithology of Huanchaca Mesetta during the Lateglacial. 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 Lateglacial had $\delta^{13}C$ values of -16‰ (Figure 5), indicating a contribution of C_4 grasses to organic matter composition. The proportion of C_3 to C_4 grass contribution was calculated by using values of C_3 and C_4 grasses and a simple two-pool mixing model (Perdue and Koprivnjak, 2007) with end member values of -27‰ for C_3 and -12‰ for C_4 plants. The contribution of C_4 vegetation was ca. 80%, higher than any other time in the Huanchaca record. Modern $\delta^{13}C$ values in the basin range from -18 to -22‰. The location of these C_4 drought adapted grasses was likely the surrounding plateau. Organic carbon concentrations gradually increased from 1% to 4% during the Lateglacial, 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 $\delta^{15}N$ values were ca. 5‰ indicating minimal denitrification during the Lateglacial. 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 Lateglacial (Figure 6). The $\delta^{15}N$ values suggest that sediments within the swamp were drier than present creating aerobic conditions and low denitrification rates.

Charcoal influx levels were low during the Lateglacial (14,500-12,000 cal yr BP). The fire return interval (FRI) was 2 fire episodes per 1000 yr (Figure 7). 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 mesetta surrounding the basin. Low charcoal influx levels coupled with low magnitude charcoal peaks, suggest that the non-analogue vegetation structure of C_3 Pooideae, 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 influx coupled with low fire frequency suggest that the Lateglacial environment was likely fire-sensitive within the basin.

3.2 Zone 2: 11,800-9000 cal yr BP early Holocene

There were decreased C_4 Panicoideae grasses, with consistent levels of C_3 Pooideae grasses, arboreal, and Asteraceae (Opaque perforated platelets) phytoliths. 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 BP The $\delta^{13}C$ contribution of C_4 grasses decreased dramatically from 60 to 20% during this period (Figure 8). 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 denitrification 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 influx at Huanchaca Mesetta increased ca. 11,200 cal yr BP coupled with an increase in the fire frequency to 5 episodes (periods of increased burning) per 1000 yr. The peak magnitude values indicated two substantial fire episodes (periods of increased burning) ca. 10,200 and 9100 cal yr BP 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 influx 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: 8000-3750 cal yr BP middle Holocene

Significant vegetation changes occur through the middle Holocene. From 8000 to 5500 cal yr BP, C_4 Panicoideae (warm/wet) grasses were at the lowest values in the record. C_3 Pooideae (cold/wet) grasses diminished after ca. 7000 cal yr BP and remain absent for the remainder of the record. Arboreal phytoliths reached the highest levels in the record at 8000 cal yr BP followed by a slight decline to 3500 cal yr BP $\delta^{13}C$ values ranged between -24 and -22‰ from 7900 cal yr BP to 5100 cal yr BP These values corresponded to a diminished C_4 contribution to organic matter (approximately 18%). Decreased C_4 grass phytoliths from 8000 to 5000 cal yr BP was interpreted as a decrease in vegetation density in the open mesetta surrounding the basin caused by drying conditions on the mesetta. After 5000 cal yr BP, C_4 Panicoideae grasses and C_4 Chloride (warm/dry) grasses gradually increased in the surrounding watershed, coupled increased $\delta^{13}C$ values to -19‰. *M. flexuosa* phytoliths first appeared at 5000 cal yr BP, and gradually increased to modern levels by 3750 cal yr BP. The $\delta^{13}C$ values decreased, potentially associated with the development of the C_3 *M. flexuosa* community. A dark-brown clay-sand mixture from 8000 to 3750 cal yr BP dominated the lithology that transitioned to black detrital peat ca. 3750 cal yr BP associated with the establishment of *M. flexuosa.* After 4000 cal yr BP LOI, magnetic susceptibility, and C:N values increased, indicating increased organic material. Nitrogen cycling continued to fluctuate throughout this period. $\delta^{15}N$ values exhibited the greatest frequency and amplitude of variability from 8000 to 3750 cal yr BP ranging from 2 to 12‰ indicating repeated and extensive dry periods on the mesetta.

Increased charcoal influx ca. 8000 cal yr BP was followed by an abrupt decrease to the lowest values during the record from ca. 7900 to ca. 3800 cal yr BP. Peak frequency reached the highest levels of 6 fire episodes (periods of increased burning) per 1000 yr 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. 6500 cal yr BP suggesting a change in the fire ecology on the mesetta. From 5000 to 3750 cal yr BP, grass charcoal increased. This is coincident with the establishment of *M. flexuosa* palm swamp and increased C_4 grasses in the surrounding watershed. After 3900 cal yr BP, charcoal influx 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 3900 cal yr BP, 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: 3750 to 2000 cal yr BP: late Holocene

There is a decrease in arboreal taxa coupled with increased values of *M. flexuosa.* C_4 Panicoideae (warm, wet) grasses continued to dominate the surrounding watershed. The lithology consisted of black detrital peat ca. 2450-2050 cal yr BP associated with high LOI values (ca. 22 % organics) and magnetic susceptibility values (ca. 1000 10^{-5} SI). After 2500 cal yr BP the %C, %N, and $\delta^{15}N$ 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 $\delta^{13}C$ values reached modern levels by 2800 cal yr BP although, values exhibit increased variability, fluctuating between -19 and -24‰ co-varying with the C_4 grass contribution between 10-20%.

Charcoal influx at Huanchaca Mesetta remained low 3750 to 2000 cal yr BP with a FRI of 5 episodes (periods of increased burning) per 1000yrs. Grass charcoal reached the highest continuous levels ca. 2800 to 2000 corresponding to high levels of fire adapted C_4 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.

3.5 Zone 5: 2000 cal yr BP to Present: late Holocene

M. flexuosa reached the highest levels in the record in ca. 1800 cal yr BP followed by decreasing values towards present. The presence of hat shaped phytoliths ca. 200 cal yr BP indicate very low concentrations of other palm species during this time. There was a gradual decrease in *M. flexuosa* towards present coupled with the highest levels of C_4 Panicoideae grasses ca. 200 cal yr BP and a decrease in C_4 Chloridoideae (warm, dry) grasses in the surrounding watershed. The lithology was dominated by dark brown detrital peat. After ca. 800 cal yr BP $\delta^{13}C$ values were ca. -18‰ and the % C_4 contribution was ca. 50%. These data corresponded to the highest levels of C_4 Panicoideae grass phytoliths in the record. The dark detrital peat lithology was interrupted by two coarse sand layers ca. 1550 cal yr BP and ca. 300-200 cal yr BP, followed by a shift back to black detrital peat ca. 200 cal yr BP to present. These sand layers were characterized by a decrease in LOI from ca. 22 to 2 % organics, C:N ratios from ca. 25 to 0, and $\delta^{15}N$ 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 BP %C values increased from ca. 1% to >20% reached the highest values in the record. The %N values increased from ca. 01 to the peak Holocene values of 1.2 at present. The dramatic increases in both %C and %N were likely the result of in situ carbon cycling and nitrogen fixation.

Charcoal influx increased after 2000 cal yr BP at ca. 1400 to 1200 cal yr BP, and reached peak Holocene values ca. 500-400 cal yr BP. Increased charcoal was coupled with the lowest FRI values in the record. Peak magnitude increased significantly around 1200 cal yr BP and the largest peak magnitude values ca. 200 cal yr BP. These charcoal values were cropped for plotting and visualization purposes. Raw counts exceed 1200 thus the values are also provided as log transformed (Figure 8). Peak frequency increased after ca. 400 cal yr BP to ca. 4 fire episodes (periods of increased burning) per 1000 yr towards present. There was a decrease in grass charcoal indicating increased woody biomass burned. The increased charcoal influx 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 *cerrãdo* savannas are largely related to edaphic factors (Colgan et al., 2012; Killeen, 1998a). Since the Lateglacial, 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 Lateglacial (Baker et al., 2001; Cruz et al., 2005), the open savanna surrounding the basin was continuously dominated by fire adapted C_4 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 C_4 grasses as indicated by the continued presence of C_4 Panicoideae grass phytoliths that co-varied with the $\delta^{13}C$ 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 species composition to C_4 drought adapted grasses. Arboreal and palm vegetation was limited to the topographic depressions present on the plateau where soil was sufficiently deep to support more complex vegetation communities.

4.2 Second Order Control: Climatological Drivers

4.2.1 Lateglacial Surazo Winds and Mauritia flexuosa

Non-analogue Lateglacial vegetation communities are documented from low elevation sites including Laguna Chaplin (14º 28'S, 61º 04'W approximately 40 km west) and Laguna Bella Vista (13º, 37'S, 61º, 33W, 140 km northwest). The absence of *Anadenanthera*, a key indicator in present-day 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 CO_2 concentrations. These conditions favored C_4 grasses, sedges and drought adapted savanna and dry forest arboreal species (Burbridge et al., 2004). Similarly, the non-analogue Lateglacial vegetation community at Huanchaca Mesetta is notable for the absence of *M. flexuosa. M. flexuosa* can tolerate a broad precipitation gradient ranging from 1500 mm to 3500 mm annually in areas with annual temperature averages above 21 ºC, roughly coinciding with the 1000 m a.s.l. 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 m a.s.l.) during the Lateglacial (Burbridge et al., 2004), indicate conditions were sufficiently warm 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 Lateglacial conditions from Laguna La Gaiba, (ca. 500 km SE of Huanchaca Mesetta), indicate temperatures reached modern conditions (ca. 25 to 26.5 ºC) around 19,500 cal yr BP and have remained relatively stable to present (Whitney et al., 2011). However, previous studies suggest the increased frequency of *surazos* 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 ºC lower (Bush & Silman, 2004). Based on a lapse rate of 6.4 ºC/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 ºC difference in average annual temperatures. Despite near modern annual temperatures ca.19, 500 cal yr BP, 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 ºC for *M. flexuosa* (Rull and Montoya, 2014). Thus, during the Lateglacial, 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 Interpreting CHAR Analysis in Paleofire Reconstructions at Huanchaca Mesetta

The charcoal record from the Huanchaca Mesetta provides one of the first sub-centennial paleofire records from the *cerrãdo* savanna ecosystem. Previous experimental studies on sedimentary charcoal from African savanna ecosystems support the use of sedimentary charcoal to reconstruct past fire activity in savanna systems (Aleman et al., 2013; Duffin et al., 2008). The Huanchaca Mesetta charcoal record presents a novel approach, combining charcoal influx data, CHAR Analysis software (Higuera et al., 2007), and arboreal/non-arboreal charcoal ratios in Neotropical savanna ecosystems. Originally, CHAR Analysis was designed as a peak-detection tool for forest ecosystems with low FRI in the Northern Hemisphere (Higuera et al., 2007). Paleoecological investigations in fire-prone systems such as savannas, which detect fire peaks or isolated fire events, can be challenging because of the annual to multi-annual FRI.

To address the challenge of reconstructing *cerrãdo* paleofire activity, charcoal influx was compared with the ratio of arboreal to non-arboreal grass charcoal to infer the primary fuel source during periods of elevated fire activity. Low charcoal influx values, coupled with low arboreal charcoal, were interpreted as the background component of charcoal influx data. Increased charcoal influx values and/or increased arboreal charcoal that exceeded the background threshold were identified as fire episodes. Because of the temporal resolution of the record, fire episodes were not interpreted as isolated fires but rather as periods of time that experienced increased fire activity (indicated by higher FRI values). Thus, an increase in the FRI from 2 to 5 episodes/1000 yrs, as seen from 8000 to 6000 cal yr BP, represents more than a 50% increase in the periods of burning over that 2000-yr period. These data indicate a substantial shift in paleofire activity during the middle Holocene, particularly as there were no significant changes in the vegetation record on the Huanchaca Mesetta during this time.

4.2.3 Holocene Precipitation, Fuel Moisture and Fuel Availability

During the middle Holocene in lowland Amazonia the presence of dry forest taxa and increased charcoal influx 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 Orícore (13º20'44.02'S, 63º31'31.86"W, 335 km NW), peaks in drought tolerant arboreal taxa, coupled with maximum charcoal concentrations indicate drier and regionally more open vegetation (Carson et al., 2014). Laguna Granja (13º15'44" S, 63º, 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 8) attributed to precipitation levels ca. 40% below present (Baker et al., 2001; Cross et al., 2000; D'Agostino et al., 2002).

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 Orícore, 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 C_4 grass connective fuels resulted in decreased burning on the mesetta.

In the late Holocene (3750 cal yr BP to present), Lake Titicaca reached modern water levels (Rowe et al., 2003) indicating wetter regional conditions with less severe dry seasons. The pollen assemblages of Laguna Bella Vista, Laguna Chaplin and Laguna Orícore, 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). 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 SASM (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 10-15ºS 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.

During the late Holocene, 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 C_4 grasses on the surrounding plateau. Lightning-caused fire is common in *cerrãdo* 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 Lateglacial, 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 influx have been seen in numerous paleoecological records from savanna ecosystems in Colombia (Behling and Hooghiemstra, 1998, 1999; Berrio et al., 2002a, 2002b), Venezuela (Montoya et al., 2011b; Rull and Montoya, 2014; Rull, 1999, 2009) and Brazil (DaSilva 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 influx 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 suggest 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 BP recovered from anthosols (terra preta) throughout La Chonta ca. 150 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 1000 to 400 cal yr BP, approximately 2000 years after the initial increase in *M. flexuosa* at these sites (B. Whitney personal communication, 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; Ramos-Neto and Pivello, 2000; Rull and Montoya, 2014) (Arroyo-Kalin, 2012; Behling and Hooghiemstra, 1998, 1999; Behling, 2002; Berrio et al., 2002a; 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 Lateglacial 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 (DaSilva 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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Tables and Figures

Table 1 AMS Radiocarbon Dates from Huanchaca Mesetta

Lab Number	Material	Depth (cm)	^{14}C age (yr BP)	$\delta^{13}C$ Ratio	Intcal 13 2 sigma (cal yr BP)
UGAMS 15158	Macrofossil	17	190 ± 20	-28.8	0-289
UGAMS 17252	Bulk Sediment	58	2310 ± 25	-18.8	2211-2356
UGAMS 15264	Bulk Sediment	118	1360 ± 20	-22.9	1272-1305
UGAMS 12023	Bulk Sediment	190	2480 ± 20	-22.62	2473-2715
UGAMS 17253	Bulk Sediment	225	3365 ± 25	-20.7	3561-3689
UGAMS 17254	Bulk Sediment	277	6545 ± 30	-22.6	7422-9622
UGAMS 15159	Bulk Sediment	320	8600 ± 30	-22.8	9524-9622
UGAMS 17255	Bulk Sediment	380	11905 ± 35	-16.3	13577-13789

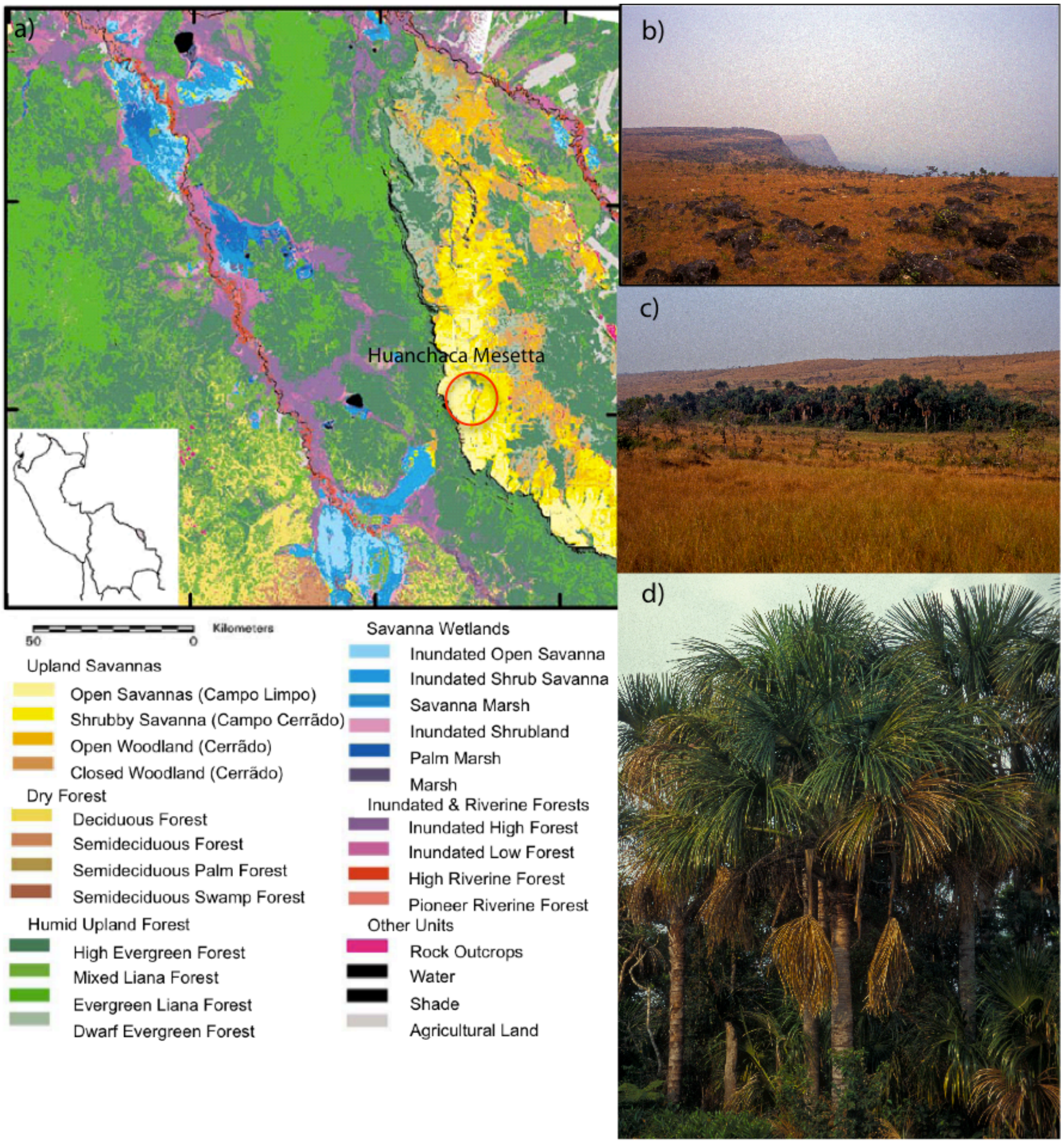

Figure 1 Huanchaca Mesetta study site a) vegetation map of Noel Kempff Mercado National Park (NKMNP) modified from Killeen et al. 1998, b) view from a top Huanchaca Mesetta, c) Huanchaca Mesetta palm swamp, d) mono-specific stand of *Mauritia flexuosa*. Photos by F. Mayle.

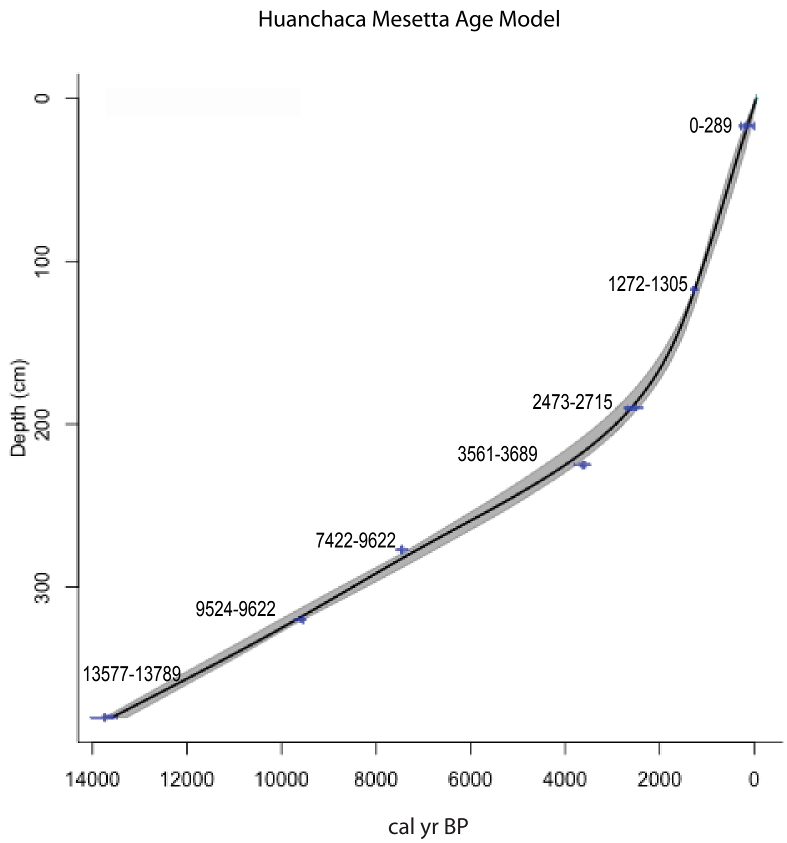

Figure 2 Clam age-depth model for Huanchaca Mesetta. Grey bars represent 2 sigma error.

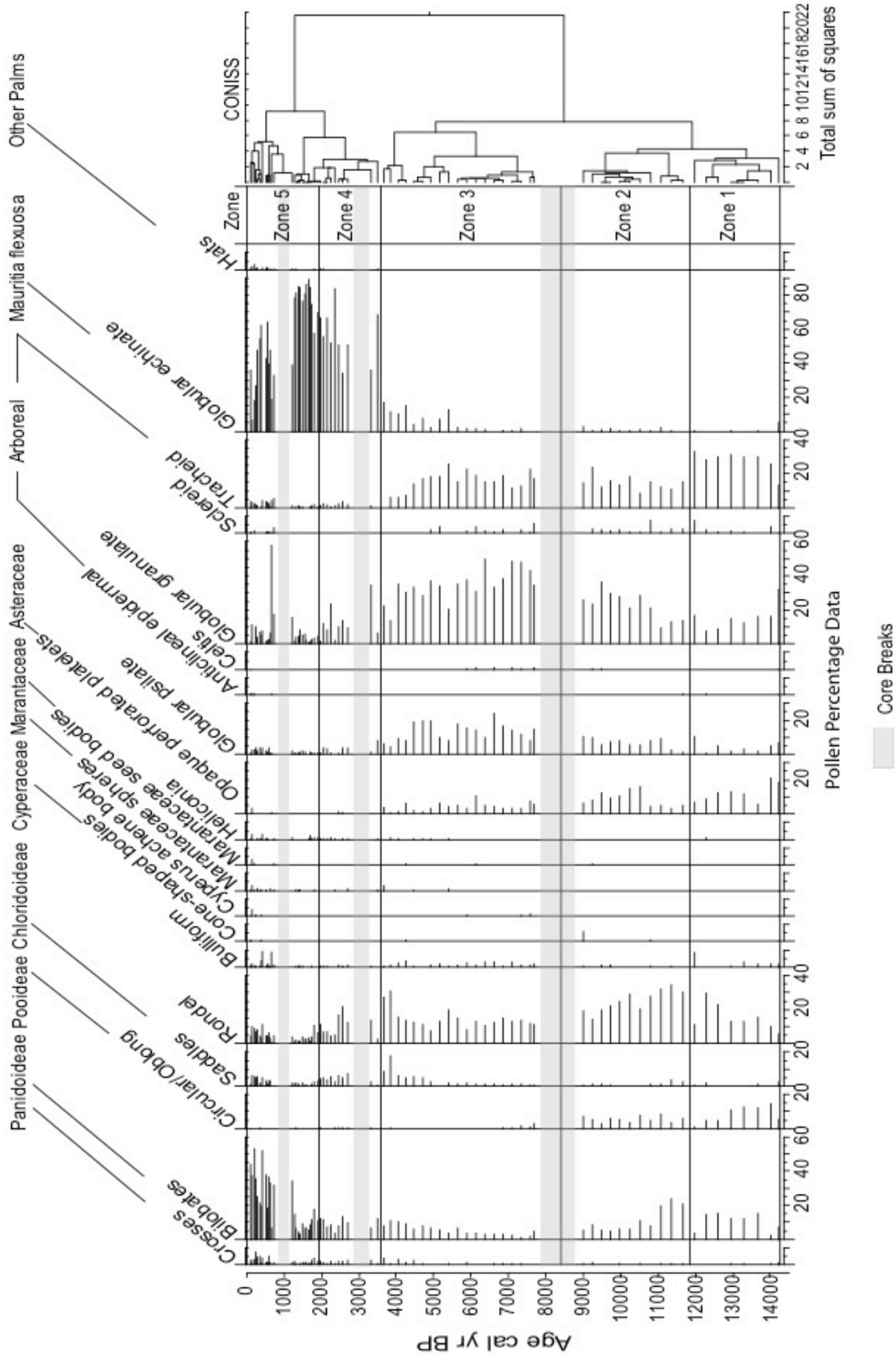

Figure 3 Huanchaca Mesetta phytolith data separated by zones created by constrained cluster analysis (CONISS). Grey bars indicate core breaks.

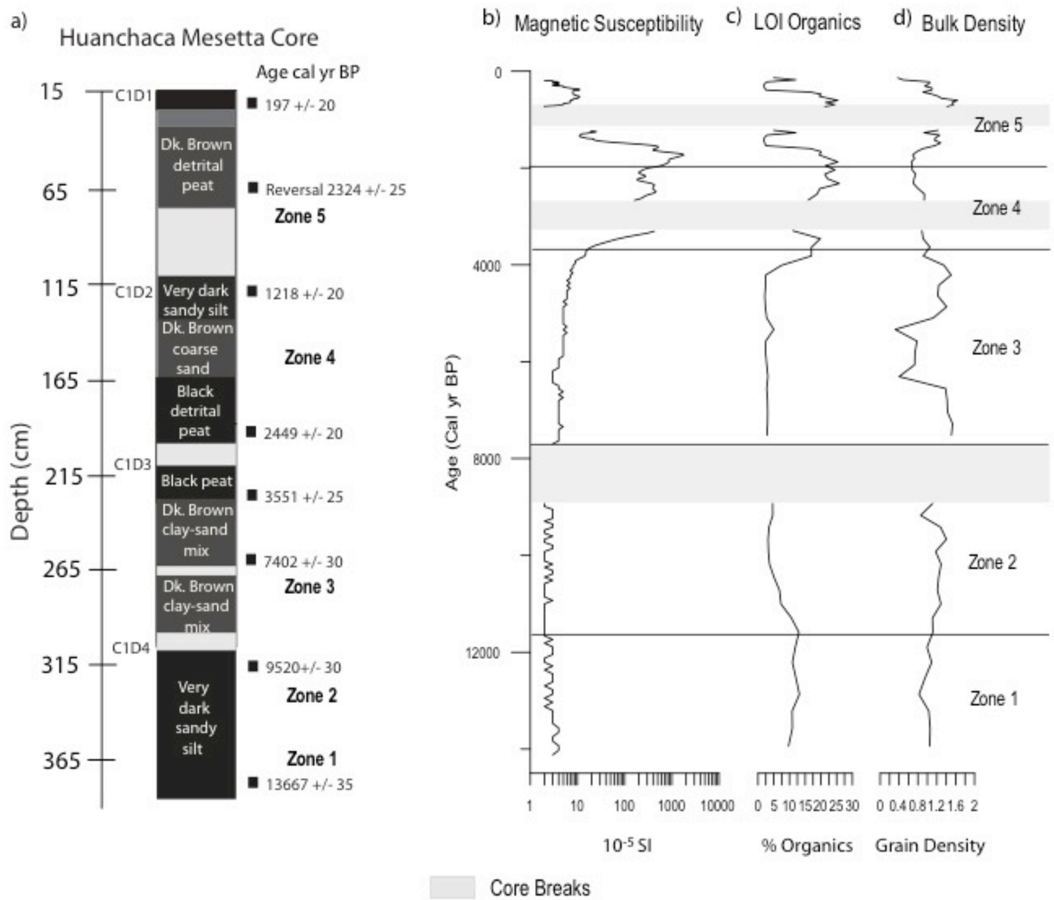

Figure 4 Huanchaca Mesetta lithology a) lithological description of the core profile, b) magnetic susceptibility, c) loss on ignition (LOI), d) bulk density. Zones derived from phytolith data. Grey bars represent core breaks.

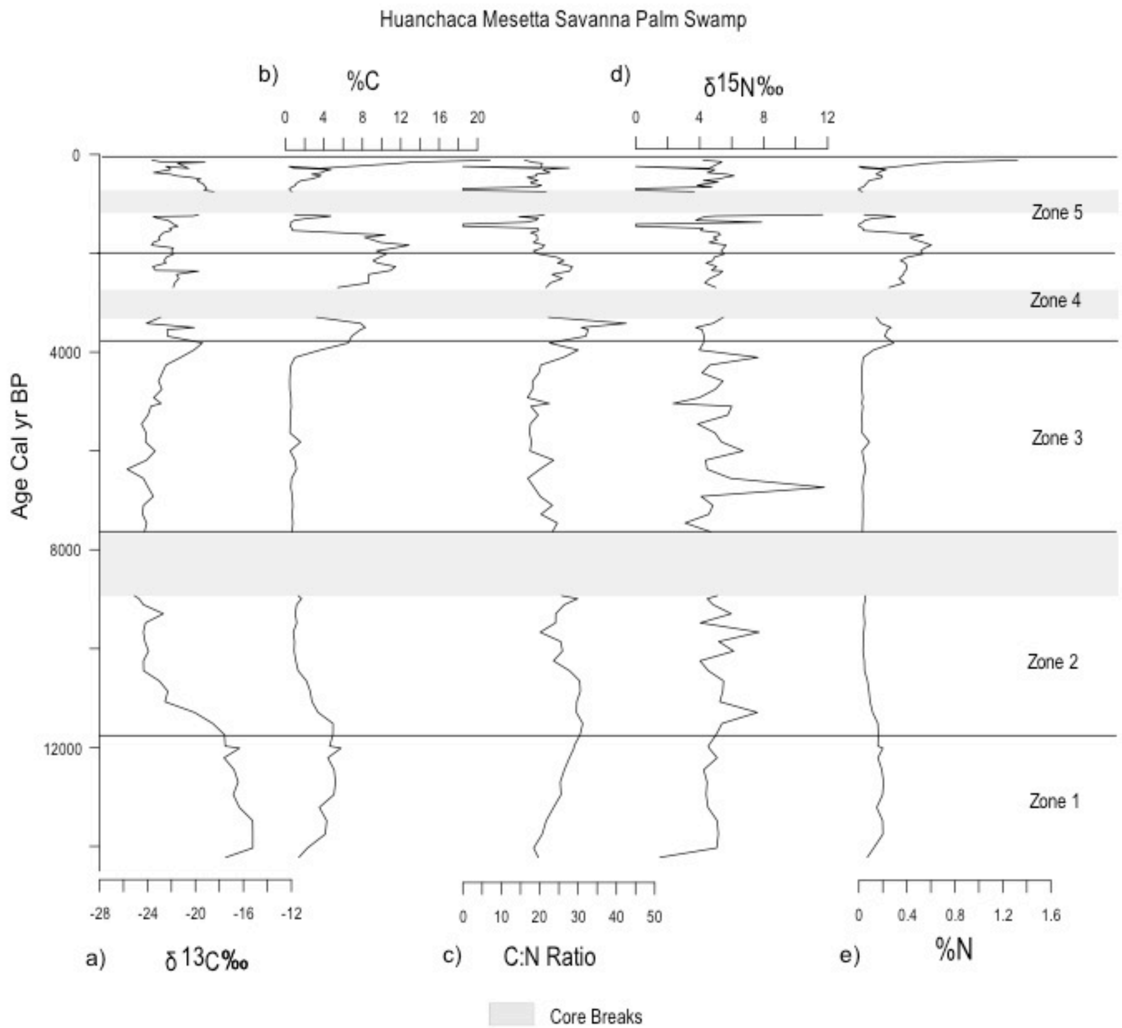

Figure 5 Huanchaca Mesetta stable isotope data a) δ13C, b) % total carbon, c) carbon to nitrogen ratio, d) δ15N, e) % total N. Zones derived from phytolith data. Grey bars indicate core breaks.

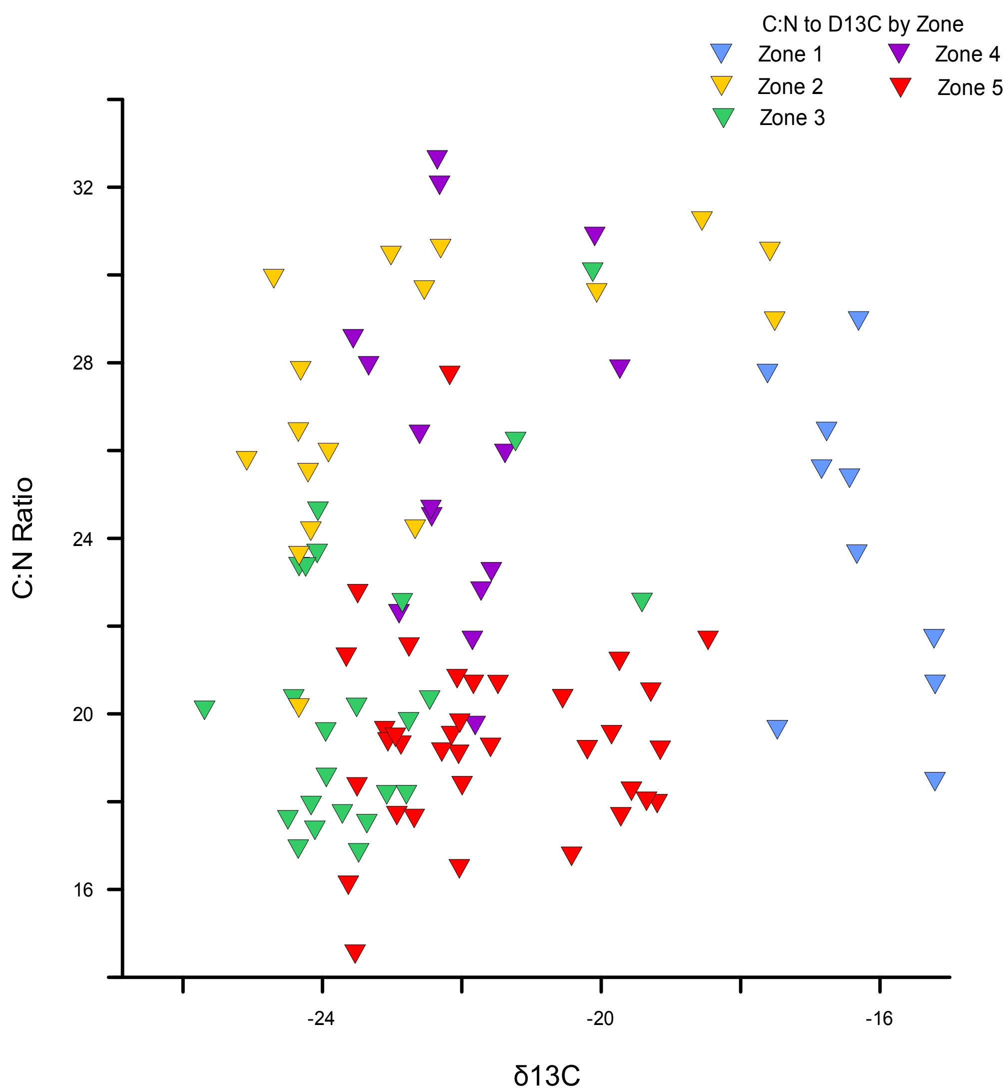

Figure 6 C:N ratio to δ13C stable isotopes by zones determined from phytolith data.

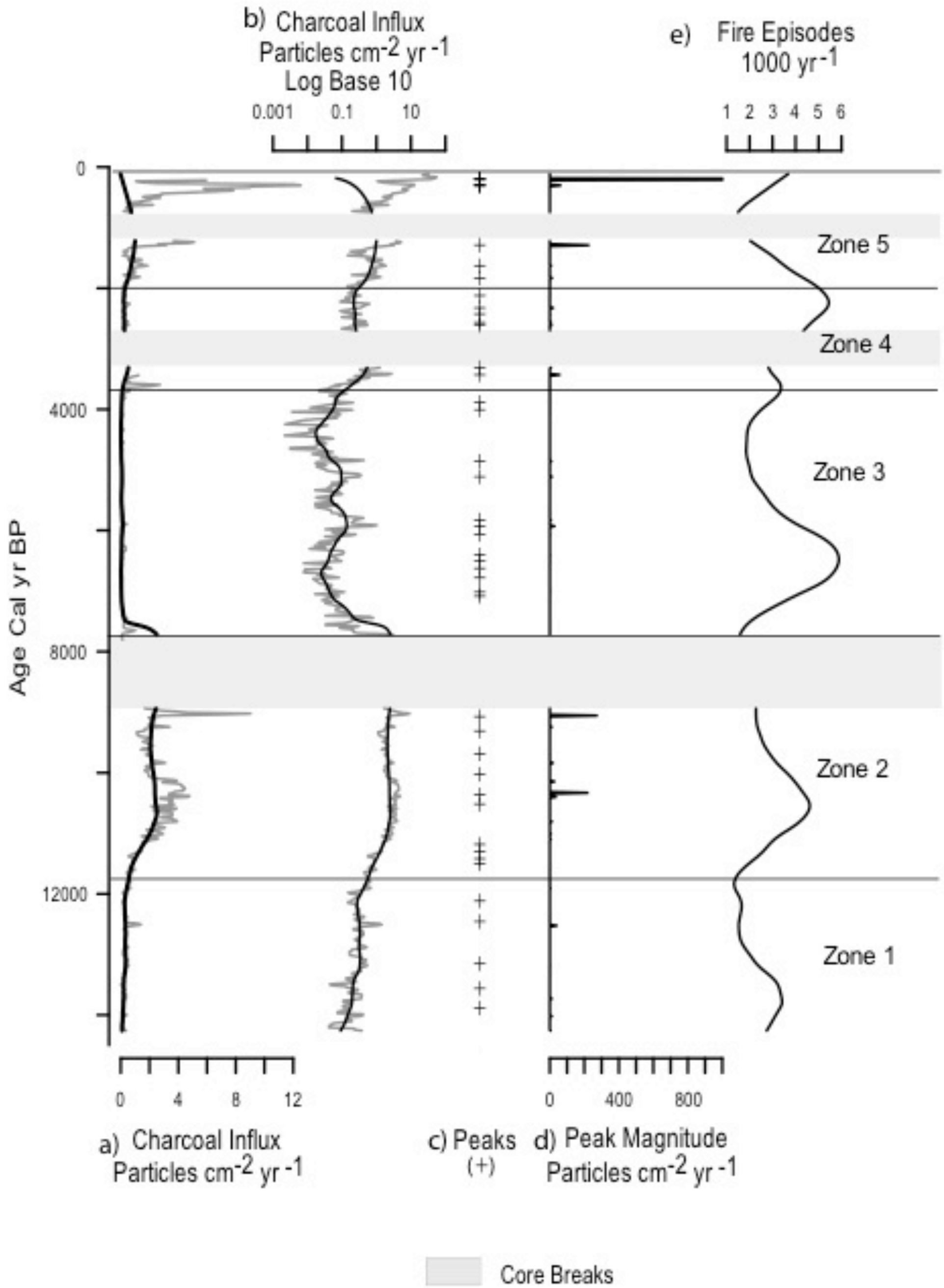

Figure 7 Huanchaca Mesetta charcoal data a) charcoal influx in grey, black background, b) charcoal influx log base 10 in grey, black background, c) peaks indicated by crosses, d) peak magnitude, e) fire episodes per 1000 years. Zones derived from phytolith data. Grey bars indicate core breaks.

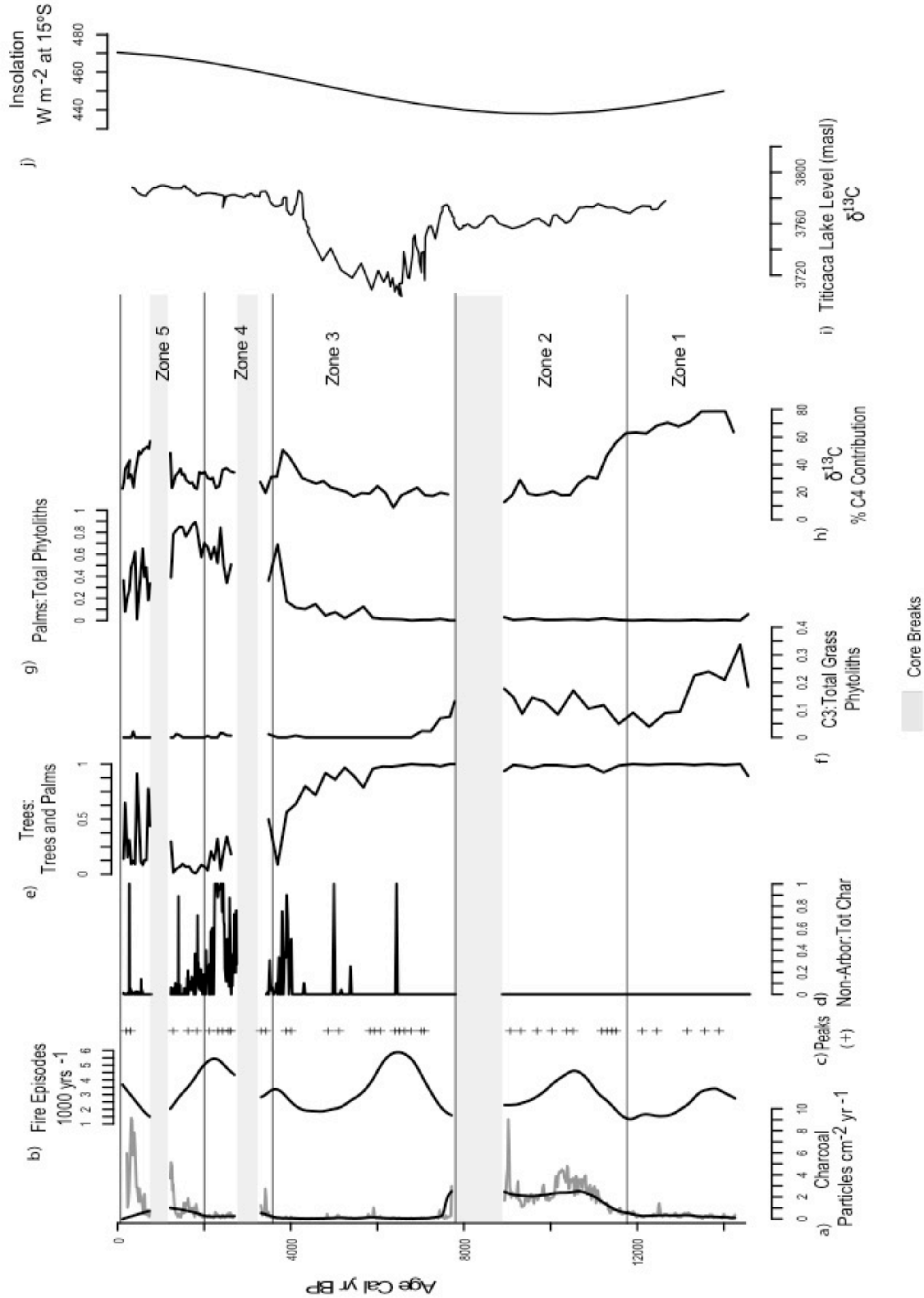

Figure 8 Huanchaca Mesetta summary figure a) charcoal influx in grey, black background, b) fire episodes per 1000 yr, c) peaks indicated by crosses, d) ratio of non-arboreal to total charcoal, e) ratio of trees to trees and palms, f) ratio of C3 to total grasses, g) ratio of palms to total phytoliths, h) % C4 contribution, i) lake level of Titicaca in m a.s.l., j) insolation at 15ºS. Zones derived from phytolith data. Grey bars indicate core breaks.