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1 The Effects of Past Climate Variability on Fire and Vegetation in the Cerrado Savanna
2 Ecosystem of the Huanchaca Mesetta, Noel Kempff Mercado National Park, NE Bolivia
3 S. Yoshi Maezumi^{1,2}, Mitchell J. Power^{1,2}, Francis E. Mayle³, Kendra McLaughlan⁴, José
4 Iriarte⁵

5
6 ¹ Department of Geography, University of Utah, 260 S. Central Campus Dr., Rm: 270,
7 Salt Lake City, UT 84112, USA

8 ² Natural History Museum of Utah, 301 Wakara Way, Salt Lake City, UT 84103, USA

9 ³ Department of Geography and Environmental Science, Centre for Past Climate Change,
10 University of Reading, Whiteknights, PO Box 227, Reading RG6, UK

11 ⁴ Department of Geography, Kansas State University, 118 Seaton Hall, Manhattan, KS
12 66506, USA

13 ⁵ Department of Archaeology, College of Humanities, University of Exeter, Laver
14 Building, North Park Road, Exeter EX4 4QE, UK

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20 Corresponding Author: shira.maezumi@gmail.com, 001-(760)-212-6613

21
22 **Abstract**

23 Cerrado savannas have the greatest fire activity of all major global land-cover types
24 and play a significant role in the global carbon cycle. During the 21st century,
25 temperatures are ^{projected} ~~predicted~~ to increase by ~3°C coupled with a precipitation decrease of ^e
26 ~20%. Although these conditions could potentially intensify drought stress, it is unknown
27 how that might alter vegetation composition and fire regimes. To assess how Neotropical
28 savannas responded to past climate changes, a 14,500-year ^{with} high-resolution sedimentary
29 record from Huanchaca Mesetta, a palm swamp located in the cerrado savanna in
30 northeastern Bolivia, was analyzed for phytoliths, stable isotopes and charcoal. A non-
31 analogue, cold-adapted vegetation community dominated the ~~Late~~ ^e Glacial-Early
32 Holocene period (14.5-9ka), that included trees and C₃ Pooideae and C₄ Panicoideae ^l
33 grasses. The Late Glacial vegetation was fire sensitive and fire activity during this period
34 was low, likely responding to fuel availability and limitation. Although similar vegetation

35 characterized the ^{e/} Early Holocene, the warming conditions associated with the onset of
36 the Holocene led to an initial increase in fire activity. Huanchaca Mesetta became
37 increasingly fire-dependent during the ^m Middle Holocene with the expansion of C₄ fire
38 adapted grasses. However, as warm, dry conditions, characterized by increased length
39 and severity of the dry season, continued, fuel availability decreased. The establishment
40 of the modern palm swamp vegetation occurred at 5,000 cal yr BP. Edaphic factors are
41 the first order control on vegetation on the rocky quartzite mesetta. Where soils are
42 sufficiently thick, climate is the second order control of vegetation on the mesetta. The
43 presence of the modern palm swamp is attributed to two factors: 1) increased
44 precipitation that increased water table levels, and 2) decreased frequency and duration of
45 ^{explain} *surazos* leading to increased temperature minima. Natural (soil, climate, fire) drivers
46 rather than anthropogenic drivers control the vegetation and fire activity at Huanchaca
47 Mesetta. Thus the *cerrado* savanna ecosystem of the Huanchaca Plateau has exhibited
48 ecosystem resilience to major climatic changes in both temperature and precipitation
49 since the Late Glacial period.

50

51 1. Introduction

52 The *cerrado* savanna of central South America is the largest, richest, and likely most
53 threatened savanna in the world (Da Silva Meneses and Bates, 2002). The *cerrado* is the
54 second largest biome in South America covering 1.86 million km² and is home to over
55 10,000 plant species (Myers et al. 2000). The tropical forest-savanna ecotones within the
56 *cerrado* biome are of considerable interest to biologists because of their high habitat
57 heterogeneity (*beta* diversity), importance in rainforest speciation (Smith et al. 1997) and

58 sensitivity to climate change (IPCC, 2014). According to current estimates however, only
59 20% of the *cerrado* remains undisturbed and only 1.2% of the area is preserved in
60 protected areas (Mittermeier et al. 2000). Additionally, *cerrado* savannas have a
61 significant role in the modern global carbon cycle because of high CO₂ loss associated
62 with frequent natural fire activity (Malhi et al., 2002). Currently savanna fires are
63 considered the largest source of natural pyrogenic emissions, with the most fire activity
64 of all major global land cover types (Pereira, 2003). In the last few decades, deforestation
65 for agriculture and increased drought have resulted in increased burning in savannas,
66 contributing to approximately 12% of the annual increase in atmospheric carbon (van der
67 Werf et al., 2010).

68 The *cerrado* biome comprises forest, savanna, and campestre (open field) formations
69 (Abreu et al., 2012; Mistry, 1998). *Cerrado sensu stricto* is characterized as a woody
70 savanna formation composed of dense, thin, and rocky outcrops with *cerrado*
71 physiognomies that are distinguishable based on their densities, heights, and scattered
72 tree-shrub covers with roughly 50% trees and 50% grass (Abreu et al., 2012). The
73 principal determinants of the growth and development of the *cerrado* vegetation types are
74 largely related to edaphic factors (Colgan et al., 2012). For example the distribution of
75 major *cerrado* vegetation types are closely related to the geomorphology of the
76 Precambrian Brazilian shield in South America (Killeen, 1998a). The development of the
77 variety of *cerrado* vegetation communities is largely the result of heterogeneous nature of
78 the edaphic features (Killeen, 1998a) including the depth of the water table, drainage, the
79 effective depth of the soil profile, the presence of concretions (Haridasan, 2000), soil
80 texture and the percentage of exposed rock (Junior and Haridasan, 2005).

81 In addition to edaphic constraints, climate also has a prominent role in determining
82 *cerrado* savanna vegetation structure and fire activity (Ribeiro and Walter, 2008). The
83 *cerrado* biome is dominated by a warm, wet-dry climate associated with the seasonal X
84 migration of the Intertropical Convergence Zone (ITCZ) (Latrubesse et al., 2012; Da
85 Silva Meneses and Bates, 2002; Vuille et al., 2012). On synoptic climatological
86 timescales, temperature and precipitation are the most important effects of climate on fire
87 (e.g. months to seasons to years) (Mistry, 1998). These factors govern net primary
88 productivity (NPP) and the abundance of available fuels (Brown and Power, 2013; }
89 Marlon et al., 2013). Warmer temperatures are typically associated with increased
90 burning through vegetation productivity and the occurrence of fire-promoting climatic
91 conditions. However, the role of temperature can be mediated by precipitation (Brown
92 and Power, 2013). Fire responds differently to increases in precipitation depending on
93 whether fuel is initially abundant or limited in the ecosystem (Marlon et al., 2013; Mistry,
94 1998). In arid and semi-arid environments, such as the *cerrado*, increases in precipitation
95 tend to increase fire, whereas increased precipitation in humid environments can reduce
96 fire (Marlon et al., 2008, 2013).

97 The seasonality of the precipitation coupled with abundant wet-season lightning }
98 ignitions (Ramos-Neto and Pivello, 2000) is linked to high fire frequency in the *cerrado*
99 (Miranda et al., 2009). Wet season lightning fires typically start in open vegetation (wet
100 fields or grassy savannas) with significantly higher incidence of fire in more open
101 savanna vegetation (Ramos-Neto and Pivello, 2000). High biomass production during
102 the wet season results in abundant dry fuels favoring frequent fires throughout the year X
103 (Ramos-Neto and Pivello, 2000). Data show a positive correlation with fine fuel build-up

104 and both fire temperature and fire intensity (energy output) (Fidelis et al., 2010). Thus,
105 increased wet season fuel accumulation in the *cerrado* increases fire intensity. Based on
106 an ecosystems adaptation to fire it can be classified as independent, fire-sensitive, and
107 fire-dependent (Hardesty et al., 2005). In fire-independent ecosystems such as tundra and
108 deserts, fire is rare, either because of unsuitable climate conditions or lack of biomass to
109 burn. Fire-sensitive ecosystems such as tropical rainforests, are damaged by fire, which
110 disrupts ecological processes that have not evolved with fire (Hardesty et al., 2005). Fire-
111 dependent systems such as the well-drained grasslands of the *cerrado* biome, have
112 evolved in the presence of periodic or episodic fires and depend on fire to maintain their
113 ecological processes (Hardesty et al., 2005). Fire-dependent vegetation is fire-adapted,
114 flammable and fire-maintained (Miranda et al., 2009; Pivello, 2011).

115 The study of fire and vegetation change in the *cerrado* is increasingly important as
116 population, agricultural activity, and global warming create pressing management
117 challenges to preserve these biodiverse ecosystems (Mistry, 1998). The long-term role of
118 humans on vegetation and fire regimes of the *cerrado* remains unclear. During the Late
119 Holocene (3,000 cal yr BP) there is increasing evidence for the increase in *Mauritia*
120 *flexuosa* and fire activity in Bolivia, Colombia, Venezuela and Brazil that has been
121 attributed to both natural and anthropogenic drivers (Behling and Hooghiemstra, 1999;
122 Berrio et al., 2007; Kahn and de Castro, 1985; Kahn, 1987, 1988; Montoya and Rull,
123 2011; Rull, 2009; Da Silva Meneses et al., 2013).

124 To investigate the drivers of vegetation and fire in the *cerrado* a long-term
125 perspective is needed. The past few decades have experienced increased global
126 temperatures, increased atmospheric CO₂, and unprecedented levels of deforestation

127 (Malhi et al., 2002). These recent changes heavily influence modern ecological studies,
128 thus limiting the understanding of the role of natural variability in these systems. Long-
129 term paleoecological studies can provide baseline information on processes shaping
130 forest-savanna fire-vegetation dynamics from centennial-to-millennial timescales (Mayle
131 and Whitney 2012). These long-term studies can inform whether recent shifts in ecotones
132 are the result of a minor short-term oscillation around a relatively stable ecotone or a
133 longer-term (e.g. millennial scale) unidirectional ecotonal shift forced by climate change
134 (Mayle et al. 2000; Mayle and Whitney 2012). Additionally, long-term paleoecological
135 records help form realistic conservation goals and identify fire management strategies for
136 the maintenance or restoration of a desired biological state (Willis et al., 2007).

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

145

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

148 (2) Climate is the dominant control on savanna structure and floristic composition.

149 (3) The Late Holocene rise in *Mauritia flexuosa* was driven by climate rather than a
150 change in human land-use.

151

152 1.1 Study Site

153 Noel Kempff Mercado National Park (NKMNP), a 15,230 km² biological reserve in
154 northeastern Bolivia, is located on the Precambrian Shield near the southwestern margin
155 of the Amazon Basin, adjacent to the Brazilian States of Rondônia and Mato Grosso
156 (Burbridge et al., 2004). It is a UNESCO World Heritage Site, in recognition of its
157 globally important biodiversity and largely undisturbed ecosystems, including *terra firme*
158 (non-flooded) evergreen rainforest, riparian and seasonally-flooded humid evergreen
159 forest, seasonally flooded savanna, wetlands, upland *cerrado* savannas, and semi-
160 deciduous dry forests (Mayle et al., 2007). NKMNP occupies an ecotone between
161 Amazon rainforest to the north and dry forests and savannas to the south, containing 22
162 plant communities (Figure 1) (Burn et al., 2010). Huanchaca Mesetta palm swamp
163 (14°32'10.66"S, 60° 43'55.92"W, elevation: 1070 m a.s.l.) is located within NKMNP on
164 the Huanchaca Mesetta – an 800-900 m elevation table mountain. The palm swamp is
165 approximately 200 by 50 meters, comprised entirely of a mono-specific stand of the palm
166 *Mauritia flexuosa*.

167

168 1.2 Climate

169 The climate of NKMNP is characterized by a tropical wet and dry climate (Da Silva
170 Meneses and Bates, 2002). The mean annual precipitation at NKMNP derived from
171 nearby weather stations (Concepción, Magdalena, San Ignacio) is ca. 1400-1500 mm per

172 year, with mean annual temperatures between 25° and 26° C (Hanagarth, 1993; Montes
173 de Oca, 1982; Roche and Rocha, 1985). There is a three to five month dry season during
174 the Southern Hemisphere winter (May to September-October), when the mean monthly
175 precipitation is less than 30 mm (Killeen, 1990). Precipitation falls mainly during the
176 austral summer (December to March), originating from a combination of deep-cell
177 convective activity in the Amazon Basin from the South American Summer Monsoon
178 (SASM) and the Intertropical Convergence Zone (ITCZ) (Vuille et al., 2012). The SASM
179 transports Atlantic moisture into the basin and corresponds to the southern extension of
180 the ITCZ. The ITCZ is driven by seasonal variation in insolation; thus, maximum
181 southern hemisphere insolation and precipitation occur in the austral summer (Bush and
182 Silman, 2004; Vuille et al., 2012). During winter (June, July, August), cold, dry polar
183 advections from Patagonia, locally known as *surazos*, can cause short-term cold
184 temperatures to frequently decrease down to 10°C for several days at a time (Latrubesse
185 et al., 2012; Mayle and Whitney, 2012). These abrupt decreases in temperature may
186 potentially influence the distribution of temperature-limited species on the Huanchaca
187 Mesetta.

188

189 *1.3 Geomorphology*

190 The Huanchaca Mesetta table mountain is near the western limit of the Brazilian
191 Shield and dominates the eastern half of NKMNP. It is composed of Precambrian
192 sandstone and quartzite (Litherland and Power, 1989). The top of the mesetta is flat, with
193 a gently rolling surface and at elevations ranging from 500-900 m above sea level (a.s.l.)
194 (Da Silva Meneses and Bates, 2002). The substrate of the mesetta is rocky, and soils are

195 thin and low in organic material (Litherland and Power 1989). Continuity of the
196 crystalline or sedimentary blocks of the mesetta is broken by an extensive network of
197 peripheral or inter-mesetta depressions formed from a combination of erosion, dolerite
198 dike intrusions and faulting on the mesetta (Litherland and Power, 1989; Da Silva
199 Meneses and Bates, 2002). These depressions act as catchments for sediment and water,
200 resulting in sediment accumulation, which supports more complex vegetation
201 communities. High species diversity exhibited on the Huanchaca Mesetta, compared
202 with other savanna regions of South America, is attributed to the long history of isolation
203 of this edaphically-controlled table-mountain savanna (Mayle et al. 2007).

204

205 1.4 Vegetation

206 The *cerrádo* savanna on Huanchaca Mesetta is dominated by a continuous grass
207 cover with sparsely scattered small trees and shrubs that grows on the thin, well-drained,
208 nutrient-poor soils (Killeen, 1998b). Woody species include *Byrsonima coccolobifolia*,
209 *Caryocar brasiliensis*, *Erythroxylum suberosum*, *Vochysia haenkeana*, and *Callisthene*
210 *fasciculata*. Trees and shrubs include *Qualea multiflora*, *Emmotum nitens*, *Myrcia*
211 *amazonica*, *Pouteria ramiflora*, *Diptychandra aurantiaca*, *Kielmeyera coriacea*, *Ouratea*
212 *spectabilis*, and *Alibertia edulis*. ^{Small shrubs?} Sub-shrubs include *Eugenia punctifolia*, *Senna velutina*,
213 and herbaceous species include *Chamaecrista desvauxii* and *Borreria sp.* Grass families
214 include the Rapataceae (C₃) (*Cephalostemon microglochis*), Orchidaceae (*Cleistes*
215 *paranaensis*) (CAM, C₃), Iridaceae (*Sisyrinchium spp.*) (C₄), Xyridaceae (*Xyris spp.*)
216 (C₄), and Eriocaulaceae (*Eriocaulon spp.*, *Paepalanthus spp.*, *Syngonanthus spp.*) (C₄)
217 (Killeen, 1998b). In the inter-fluvial depressions organic rich soil is sufficiently deep to

218 support humid evergreen forests islands which are typically dominated by mono-specific
219 stands of *Mauritia flexuosa* (Mayle and Whitney, 2012; Da Silva Meneses and Bates,
220 2002). *M. flexuosa* is a monocaulous, aborescent palm, averaging 20-30 meters tall which
221 is typically associated with a low, dense understory (da Silva and Bates, 2002; Furley and
222 Ratter, 1988; Kahn, 1988;). *M. flexuosa* is confined to lower elevations (< ca. 1000m
223 elevation) in warm/wet climates (Rull and Montoya, 2014). *M. flexuosa* swamps favor
224 inter-fluvial depressions that remain flooded during the dry season, when the surrounding
225 terrains dry out (Huber, 1995a, 1995b; Kahn and de Granville, 1992). The abundance of
226 *M. flexuosa* in permanently flooded, poorly drained soils is the result of pneumatophores
227 (aerial roots) which enable its growth in anaerobic conditions (Kahn, 1988; Rull and
228 Montoya, 2014). Seasonal water deficits saturate the soil profile in the wet season and
229 desiccate soil during the dry season resulting in a dominance of herbaceous versus woody
230 plants surrounding the inter-fluvial depressions (Killeen, 1998b). The seasonal dryness
231 leads to drought, plant water stress, and frequent fire activity resulting in the development
232 of xeromorphic and sclerophyllous plant characteristics on the open mesetta (Killeen,
233 1998b). The spatial distribution of evergreen forest versus drought-tolerant savanna
234 vegetation is additionally constrained by edaphic conditions limiting the expansion of
235 forest vegetation because of the heavily weathered sandstone soils dominant outside the
236 inter-fluvial depressions (Killeen and Schulenberg, 1998). Limited soil development
237 precludes rainforest from developing on the large, rocky expanses of the mesetta (Killeen
238 and Schulenberg, 1998). The essentially treeless campo *cerrado* that grows around
239 Huanchaca Mesetta palm swamp is edaphically constrained and has likely grown on this
240 mesetta for millions of years (Mayle and Whitney, 2012). Thus, the vegetation of the

241 Huanchaca Mesetta is influenced by both climatic and non-climatic controls including
242 seasonal hydrologic conditions, edaphic soil constraints and frequent fire activity (Killeen
243 and Schulenberg, 1998).

244

245 **2 Materials & Methods**

246 *2.1 Sediment core*

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

255

256 *2.2 Chronology*

257 The chronological framework for Huanchaca Mesetta was based on eight (AMS)
258 radiocarbon dates from non-calcareous bulk sediment and wood macrofossils analyzed at
259 the University of Georgia Center for Applied Isotope Studies (Table 1). The uncalibrated
260 radiometric ages are given in radiocarbon years before 1950 AD (years 'before present',
261 yr BP). The errors are quoted at one standard deviation and reflect both statistical and
262 experimental errors. Radiocarbon ages were calibrated using CALIB 7.0 and the
263 IntCal13 calibration dataset (McCormac et al., 2004). IntCal13 was selected in place of

264 the SHcal13 calibration curve because of the latitudinal location (14°S) of Huanchaca
265 Mesetta and the proximal hydrologic connection with the origin of the South American
266 Monsoon in the northern hemisphere. The seasonal migration of the ~~Intertropical~~
267 ~~Convergence Zone~~ (ITCZ) is thought to introduce a northern hemisphere ¹⁴C signal to the
268 low latitude southern hemisphere (McCormac et al., 2004). This study area is located in
269 the low latitudes (14°S) and within the range of the ITCZ migration; thus, the IntCal13
270 calibration curve was selected for the radiocarbon calibrations. Following calibration, the
271 mean age value ^(cal yr BP) of the largest probability at 2 sigma was used to create the smoothing
272 spline age model using classical age-depth modeling, in the package CLAM (Blaauw,
273 2010) within the open-source statistical software R (Figure 2):

274

275

276

277 2.3 Loss on Ignition

278 The variability in the organic and carbonate content of sediments is used, in
279 conjunction with magnetic susceptibility, to identify periods of variability in sediment
280 composition and organic content throughout the Holocene. Organic and carbonate
281 sediment composition was determined by Loss-on-Ignition, conducted at contiguous 1
282 cm increments throughout the cores. For each sample, 1 cm³ of sediment was dried in an
283 oven at 100°C for 24 hours. The samples underwent a series of 2-hour burns in a muffle
284 furnace at 550°C and 1000°C to determine the relative percentage of the sample
285 composed of organics and carbonates. Concentration was determined by weight
286 following Dean (1974) standard methodology.

287

288 *2.4 Magnetic Susceptibility*

289 Magnetic susceptibility (MS) was measured to identify mineralogical variation in the
290 sediments (Nowaczyk, 2001). The MS of sediments is reflective of the relative
291 concentration of ferromagnetic (high positive MS), paramagnetic (low positive MS), and
292 diamagnetic (weak negative MS) minerals or materials. Typically, sediment derived from
293 freshly eroded rock has a relatively high MS, whereas sediments that are dominated by
294 organic debris, evaporites, or sediments that have undergone significant diagenetic
295 alteration typically have a low or even negative MS (Reynolds, 2000). Shifts in the
296 magnetic signature of the sediment can be diagnostic of a disturbance event (Gedye et al.
297 2000). Sediment cores were scanned horizontally, end to end through the ring sensor.
298 MS was conducted at 1 cm intervals using a Barington ring sensor equipped with a 75
299 mm aperture.

300

301 *2.5 Charcoal*

302 Sediment samples were analyzed for charcoal pieces greater than 125 μm using a
303 modified macroscopic sieving method (Whitlock and Larsen 2001) to reconstruct the
304 history of local and extra-local fires. Charcoal was analyzed in contiguous 0.5 cm
305 intervals for the entire length of the sediment core at 1 ~~cc~~^{cm³} volume. Samples were treated
306 with 5% potassium hydroxide in a hot water bath for 15 minutes. The residue was gently
307 sieved through a 125 μm sieve. Macroscopic charcoal (particles >125 μm in minimum
308 diameter) was counted in a gridded petri dish at 40 \times on a dissecting microscope. Non-
309 arboreal charcoal was characterized by two morphotypes: (1) cellular 'graminoid' (thin

310 rectangular pieces; one cell layer thick with pores and visible vessels and cell wall
311 separations) and (2) fibrous (collections or bundles of this filamentous charcoal clumped
312 together). Arboreal charcoal was characterized by three morphotypes: (1) dark (opaque,
313 thick, solid, geometric in shape, some luster, and straight edges), (2) lattice (cross-
314 hatched forming rectangular ladder-like structure with spaces between) and (3) branched
315 (dendroidal, generally cylindrical with successively smaller jutting arms) (Jensen et al.,
316 2007; Mueller et al., 2014; Tweiten et al., 2009). Charcoal pieces were grouped into non-
317 arboreal and arboreal categories based on their morphology, which enabled the
318 characterization of fuel sources in the charcoal record (Mueller et al., 2014).

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

328

329 2.6 Stable Isotopes

330 Stable carbon isotopes were analyzed as an additional proxy for changes in vegetation
331 structure and composition. Carbon isotopic composition of terrestrial organic matter is
332 determined primarily by the photosynthetic pathway of vegetation (Malamud-Roam et

333 al., 2006). Previous research on $\delta^{13}\text{C}$ values of the Huanchaca Mesetta have been used to
334 determine the relative proportions of C_4 savanna grasses versus C_3 woody ^{and herbaceous} vegetation
335 (Killeen et al., 2003; Mayle, Langstroth, Fisher, & Meir, 2007).

336 Sediment $\delta^{15}\text{N}$ integrates a variety of nutrient cycling processes including the loss of
337 inorganic N to the atmosphere through denitrification (McLauchlan et al., 2013;
338 Robinson, 1991). Denitrification and the subsequent enrichment of $\delta^{15}\text{N}$ requires
339 abundant available carbon, available nitrate, and anaerobic conditions (Seitzinger et al.,
340 2006). Thus, wet, anoxic soils tend to have enriched values of $\delta^{15}\text{N}$. Environmental
341 conditions that alter from wet (anaerobic) to dry (aerobic) conditions also enrich $\delta^{15}\text{N}$
342 values (Codron et al., 2005). During dry periods, denitrification is shut off because of an
343 increase in available oxygen in sediments, thus $\delta^{15}\text{N}$ values decrease. If dry soils become
344 hydrated, there is a preferential loss of ^{14}N , enriching $\delta^{15}\text{N}$ values (Codron et al., 2005).
345 Stable isotope analysis was conducted at 3-cm resolution for total carbon (C) and
346 nitrogen (N) throughout the length of the sediment core. One cm^3 of bulk sediment was
347 dried, powdered, and treated with 0.5 molar hydrochloric acid to remove carbonates. A
348 range of 1-25 mg of the dried carbonate-free sediment was weighed into tin capsules
349 depending on organic matter content. The samples were analyzed on a Finnigan Delta
350 dual inlet elemental analyzer at the Sirfer Lab at the University of Utah. $^{13}\text{C}/^{12}\text{C}$ and
351 $^{15}\text{N}/^{14}\text{N}$ ratios are presented in delta (δ) notation, in per mil (‰) relative to the PDB and
352 N_2 air standards) (Codron et al. 2005).

353

354 *2.7 Phytoliths*

355 Phytoliths preserve well in sediment records and are especially useful in areas with
356 intermittent dry periods. Phytoliths were used as a proxy to reconstruct past vegetation
357 composition and are especially useful in the lower taxonomic identification of grasses
358 (Piperno and Pearsall, 1998). Grass phytoliths can provide important paleoecological
359 information. Tropical C₄ grasses, adapted to open environments with high seasonality of
360 rainfall, typically expand at the expense of C₃ grasses and other tropical forest species
361 during drier intervals (Hartley and Slater, 1960; Hartley, 1958a, 1958b; Piperno, 1997).
362 C₄ Panicoideae grasses are generally adapted to warm moist conditions, whereas C₄
363 Chloride grasses are adapted to warm, dry conditions (Hartley and Slater, 1960). C₃
364 subfamilies, including the Pooideae, are adapted to cool and moist conditions, are
365 currently confined to temperate climates with lower temperatures (Hartley, 1961, 1973;
366 Iriarte, 2006). The presence of C₃ Pooideae grasses from phytolith data from southeastern
367 Pampa grasslands in Uruguay have been interpreted to indicate a shorter dry season with
368 overall conditions that were cooler than during the Holocene (Iriarte, 2006). Phytolith
369 samples were taken every 4 cm along the sediment core. The extraction and slide preparation of phytoliths were
370 conducted at the University of Exeter, UK, following standard procedures described by
371 Piperno (2005). Slides were scanned and counted at the University of Utah Power
372 Paleocology Lab using a Leica EMED compound light microscope (400-1000x). The
373 number of phytoliths counted varied from 101-320 per slide. The modern palm swamp is
374 a monospecific stand of *Mauritia flexuosa* that produces globular echinate phytoliths but
375 does not produce hat-shaped phytoliths characteristic of other Arecaceae (Piperno, 2005).
376 Although other palms produce globular echinate phytoliths, the current monospecific
377 stand supports the identification of globular echinate phytoliths as belonging to this palm.

378 Given the abundance of *Mauritia flexuosa* during the Middle and Late Holocene,
379 phytolith percentages from globular echinate phytoliths were calculated using a separate
380 sum. Percentages of non-*Mauritia* phytoliths were calculated on the basis of the total sum
381 of phytoliths. Phytolith identification was made by comparison with modern plant
382 reference collections curated at the University of Exeter Archaeobotany Lab. The
383 classification of Poaceae implemented a three-partite morphological classification related
384 to grass taxonomy (Panicoideae-Chloridoideae-Pooideae) (Twiss et al., 1969) and further
385 developed in both North America (Fredlund and Tieszen, 1994) and the Neotropics
386 (Bertoli de Pomar, 1971; Iriarte and Paz, 2009; Iriarte, 2003; Piperno and Pearsall, 1998;
387 Piperno, 2005; Sendulsky and Labouriau, 1966; Söndahl and Labouriau, 1970; Teixeira
388 da Silva and Labouriau, 1970; Zucol, 1999, 2000, 1996, 1998). The phytolith percentage
389 diagrams were plotted using Tilia and Tilia Graphing software (Grimm, 1987).

how compared?

391 3 Results

392 Four distinct vegetation types were identified based on constrained cluster analysis
393 (CCA) of phytolith assemblages. These four zones are: the Late Glacial (14,500-11,500
394 cal yr B.P.), the Early Holocene (11,500-9,000 cal yr B.P.), the Middle Holocene (8,000-
395 3,500 cal yr B.P.), and the Late Holocene (3,500 cal yr B.P. to present).

397 3.1 Zone 1: 14,500-11,500 cal yr B.P. Late glacial

399 The Late Glacial vegetation on Huanchaca Mesetta was dominated by arboreal taxa,
400 grasses and Asteraceae (Opaque Perforated platelets) phytoliths (Figure 3). The phytolith

to keep the logic here
"Late Glacial" should be
written as "Lateglacial"
in order to keep it in
harmony with "Pleniglacial"
etc.

better BP
"units" have no points

401 assemblage likely contains both in-situ vegetation production and wind-blown vegetation
402 from the surrounding rocky savanna. Both C₄ Panicoideae and C₃ Pooideae grass
403 phytoliths were present during the Late Glacial. The presence of C₃ Pooideae grasses is
404 interpreted as cooler Late Glacial conditions compared to present. The Late Glacial
405 vegetation community at Huanchaca Mesetta lacks a modern analogue plant community
406 in NKMNP. The presence of both of C₃ Pooideae and C₄ Panicoideae grasses suggest
407 some degree of landscape heterogeneity. A consistent layer of very dark sandy silt
408 dominated the lithology of Huanchaca Mesetta during the Late Glacial. The magnetic
409 susceptibility and bulk density values were low and exhibit minimum variability
410 compared to the rest of the record (Figure 4). Coupled with LOI organic values below
411 10%, the sediment lithology was summarized as a low-energy depositional environment
412 with relatively low nutrient input. Organic matter deposited during the Late Glacial had
413 $\delta^{13}\text{C}$ values of -16‰ (Figure 5) indicating a contribution of C₄ grasses to organic matter
414 composition. The proportion of C₃ to C₄ grass contribution was calculated by using
415 values of C₃ and C₄ grasses and a simple two-pool mixing model as described by Perdue
416 and Koprivnjak (2007) with end member values of -27‰ for C₃ and -12‰ for C₄ plants
417 (Figure 7). The contribution of C₄ vegetation was ca. 80%, higher than any other time in
418 the Huanchaca record. Modern $\delta^{13}\text{C}$ values in the basin range from -18 to -22‰. The
419 location of these C₄ drought adapted grasses was likely the surrounding plateau. Organic
420 carbon concentrations gradually increased from 1% to 4% during the Late Glacial,
421 indicating relatively low amounts of organic matter in the system compared to those of
422 today. The C:N ratio ranged from 20 to 30, indicating a terrestrial organic matter source.
423 N concentrations were low from 0.1 to 0.2% and the $\delta^{15}\text{N}$ values were ca. 5‰ indicating

introduce acronym in line 281

Where is Figure 6?

(re-numbered to Fig. 6)

424 minimal denitrification during the Late Glacial. The $\delta^{13}\text{C}$, % C_4 contribution, and high
425 C:N values coupled with the phytolith data dominated by trees and grasses, suggest a
426 predominantly terrestrial signal, characterized by an open savanna grassland during the
427 Late Glacial. The $\delta^{15}\text{N}$ values suggest that sediments within the swamp were drier than
428 present creating aerobic conditions and low denitrification rates.

429 Charcoal accumulation levels were low during the Late Glacial (14,500-12,000 cal yr
430 B.P.). Fire return interval (FRI) was 2 fire episodes per 1000 years (Figure 6). Based on
431 the 0.5 cm sampling resolution of this record, fire "episodes" were interpreted as periods
432 of increased fire activity rather than isolated fire "event". The charcoal signature was
433 consistent with frequent, low intensity fires that likely occurred in the open, grass
434 dominated mesetta surrounding the basin. Low charcoal accumulation levels coupled
435 with low magnitude charcoal peaks, suggest that the non-analogue vegetation structure of
436 C_3 Pooideae, C_4 Panicoideae, and arboreal phytoliths likely created a fuel structure that
437 lacked sufficient density or fuel connectivity to produce abundant arboreal or grass
438 charcoal. Low charcoal accumulation coupled with low fire frequency suggest that the
439 Late Glacial environment was likely fire-sensitive within the basin.

440 3.2 Zone 2: 11,500-9,000 cal yr B.P., Early Holocene

443 Decreased C_4 Panicoideae grasses and consistent C_3 Pooideae grasses, arboreal, and
444 Asteraceae (Opaque perforated platelets) phytoliths dominated the assemblage. The
445 presence of C_3 grasses, and the absence of *M. flexuosa*, the dominant component of the
446 modern basin vegetation, suggest temperatures cooler than present. The lithology,

(re-number to Fig. 7)

in flux
I do not understand the word "accumulation" here. What is the unit of accumulation? I guess you mean charcoal in flux (particles $\text{cm}^{-2} \text{yr}^{-1}$)

447 magnetic susceptibility, bulk density, and LOI values indicate minimal shift during the
448 vegetation transition. Organic geochemistry reflected a change in organic matter source,
449 with $\delta^{13}\text{C}$ values becoming more negative, indicating an increase in the contribution of C_3
450 vegetation ca. 11,000 cal yr B.P. The $\delta^{13}\text{C}$ contribution of C_4 grasses decreased
451 dramatically from 60 to 20% during this period. These data correspond to a decrease in
452 C_4 Panicoideae grass phytoliths and an increase in arboreal phytoliths. Low levels of
453 terrestrial organic input into the system were indicated by low carbon concentrations and
454 C:N values ranging between 25 and 30. N cycling changed during this zone, with $\delta^{15}\text{N}$
455 values exhibiting greater amplitude and higher frequency variability. The $\delta^{15}\text{N}$ values
456 ranged between 4 and 8‰ indicating increased variability in denitrification rates
457 associated with increasing wet (anaerobic) to dry (aerobic) conditions. The N
458 concentrations were low, between 0.05 and 0.01%, indicating minimal nitrogen
459 availability in the system.

460 Charcoal accumulation at Huanchaca Mesetta increased ca. 11,200 cal yr B.P. coupled
461 with an increase in the fire frequency to 5 episodes (periods of increased burning) per
462 1000 years. The peak magnitude values indicated two substantial fire episodes (periods of
463 increased burning) ca. 10,200 and 9,100 cal yr B.P. The lack of significant change in the
464 lithology suggests that taphonomic conditions were consistent during this interval. The
465 increase in grass phytoliths during this period coupled with the increase in charcoal
466 accumulation and fire episodes suggest that the ^eEarly Holocene vegetation community
467 was becoming increasingly more fire dependent and vegetation was likely adapting to the
468 increase in fire frequency associated with the period.

469

470 3.3 Zone 3: 8,000-3,750 cal yr B.P. Middle Holocene

471

472 Significant vegetation changes occur through the Middle Holocene. From 8,000 to
473 5,500 cal yr B.P., C₄ Panicoideae (warm/wet) grasses were at the lowest values in the
474 record. C₃ Pooideae (cold/wet) grasses diminished after ca. 7,000 cal yr B.P. and remain
475 absent for the remainder of the record. Arboreal phytoliths reached the highest levels in
476 the record at 8,000 cal yr B.P. followed by a slight decline to 3,500 cal yr B.P. $\delta^{13}\text{C}$
477 values ranged between -24 and -22‰ from 7,900 cal yr B.P. to 5,100 cal yr B.P. These
478 values corresponded to a diminished C₄ contribution to organic matter (approximately
479 18%). Decreased C₄ grass phytoliths from 8,000 to 5,000 cal yr B.P. was interpreted as a
480 decrease in vegetation density in the open mesetta surrounding the basin caused by
481 drying conditions on the mesetta. After 5,000 cal yr B.P., C₄ Panicoideae grasses and C₄
482 Chloride (warm/dry) grasses gradually increased in the surrounding watershed, coupled
483 increased $\delta^{13}\text{C}$ values to -19‰. *Mauritia flexuosa* phytoliths first appeared at 5,000 cal yr
484 B.P., and gradually increased to modern levels by 3,750 cal yr B.P. The $\delta^{13}\text{C}$ values
485 decreased, potentially associated with the development of the C₃ *M. flexuosa* community.
486 A dark-brown clay-sand mixture from 8,000 to 3,750 cal yr B.P. dominated the lithology
487 that transitioned to black detrital peat ca. 3,750 cal yr B.P. associated with the
488 establishment of *M. flexuosa*. After 4,000 cal yr B.P. LOI, magnetic susceptibility, and
489 C:N values increased, indicating increased organic material. Nitrogen cycling continued
490 to fluctuate throughout this period. $\delta^{15}\text{N}$ values exhibited the greatest frequency and
491 amplitude of variability from 8,000 to 3,750 cal yr B.P. ranging from 2 to 12‰ indicating
492 repeated and extensive dry periods on the mesetta.

etc

493 Increased charcoal accumulation ca. 8,000 cal yr B.P. was followed by an abrupt
494 decrease to the lowest values during the record from ca. 7,900 to ca. 3,800 cal yr B.P.
495 Peak frequency reached the highest levels of 6 fire episodes (periods of increased
496 burning) per 1000yrs during the Middle Holocene. These data corresponded to the
497 highest levels of $\delta^{15}\text{N}$ values indicating extended dry periods that likely promoted
498 frequent fires on the mesetta. The first evidence of grass charcoal appeared ca. 6,500 cal
499 yr B.P. suggesting a change in the fire ecology on the mesetta. From 5,000 to 3,750 cal yr
500 B.P., grass charcoal increased. This is coincident with the establishment of *M. flexuosa*
501 palm swamp and increased C₄ grasses in the surrounding watershed. After 3,900 cal yr
502 B.P., charcoal accumulation and fire frequency increased. Significant increases in grass
503 charcoal reflected a change in the fuel composition in the watershed. Phytolith, isotope
504 and charcoal data suggest that after 3,900 cal yr B.P., the *M. flexuosa* within the basin
505 became increasingly fire-sensitive and the occurrence of a fire within the palm stand
506 would have had consequences for the vegetation not adapted to fire. The fire adapted C₄
507 grass dominated watershed continued to be fire-dependent.

508

509

510 3.4 Zone 4: 2,800 cal yr B.P.- Present: Late Holocene

511

512 During the Late Holocene arboreal taxa was replaced by a pure stand of *M. flexuosa*.
513 C₄ Panicoideae (warm, wet) grasses continued to dominate the surrounding watershed.
514 *Mauritia flexuosa* values reached the highest levels during the Holocene from 2,000-
515 1,200 cal yr B.P. The hat shaped phytoliths indicate very low concentrations of other

516 palms during this time. There was a gradual decrease in *M. flexuosa* towards present
517 coupled with the highest levels of C₄ Panicoideae grasses ca. 200 cal yr B.P. and a
518 decrease in C₄ Chloridoideae (warm, dry) grasses in the surrounding watershed. The
519 lithology consisted of black detrital peat ca. 2450-2050 cal yr B.P. associated with high
520 LOI (ca. 22) and magnetic susceptibility values (ca. 1000). After 2,500 cal yr B.P. the
521 %C, %N, and $\delta^{15}\text{N}$ increased suggesting moist, anoxic conditions that enabled moderate
522 denitrification from the swamp. These lithologic and isotopic data represented the
523 establishment of modern palm swamp characterized by increased autochthonous organic
524 accumulation. The $\delta^{13}\text{C}$ values reached modern levels by 2,800 cal yr B.P. although,
525 values exhibit increased variability, fluctuating between -19 and -24‰ co-varying with
526 the C₄ grass contribution between 10-20%. After ca. 800 cal yr B.P. $\delta^{13}\text{C}$ values were ca.
527 -18‰ and the % C₄ contribution was ca. 50%. These data corresponded to the highest
528 levels of C₄ Panicoideae grass phytoliths in the record. The dark detrital peat lithology
529 was interrupted by two coarse sand layers ca. 1550 cal yr B.P. and ca. 300-200 cal yr
530 B.P., followed by a shift back to black detrital peat ca. 200 cal yr B.P. to present. These
531 sand layers were characterized by a decrease in LOI from ca. 22 to 2, C:N ratios from ca.
532 25 to 0, and $\delta^{15}\text{N}$ from ca. 5 to 0‰ coupled with increased magnetic susceptibility and
533 bulk density values suggesting clastic flood events associated with sandy sediments low
534 in organic material. From 300 cal yr B.P. %C values increased from ca. 1% to >20%
535 reached the highest values in the record. The %N values increased from ca. 0.1 to the peak
536 Holocene values of 1.2 [near] at present. The dramatic increases in both %C and %N were
537 likely the result of in situ carbon cycling and nitrogen fixation.

538 Charcoal accumulation at Huanchaca Mesetta remained low 2,800 to 1,800 cal yr
539 B.P. with a FRI of 5 episodes (periods of increased burning) per 1000yrs from 2,800 to
540 1,800 cal yr B.P. Grass charcoal reached the highest continuous levels ca. 2,800 to 2,000
541 corresponding to high levels of fire adapted C₄ grass phytoliths. Increased grass charcoal
542 coupled with low peak magnitude values and high fire frequency indicated that the
543 vegetation surrounding the palm swamp was fire dependent and fire adapted. However
544 within the moist *M. flexuosa* palm stand, the vegetation remained fire sensitive. Charcoal
545 accumulation increased ca. 1,400 to 1,200 cal yr B.P. and 700 cal yr B.P., and reached
546 peak Holocene values ca. 500-400 cal yr B.P. Increased charcoal was coupled with the
547 lowest FRI values in the record. Peak magnitude increased significantly around 1,200 cal
548 yr B.P. and the largest peak magnitude values ca. 200 cal yr B.P. These charcoal values
549 were cropped for plotting and visualization purposes. Raw counts exceed 1,200 thus the
550 values are also provided as log transformed (Figure 7). Peak frequency increased after ca.
551 400 cal yr B.P. to ca. 4 fire episodes (periods of increased burning) per 1000yrs towards
552 present. There was a decrease in grass charcoal indicating increased woody biomass
553 burned. The increased charcoal accumulation coupled with low FRI and more woody
554 charcoal was interpreted as fire episodes that infrequently penetrated the fire sensitive
555 palm stand and burned the *M. flexuosa* woody biomass.
556 The charcoal, phytolith, and isotope data collectively suggest that the vegetation
557 surrounding the palm swamp was fire dependent and fire adapted while the vegetation
558 within the palm swamp was fire sensitive.

559

560 **4 Discussion**

561

562 *4.1 First Order Control: Edaphic Constraints*

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

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

species composition
are basins located in between rivers? unlikely.
I guess this needs re-formulation

580

581 *4.2 Second Order Control: Climatological Drivers*

582

583 *4.2.1 Late Glacial Surazo Winds and Mauritia flexuosa*

584 Non-analogue Late Glacial vegetation communities are documented from low
585 elevation sites including Laguna Chaplin (14° 28'S, 61° 04'W approximately 40 km west)
586 and Laguna Bella Vista (13°, 37'S, 61°, 33W, 140 km northwest). The absence of
587 *Anadenanthera*, a key indicator in ^{present-day} deciduous and semi-deciduous dry forests was
588 interpreted as reduced precipitation (e.g. longer and/or more severe dry season), increased
589 aridity and lowered atmospheric CO₂ concentrations. These conditions favored C₄
590 grasses, sedges and drought adapted savanna and dry forest tree species (Burbridge et al.,
591 2004). Similarly, the non-analogue Late Glacial vegetation community at Huanchaca
592 Mesetta is notable for the absence of *M. flexuosa*. *Mauritia flexuosa* can tolerate a broad
593 precipitation gradient ranging from 1500 mm to 3500 mm annually in areas with annual
594 temperature averages above 21°C, roughly coinciding with the 1000 masl contour line
595 (Rull and Montoya, 2014). *M. flexuosa* is dependent on local hydrology including water
596 table depth and flooded conditions (Kahn, 1987). The presence of *M. flexuosa* in the
597 lowland records at Laguna Chaplin and Laguna Bella Vista (ca. 200 masl) during the
598 Late Glacial (Burbridge et al., 2004), indicate conditions were sufficiently warm and with
599 a locally wet habitat below the mesetta to support the palms despite an estimated 20%
600 decrease in precipitation (Mayle et al., 2004; Punyasena, 2008). Temperature was thus,
601 likely a limiting factor for the establishment of *M. flexuosa* on the mesetta. However,
602 temperature reconstructions of Late Glacial conditions from Laguna La Gaiba, (ca. 500
603 km SE of Huanchaca Mesetta), indicate temperatures reached modern conditions (ca. 25
604 to 26.5°C) around 15,900 cal yr B.P. and have remained relatively stable to present
605 (Whitney et al., 2011). However, previous studies have suggested the increased
606 frequency of *surazos* winds (Bush and Silman, 2004). An ice cap located on the

arboreal

I think we should consider this as an acronym.

Once introduced (where?) be contingent

a.s.l.

607 Patagonian Andes generated an anomalously high pressure center in northwestern
608 Patagonia resulting in increased *surazo* cold fronts blowing cold, dry, southerly winds
609 northward penetrating the NKMNP region (Iriondo and Garcia, 1993; Latrubesse and
610 Ramonell, 1994). The *surazos* may have been no more intense than those of present, but
611 likely occurred more often and lasted more of the year (Bush and Silman, 2004).
612 Increased frequency of *surazos* would have had little effect on the absolute temperature
613 minima but the mean monthly and annual temperature minima may have been ca. 5°C
614 lower (Bush & Silman, 2004). Based on a lapse rate of 6.4°C/km (Glickman, 2000), the
615 400 m difference between the lowland sites (Laguna Chaplin and Laguna Bella Vista, ca.
616 250 m a.s.l.) and Huanchaca Mesetta (ca. 650-800 m a.s.l.) could have resulted in up to ca.
617 2.6°C difference in average annual temperatures. Despite near modern annual
618 temperatures ca. 15,900 cal yr B.P., the elevational lapse rate coupled with lower mean
619 monthly and annual temperature minima accompanying more frequent *surazos*, likely
620 resulted in climatic conditions below the thermal optimum of 21°C for *M. flexuosa* (Rull
621 and Montoya, 2014). Thus, during the Late Glacial, increased frequency of *surazos* likely
622 resulted in increased biological stress on the vegetation community at Huanchaca Mesetta
623 resulting in vegetation dominated by trees and grasses opposed to *M. flexuosa*.

624

625 4.2.2 Holocene Precipitation and Fuel Moisture and Fuel Availability

626 During the ^mMiddle Holocene the presence of dry forest taxa and increased charcoal
627 accumulation at Laguna Chaplin and Laguna Bella Vista indicate a combination of
628 seasonally flooded savannas and semi-deciduous dry forests (Mayle et al., 2004). At
629 Laguna Oricore (13°20'44.02"S, 63°31'31.86"W, 335 km NW), peaks in drought tolerant

630 ^{arboreal} tree taxa, coupled with maximum charcoal concentrations indicate drier and regionally
631 more open vegetation (Carson et al., 2014). Laguna Granja (13°15'44" S, 63°, 42' 37" W)
632 350km NW was also characterized by open savanna vegetation. These data suggest lower
633 mean annual precipitation (<150 cm) and a longer dry season (>5 months with <100 cm)
634 during the ^mMiddle Holocene (Burbridge et al., 2004; Mayle et al., 2000). Additionally,
635 water levels at Lake Titicaca were ca. 100m below present (Figure 7) attributed to
636 precipitation levels ca. 40% below present (Baker et al., 2001; Cross et al., 2000;
637 D'Agostino et al., 2002). The spatial extent of the ^mMiddle Holocene dry period suggests a
638 common mechanism affecting Amazonian moisture and precipitation. During this period,
639 weakened SASM convective activity was attributed to an orbitally-driven minimum in
640 January insolation at 15-10°S (Berger and Loutre, 1991). Reduced insolation would have
641 restricted the southerly penetration of the ITCZ and deep cell convective activity over the
642 Amazon Basin, thus decreasing the length of the summer rainy season resulting in longer,
643 more severe dry seasons (Berger and Loutre, 1991).

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

651 In the ^lLate Holocene (3,550 cal yr B.P. to present) the pollen assemblages of Laguna
652 Bella Vista, Laguna Chaplin and Laguna Oricore, indicate an expansion of humid

653 evergreen closed-canopy rainforest vegetation coupled with significant decreases in
654 charcoal concentrations (Burbridge et al., 2004; Burn et al., 2010; Carson et al., 2014).
655 Additionally, Lake Titicaca reach modern water levels during this time (Rowe et al.,
656 2003) indicating wetter regional conditions with less severe dry seasons. The rainforest–
657 savanna ecotone is currently at its most southerly extent over at least the last 50,000 years
658 (Mayle et al. 2000; Mayle and Whitney, 2012; Burbridge et al. et al., 2004). The
659 progressive succession through the Holocene in the lowlands of NKMNP from
660 savanna/semi-deciduous forest to semi-deciduous/evergreen forest to evergreen rainforest
661 is part of a long-term uni-directional trend of climate-driven rainforest expansion
662 associated with the regional increase in precipitation associated with a stronger [South] SASM
663 [~~American Summer Monsoon~~] (Mayle et al., 2004). The basin wide increase in mean
664 annual precipitation and reduction in the length/severity of the dry season is attributed to
665 increasing summer insolation at 10-15°S driven by the Milankovitch precessional forcing
666 (Mayle and Whitney, 2012). The wet conditions of the Late Holocene created ideal
667 waterlogged conditions for the establishment of the *M. flexuosa* palm swamp in the
668 drainage basin.

669 The asynchrony of charcoal records between the low elevation sites and Huanchaca
670 Mesetta is attributed to fuel flammability. Increased precipitation led to different effects
671 on fire frequency, with decreases in the lowlands and increases on Huanchaca Mesetta.
672 Increased precipitation in the low elevation closed canopy rainforests decreased fuel
673 flammability along with fire activity. Whereas increased precipitation resulted in the
674 build up of fire-adapted C₄ grasses on the surrounding plateau. Lightning-caused fire is
675 common in *cerrádo* savannas today and highest in more open savanna ecosystems, such

676 as the Huanchaca Mesetta (Ramos-Neto and Pivello, 2000). Increased precipitation
677 would have been accompanied by increased incidence of lightning-caused fire, fueled by
678 the abundance of fire adapted grass fuels in the surrounding watershed.

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

686

687 4.3 Human versus Natural Drivers on the Evolution of *Mauritia Flexuosa*

688 The development of *M. flexuosa* swamps and increases in charcoal accumulation
689 have been seen in numerous paleoecological records from savanna ecosystems in
690 Colombia (Behling and Hooghiemstra, 1998, 1999; Berrio et al., 2002b, 2007),
691 Venezuela (Montoya et al., 2011b; Rull and Montoya, 2014; Rull, 1999, 2009) and Brazil
692 (Da Silva Meneses et al., 2013). Previously two hypotheses have been proposed to
693 account for the Late Holocene development of these *M. flexuosa* palm swamps. The first
694 hypothesis suggests that the increase in *M. flexuosa* and charcoal accumulation is
695 attributed to increased precipitation and wet season lightning fires driven by strengthened
696 SASM activity (Kahn and de Castro, 1985; Kahn and de Granville, 1992; Kahn, 1987).
697 The second hypothesis suggest that the simultaneous rise in *M. flexuosa* and charcoal was
698 linked to intentional planting or semi-domestication of *M. flexuosa* for human use
699 (Behling and Hooghiemstra, 1998, 1999; Montoya et al., 2011a; Rull and Montoya,

700 2014). Currently there is insufficient archaeological evidence from any of these savanna
701 sites to support a robust anthropogenic signal (Rull and Montoya, 2014). Previous
702 paleoecological studies in the lowlands demonstrate humans were the dominant driver of
703 local-scale forest-savanna ecotonal change in those areas (e.g. Bolivian *Llanos de Moxos*)
704 dominated by complex earth-moving pre-Columbian cultures (Carson et al., 2014;
705 Whitney et al., 2014). These studies suggest that even in areas with extensive geometric
706 earthworks, inhabitants likely exploited naturally open savanna landscapes that they
707 maintained around their settlement, rather than practicing labor-intensive deforestation of
708 dense rainforest (Carson et al., 2014). Evidence for human occupation of the lowlands
709 has been found with ceramics from soil pits in an interfluvial ca. 25 km northwest of
710 Laguna Chaplin and abundant ceramics and charcoal dating to ca. 470 cal yr B.P.
711 recovered from anthosols (terra preta) throughout La Chonta ca. 150 km west of NKMNP
712 (Burbridge et al., 2004). Implementing a new methodology to concentrate and isolate
713 cultigen pollen (Whitney et al., 2012), the re-analysis of pollen data from Laguna Bella
714 Vista and Laguna Chaplin revealed *Zea mays* pollen was present around 1700 to 940 cal
715 yr B.P., approximately 2000 years after the initial increase in *M. flexuosa* at these sites
716 (B. Whitney personal communication, [July 22, 2014]). Although humans were present in
717 NKMNP, there is no evidence that they drove regionally significant ecotonal changes in
718 forest-savanna boundaries. The patterns of forest-savanna shifts exhibited at these sites
719 are consistent with climate forcing (Burbridge et al., 2004). The absence of
720 archaeological data on Huanchaca Mesetta dominated by nutrient poor, rocky soil, that
721 would have been infertile for the practice of agriculture coupled with the limited access to
722 the mesetta would have made human habitation unlikely. Although the *M. flexuosa*

723 swamps may have been used for hunting and gathering purposes, these data do not
724 suggest humans were the driving mechanism behind the initial establishment or
725 proliferation of *M. flexuosa* in the interfluvial depressions of the Mesetta.

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

734

735

736 *5.0 Implications for Savanna Ecology and Conservation*

737 The presence of savanna vegetation for the past 14,500 years at Huanchaca Mesetta
738 has significant implications for understanding modern savanna ecology and for the
739 implementation of conservation strategies in the 21st century. Previous research on the
740 evolution and development of savanna ecosystems has attributed much of the
741 development of savannas to anthropogenic origins driven by the intentional use of fire
742 (Arroyo-Kalin, 2012; Behling and Hooghiemstra, 1999; Behling, 2002; Berrio et al.,
743 2002a; ^{Behling} Hooghiemstra et al., 1998; Ramos-Neto and Pivello, 2000; Rull and Montoya,
744 2014). The results from this study demonstrate that the continued presence of the savanna

745 ecosystem at Huanchaca Mesetta is attributable to edaphic and climatic controls. The
746 presence of fire in this system for the past 14,500 years indicates that naturally occurring,
747 lightning-caused fire is an integral part of the ecology of the savanna ecosystem. Despite
748 changes in floristic composition and tree density within the drainage basin, the savanna
749 ecosystem has been resilient to major climatic changes in both temperature and
750 precipitation since the Late Glacial period. These data suggest that savanna ecosystems
751 will continue to be resilient to future climate change associated with global warming.
752 The long history of ecosystem stability in the face of dramatic climate variability attests
753 to the fact that the Huanchaca Mesetta savanna is one of the most floristically diverse
754 savannas anywhere in the Neotropics (Da Silva Meneses and Bates, 2002). The continued
755 protection of the Huanchaca Mesetta savanna as a UNESCO world heritage site, coupled
756 with the savannas natural resilience to climatic change exhibited over at least the past
757 14,500 years, indicates that despite significant global warming ^{projected} ~~predicted~~ for the 21st
758 century (IPCC, 2014), the future is optimistic for the conservation and preservation of
759 biological diversity in the Huanchaca Mesetta savanna ecosystem.

760

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Tables and Figures

Table 1 AMS Radiocarbon Dates from Huanchaca Mesetta

Lab Number	Material	Depth (cm)	¹⁴ C age (yr B.P)	δ ¹³ C Ratio	Intcal 13 B.P 2. sigma
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

unit of time

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153 NK MNP
178 SAM
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193 a.v.l.
257 AMS write in full also
261 yr BP
271 cal yr BP
should be introduced here?
289 MS
393 CCA
281 LOI
400 FRI

162 Fig. 1
259 Table 1
273 Fig. 2
400 Fig. 3
410 Fig. 4
413 Fig. 5
417 Fig. 7
420 Fig. 6
inversion in numbering