NEOTROPICAL CLIMATE, VEGETATION, AND FIRE HISTORIES ON LOCAL TO REGIONAL SCALES

by

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STATEMENT OF DISSERTATION APPROVAL

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ABSTRACT

During the 21st century global change and deforestation have increased fires in the Amazon. Protection of rainforests and sustainable land-use practices in the Neotropics are critical for preserving biodiversity and buffering for climate. To make informed policy decisions it is necessary to understand how natural and anthropogenic disturbance shaped modern Neotropical ecosystems. Long-term paleoecological records can aid in understanding the susceptibility and resiliency of Amazonia ecosystems to modern disturbance. The purpose of this research is to reconstruct fire, vegetation, and soil geochemistry histories from Neotropical ecosystems to advance the understanding of long-term ecological variability on subcentennial to multimillennial temporal scales and local-to-regional spatial scales. Three primary research aims are addressed: (1) provide subcentennial resolution of ecological change and natural disturbances at control sites in savanna and rainforests ecosystems, (2) evaluate the climate-fire relationship on local-to-regional scales, and (3) synthesize existing pollen data from the Amazon basin to identify potential ecosystem thresholds in the past. Results from this study indicate edaphic/climatic controls drove *cerrãdo* savanna fire and vegetation histories for the past 15,000 years, fire activity exhibited similar patterns on local and regional scale, and regional scale vegetation change was associated with periods of increased climatic variability since the last Glacial period, the last 21,000 years. The combined pressures of climate and human activities over the past 1,500 years have resulted in the highest levels of regional vegetation change. Increased ecosystem variability, a result of both human and natural drivers, in recent times suggests greater ecological instability and lowered buffering capacity of tropical ecosystem. These data can inform adaptive management policy to preserve diversity across a range of ecosystems in the Neotropical South America.

Dedicated to my family and friends.

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CHAPTER 1

INTRODUCTION

During the 21st century global change and deforestation have increased fires in the Amazon (Malhi & Phillips, 2004; van der Werf et al., 2010). Protection of rainforests and sustainable land-use practices in the Neotropics are critical for biodiversity and climate (Bonan, 2008; Lewis, 2006). To make informed policy decisions it is necessary to understand how natural and anthropogenic disturbance shaped modern Neotropical ecosystems. Long-term paleoecological records can aid in understanding the resiliency and susceptibility of Amazonia ecosystems to modern disturbance. Data presented in this dissertation have practical applications for planning, management, and resource conservation across a range of ecosystems in the Neotropical South America.

Recent studies indicate land use (deforestation and logging), severe drought episodes, and increased frequency of forest fire interact synergistically to drive transitions in Amazon forests to low-biomass, low-moisture, fire-adapted woody vegetation (IPCC, 2014). Some processes are self-reinforcing through positive feedbacks that create the potential for large-scale ecological tipping points or vegetation transitions (Figure 1). Deforestation provides increased ignition sources to flammable forests, contributing to forest dieback. Climate change contributes to tipping points by increasing drought severity, reducing rainfall, and raising air temperatures (IPCC, 2014). Forest fires kill trees, increasing the likelihood of subsequent burning. This is magnified when tree death enables forests to be invaded by flammable grasses, which can inhibit regional rainfall through changes in albedo and evapotranspiration (IPCC, 2014).

The combustion of biomass leads to the release of carbon dioxide (CO_2), methane (CH_4), carbon monoxide (CO), and nitrous oxide (N_2O; Pyne, 2001). These emissions, particularly CO_2 and CH_4, affect global climate as long-lived GHGs (Harrison, Marlon, & Bartlein, 2010). From 1997–2001 pyrogenic emissions from South America contributed 30% of the mean annual emissions of biomass burned (van der Werf et al., 2010).

The impact of positive feedbacks was exemplified in 2005 when a combination of human disturbance and climatic conditions resulted in a large increase in tree mortality in the Amazon (Howard, 2014). In 2010 climatic conditions combined with abundant available fuels from deforestation, resulted in one of the most extensive fire seasons on record (Fernandes et al., 2011; Lewis, Brando, Phillips, van der Heijden, & Nepstad, 2011). More than 25,000 fires burned 1.5 million hectares (2.47 million acres) in Bolivia, Brazil, Paraguay, and Argentina (Casey, 2010; CNN Wire Staff, 2010). Most of these fires were likely set deliberately to clear land for crops or pasture (Schmaltz, 2010).

Factors that may decrease the likelihood of a tipping point include less frequent extreme droughts (Marengo et al. 2011), suppression of land management fires, forest fires extinguished on a large scale (Soares-Filho et al., 2012), decreased deforestation, and reforestation of cleared lands (Nepstad, Stickler, Soares-Filho, & Merry, 2008). As of 2013, there has been a 77% decline in deforestation in the Brazilian Amazon (INPE, 2013). Currently, 80% of the region's forests remain intact, evidencing that policy-led avoidance of a fire-mediated tipping point is plausible.

The modern increase of anthropogenic fire activity in the Neotropics has stimulated research interest in the long-term legacy of human-biosphere interactions on the resiliency of Neotropical ecosystems. However, the nature and scale of pre-Columbian land use and its modern legacy on Amazonian landscapes are among the most debated topics in New World archaeology, paleoecology, and conservation (Balée, 2006; Bradshaw, 2003; Denevan, 2012; Heckenberger, 2008; Iriarte et al., 2012; Mayle, Langstroth, Fisher, & Meir, 2007; McKey et al., 2010; Schaan, 2010). This debate hinges on the geographic scale and ecological legacy of pre-Columbian human impacts in Amazonia (Carson et al., 2014; McMichael et al., 2012). The prevailing paradigm of the early 21st century characterized human disturbance in the Neotropics as negligible: small tribes living in harmony with ancient Neotropical forests, exerting minimal impact on their surroundings (Meggers, 1979, 2003).

During the past decade increasing archaeological evidence from central lowland Amazonia suggest large, socially complex, pre-Columbian societies inhabited regions within the Amazon evidenced by geoglyphs, earth-mounds, causeways, and canals (Denevan, 1992; Erickson, 2001; Erickson & Balée, 2006; Heckenberger, 2008; Heckenberger & Neves, 2009; Pärssinen & Schaan, 2009; Schaan, 2010). This evidence challenged the pristine forest paradigm, resulting in an alternative hypotheses of extensive humanized landscapes or cultural parklands heavily altered by deforestation and anthropogenic burning (Erickson, 2010; Erickson & Balée, 2006; Heckenberger, 2008).

Recently Carson et al. (2014) used coupled local and regional scale paleoecological records to reconstruct land use from seasonal western and central Amazonia (Carson et al., 2014). Carson et al. (2014) found that in areas of dense human occupation, inhabitants exploited natural forest features in ecotonal zones that did not necessitate large scale deforestation (Carson et al., 2014). These data suggest highly localized versus spatially extensive human impact on surrounding ecosystems. To aid in understanding the scale of human disturbance in the Neotropics, it is necessary to identify dominant controls in savanna-rainforest ecotones. Thus, more long-term paleoecological records from ecotonal control sites, devoid of human occupation, are needed.

Paleoecological archives can improve the understanding of the pre-Columbian legacy on modern ecosystem resiliency to climatic changes and increased anthropogenic disturbance. Paleoproxy records of fire, vegetation, and soil geochemistry aid in clarifying ecosystem response to past disturbance (Cronin, 2013). Extending the spatial and temporal scale of paleoecological archives can be achieved through high-resolution sampling and the synthesis of existing paleoecological records (Figure 2). A broader space-time scale enables the analysis of climatically driven changes in fire activity, the legacy of past disturbances on modern Neotropical ecosystems, and ecosystem thresholds (tipping points).

The purpose of this research study is to reconstruct fire, vegetation, and soil geochemistry histories from Neotropical ecosystems to advance the understanding of natural long-term ecological variability on subcentennial to multimillennial temporal scales and local, meso, and regional spatial scales. This work has three primary research aims that will be addressed in the subsequent chapters:

(1) Provide subcentennial resolution control sites in savanna and rainforests

ecosystems

(2) Evaluate the climate-fire relationship on local, meso, and regional scales

(3) Synthesize regional pollen data to identifying potential ecosystem thresholds

Sediment cores were collected from Noel Kempff Mercado National Park (NKMNP), Bolivia, near an ecotonal region with *cerrãdo* savanna and *terra firme* rainforest ecosystems. To date, evidence suggests negligible anthropogenic impact in the ecosystems in NKMNP (Burbridge, Mayle, and Killeen, 2004; Mayle, Burbridge, amd Killeen, 2000). These study sites thus provide paleoecological records of natural controls on fire, vegetation, and soil geochemistry. These data will attempt to evaluate aid in clarifying the extent of anthropogenic disturbance in pre-Columbian settlements by providing baseline records of natural paleoecological change since the Last Glacial period.

Chapter 2 analyzes sediment cores collected from the Huanchaca Mesetta palm swamp in the upland *cerrãdo* savanna ecosystem of NKMNP. The objective of this chapter is to investigate drivers of fire and vegetation in *cerrãdo* savanna ecosystems. The tropical forest-savanna ecotone 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). Additionally carbon emissions from savanna fires contributed ca. 12% of the annual increase in atmospheric carbon in the past decade (van der Werf et al., 2010). According to current estimates, 20% of the *cerrãdo* remains undisturbed, and only 1.2% of the area is preserved in protected areas (Mittermeier, Myers, Mittermeier, & Robles Gil, 1999), making the *cerrãdo* likely the most threatened savanna in the world (Da Silva

Meneses & Bates, 2002). Despite these important ecological roles, there are currently a limited number of paleoecological archives from the *cerrãdo* savanna ecosystems in the Neotropics.

A common perception in Neotropical savanna ecology is that fire, particularly in the Late Holocene, is largely an artifact of anthropogenic disturbance (Behling, Berrio, & Hooghiemstra, 1999; Behling & Hooghiemstra, 1998; Montoya, Rull, & Nogué, 2011; Rull & Montoya, 2014; Rull, 2008). However, studies of fire in the *cerrãdo* of Brazil demonstrate that lightning fires are an integral part of fire in these savanna ecosystems (Ramos-Neto & Pivello, 2000). This study provides a subcentennial record of fire activity and vegetation change, devoid of significant human occupation, to help address these perceptions. Three hypotheses are tested in this research:

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

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

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

The Huanchaca Mesetta record extends the space-time scale of fire activity and vegetation change in *cerrãdo* savanna ecosystems by providing one of the longest subcentennial resolution records of fire activity and vegetation change in Neotropical savanna ecosystems. This long-term perspective of savanna resiliency and natural fire activity are integral to management and conservation efforts in the 21st century.

Chapter 3 analyzes sediment cores for Cuarto Vientos palm swamp from the *terra firme* rainforest in NKMNP. The objective of this chapter is to investigate subcentennial fire and soil geochemistry histories devoid of significant human impact since the Last Glacial period. *Terra firme* rainforests have the highest local species richness (*alpha* diversity) of ecosystems in NKMNP (Mayle et al. 2007). High soil moisture in the *terra firma* results in dense, lush vegetation accompanied by negligible fire activity (Bassini & Becker, 1990; Bush et al., 2007; Glaser, Haumaier, Guggenberger, & Zech, 2014). Today human induced fire activity for agricultural is the primary cause of fire in rainforest ecosystems (IPCC, 2014).

Previous paleoecological research indicates the current southerly extent of the *terra firme* ecosystem in NKMNP is a recent phenomena characteristic of the Late Holocene (past few thousand years; Burbridge et al., 2004; Mayle et al., 2000). A paleoecological record from Laguna Chaplin (10 km east of Cuatro Vientos) was characterized by seasonally dry tropical forests (SDTF) with greater than present fire activity (Burbridge et al., 2004). Fire activity in SDTF was likely frequent and potentially left ecological legacies for the subsequent *terra firme* ecosystems. Subcentennial sampling resolution of past fire activity can help inform the long-term role of fire in past and present ecosystems.

To extend the spatial scale of past fire activity, subcentennial charcoal data from Cuatro Vientos (local scale) were compared to existing charcoal records within NKMNP (meso scale) and to regional charcoal records (regional scale). These data were interpreted with existing paleoclimate records (Cross, Baker, Seltzer, Fritz, & Dunbar, 2000; Cruz, Burns, & Karmann, 2005; Rowe et al., 2003; Thompson et al., 1998) to assess the response of fire to long-term climatic variations. Previous regional charcoal syntheses suggest that periods of increased climatic variability can result in greater fire activity (Brown & Power, 2013; Marlon et al., 2008; Marlon et al., 2013). To explore fire-climate linkages, three hypotheses are tested:

(1) Climate is the first order control of fire activity and soil geochemistry at Cuatro Vientos
(2) Fire activity at Cuatro Vientos follows patterns of biomass burning in NKMNP
(3) Periods of increased climatic variability result in increased regional fire activity

The Cuatro Vientos record extends the space-time scale of fire activity and soil geochemistry in *terra firme* rainforest ecosystems by providing one of the longest subcentennial resolution records of fire activity and vegetation change in *terra firme* ecosystems and in the synthesis of broader spatial scale fire records. A better understanding of climatically driven fire behavior of different spatial scales will be valuable to making informed fire management policies in the Neotropics.

Chapter 4 synthesizes existing pollen data from the Amazon lowlands (<2,000 m elevation). The objective of this chapter is to investigate the use of pollen data in identifying past ecosystem thresholds (tipping points or accelerated succession). Past ecosystem thresholds have the potential to inform future Neotropical tipping points predicted as a response to positive feedback and global climate change (IPCC, 2014).

To investigate past ecosystem thresholds, regional pollen data were synthesized extending the spatial and temporal range of a single site vegetation record. Data for this analysis are compiled from the Latin American Pollen Database (LAPD), Neotoma, and coauthor contribution. This chapter implements square cord distance (SCD) dissimilarity analysis to detect rate of change (R.O.C.) in vegetation change across the Neotropics over the last 15,000 years. This time period was selected based on the chronological resolution of the existing pollen data and oribitally driven climatic changes span this period. Three hypotheses were addressed in this chapter:

(1) Variability in the R.O.C. was not constant over time

(2) Regional patterns of variability in the R.O.C. were synchronous

(3) Periods of nonrandom variability were linked to regional drivers (e.g., climate, humans)

The successful identification of ecosystem transitions through the synthesis of pollen data can help to identify ecosystem thresholds. These data will be crucial to management and conservation policies as positive feedback exert increasing challenges of Neotropical ecosystems.

Chapter 5 summarizes the major findings from this dissertation and discusses how this study contributes to the understanding of natural climate-fire-vegetation linkages in the Neotropics in three ways. First, data presented in this dissertation extend the spatial and temporal scale of paleoecological change in the Neotropics. Second, local-meso-regional charcoal syntheses extend the understanding of climate variability on millennial scale fire activity in the Neotropics. Third implementing SCD dissimilarity analysis of synthesized pollen records can aid in understanding ecosystem resiliency and vulnerability to climatic variability in Neotropical ecosystems since the Last Glacial period.

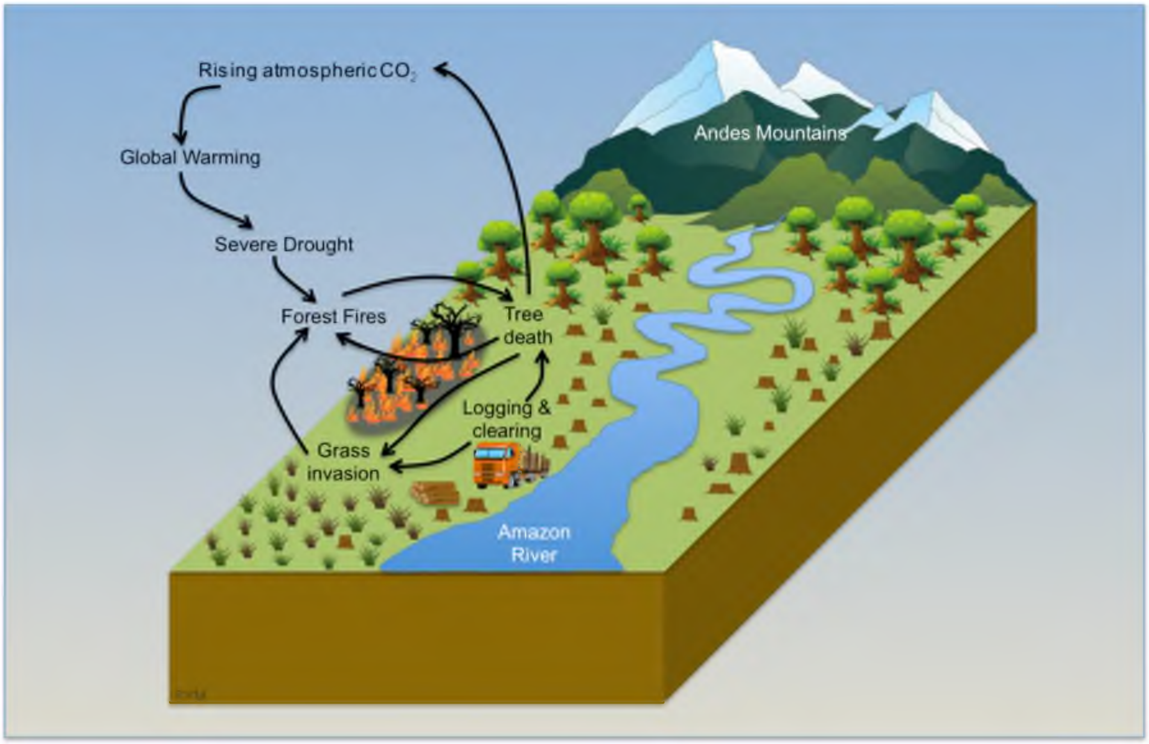


Figure 1 Climate-fire feedbacks in the Amazon. Modified from the IPCC, 2014

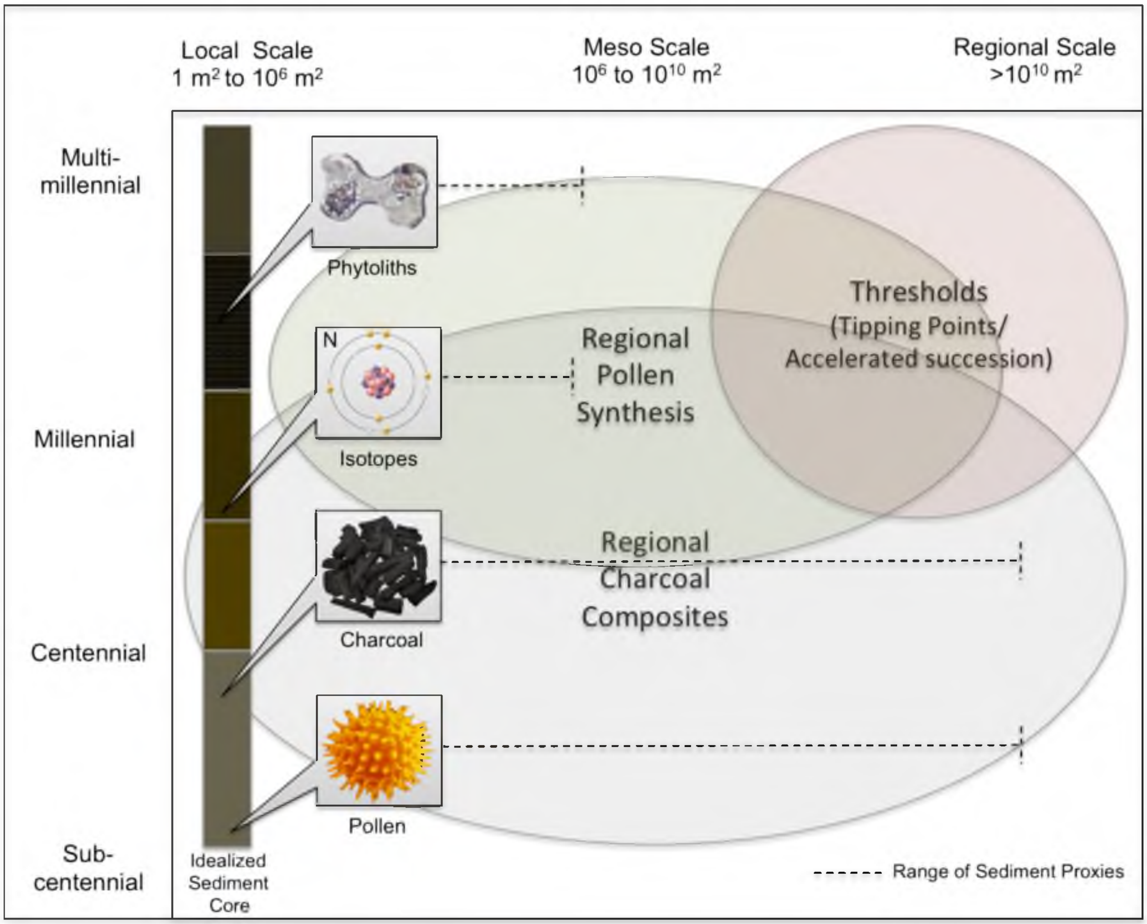


Figure 2 Extending the space-time scale: subcentennial sampling and paleoecological proxy syntheses

CHAPTER 2

THE EFFECTS OF PAST CLIMATE VARIABILITY ON FIRE AND VEGETATION IN THE CERRÃDO SAVANNA OF THE HUANCHACA MESETTA, NE BOLIVIA

Introduction

The *cerrãdo* savanna of central South America is the largest, richest, and likely most threatened savanna in the world (Da Silva Meneses & 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, Mittermeier, Mittermeier, Da Fonseca, & Kent, 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 (Smith el 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, Meir, & Brown, 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, Asner, Levick, Martin, & Chadwick, 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, 1998). The development of the variety of *cerrãdo* vegetation communities is largely the result of the heterogeneous nature of the edaphic features (Killeen, 1998), 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 & Haridasan, 2005).

In addition to edaphic constraints, climate also has a prominent role in determining *cerrãdo* savanna vegetation structure and fire activity (Ribeiro & Walter, 2008). The *cerrãdo* biome is dominated by a warm, wet-dry climate associated with the seasonal migration of the Intertropical Convergence Zone (ITCZ; Da Silva Meneses & 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 & 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 & 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 semiarid environments, such as the *cerrādo*, increases in precipitation tend to increase fire, whereas increased precipitation in humid environments can reduce fire (Marlon et al., 2008; Marlon et al., 2013).

The seasonality of the precipitation coupled with abundant wet-season lightning ignitions (Ramos-Neto & Pivello, 2000) is linked to high fire frequency in the *cerrādo* (Miranda, Sato, Neto, & Aires, 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 & Pivello, 2000). High biomass production during the wet season results in abundant dry fuels favoring frequent fires throughout the year (Ramos-Neto & 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 *cerrādo* increases fire intensity. Based on an ecosystem's adaptation to fire it can be classified as independent, fire-sensitive, and fire-dependent (Hardesty, Myers, & Fulks, 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 (3,000 cal yr BP) there is increasing evidence for the increase in *Mauritia flexuosa* and fire activity in Bolivia, Colombia, Venezuela, and Brazil that has been attributed to both natural and anthropogenic drivers (Behling & Hooghiemstra, 1999; Berrio, Hooghiemstra, Behling et al., 2002; Berrio, Hooghiemstra, Marchant et al., 2002; Da Silva Meneses et al., 2013; Kahn & de Castro, 1985; Kahn, 1987, 1988; Montoya, Rull, Stansell, Bird, et al., 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 the long-term environmental change of *cerrãdo* savanna palm swamps in Bolivia from the Late Glacial (ca. 15,000 cal yr BP) to present. Paleoecological proxies including lithology, magnetic susceptibility, loss on ignition, charcoal, stable isotope, and phytolith data are used to investigate long-term ecosystem processes in the *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, and (3) the Late Holocene rise in *Mauritia flexuosa* was driven by climate rather than a change in human land-use.

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* (nonflooded) evergreen rainforest, riparian and seasonally-flooded humid evergreen forest, seasonally flooded savanna, wetlands, upland *cerrãdo* savannas, and semideciduous 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 3; Burn, Mayle, & Killeen, 2010). Huanchaca Mesetta palm swamp (14°32’10.66”S, 60° 43’55.92”W, elevation: 1070 m a.s.l.) is located within NKMNP on the Huanchaca Mesetta – an 800–900 m elevation table mountain. The palm swamp is approximately 200 by 50 meters, comprised entirely of a monospecific stand of the palm *Mauritia flexuosa*.

Climate

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

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 & Power, 1989). The top of the mesetta is flat, with a gently rolling surface and at elevations ranging from 500–900 m above sea level (a.s.l.; Da Silva Meneses & 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 intermesetta depressions formed from a combination of erosion, dolerite dike intrusions, and faulting on the mesetta (Da Silva Meneses & Bates, 2002; Litherland & 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).

Vegetation

The *cerrãdo* savanna on Huanchaca Mesetta is dominated by a continuous grass cover with sparsely scattered small trees and shrubs that grow on the thin, well-drained, nutrient-poor soils (Killeen, 1998). 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.* Subshrubs include *Eugenia puncifolia and Senna velutina,* and herbaceous species include *Chamaecrista desvauxii* and *Borreria sp.* Grass 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, 1998). In the interfluvial depressions organic rich soil is sufficiently deep to support humid evergreen forests islands, which are typically dominated by monospecific stands of *Mauritia flexuosa* (Da Silva Meneses & Bates, 2002; Mayle & 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. 1,000 m elevation) in warm/wet climates (Rull & Montoya, 2014). *M flexuosa* swamps favor interfluvial depressions that remain flooded during the dry season, when the surrounding terrains dry out (Huber, 1995a, 1995b; Kahn & 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 & 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 interfluvial depressions (Killeen, 1998). 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, 1998). 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 interfluvial depressions (Killeen & Schulenberg, 1998). Limited soil development precludes rainforest from developing on the large, rocky expanses of the mesetta (Killeen & Schulenberg, 1998). The essentially treeless campo *cerrado* that grows around Huanchaca Mesetta palm swamp is edaphically constrained and has likely grown on this mesetta for millions of years (Mayle & Whitney, 2012). Thus, the vegetation of the Huanchaca Mesetta is influenced by both climatic and nonclimatic controls including seasonal hydrologic conditions, edaphic soil constraints and frequent fire activity (Killeen & Schulenberg, 1998).

Materials and Methods

Sediment Core

A 5.48 meter-long sediment core from Huanchaca Mesetta palm swamp was collected in 1995 using a Livingstone modified square-rod piston corer from the center of the swamp. The uppermost 15 cm, containing a dense root mat, were 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 paleoenvironmental data.

Chronology

The chronological framework for Huanchaca Mesetta was based on eight AMS radiocarbon dates from noncalcareous bulk sediment and wood macrofossils analyzed at the University of Georgia Center for Applied Isotope Studies (Table 1). The uncalibrated radiometric ages are given in radiocarbon years before 1950 AD (years 'before present', yr BP). The errors are quoted at 1 standard deviation and reflect both statistical and experimental errors. Radiocarbon ages were calibrated using CALIB 7.0 and the IntCal13 calibration dataset (McCormac et al., 2004). IntCal13 was selected in place of the SHcal13 calibration curve because of the latitudinal location (14°S) of Huanchaca Mesetta and the proximal hydrologic connection with the origin of the South American Summer Monsoon in the northern hemisphere. The seasonal migration of the Intertropical Convergence Zone (ITCZ) is thought to introduce a northern hemisphere ^{14}C signal to the low latitude southern hemisphere (McCormac et al., 2004). This study area is located in the low latitudes (14°S) and within the range of the ITCZ migration; thus, the IntCal13 calibration curve was selected for the radiocarbon calibrations. Following calibration, the mean age value of the largest probability at 2 sigma was used to create the smoothing spline age model using classical age-depth modeling, in the package CLAM (Blaauw, 2010) within the open-source statistical software R (Figure 4).

Loss on Ignition

The variability in the organic and carbonate content of sediments is used, in conjunction with magnetic susceptibility, to identify periods of variability in sediment composition and organic content throughout the Holocene. Organic and carbonate sediment composition was determined by Loss-on-Ignition, conducted at contiguous 1 cm increments throughout the cores. For each sample, 1 cm^3 of sediment was dried in an oven at 100 ˚C for 24 hours. The samples underwent a series of 2-hour burns in a muffle furnace at 550 ˚C and 1,000 ˚C to determine the relative percentage of the sample composed of organics and carbonates. Concentration was determined by weight following Dean's (1974) standard methodology.

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, Belnap, Reheis, Lamothe, & Luiszer, 2001). Shifts in the magnetic signature of the sediment can be diagnostic of a disturbance event (Gedye, Jones, Tinner, Ammann, & Oldfield, 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.

Charcoal

Sediment samples were analyzed for charcoal pieces greater than 125 µm using a modified macroscopic sieving method (Whitlock & 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 cc 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.

Nonarboreal 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, Lynch, Calcote, & Hotchkiss, 2007; Mueller, Long, Williams, Nurse, & McLauchlan, 2014; Tweiten, Hotchkiss, Booth, Calcote, & Lynch, 2009). Charcoal pieces were grouped into nonarboreal and arboreal categories based on their morphology, which enabled the characterization of fuel sources in the charcoal record (Mueller et al., 2014).

Charcoal counts were converted to charcoal concentration (number of charcoal particles cm^{-3}) and charcoal accumulation rates by dividing the deposition time (yr cm^{-1}) using CHAR statistical software (Higuera, Brubaker, Anderson, Feng, & Brown, Thomas, 2009). In CHAR, charcoal data were 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, Peters, Brubaker, & Gavin, 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.

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, Ingram, Hughes, & Florsheim, 2006). Previous research on δ^{13}C values of the Huanchaca Mesetta have been used to determine the relative proportions of C_4 savanna grasses versus C_3 woody vegetation (Killeen et al., 2003; Mayle, Langstroth, Fisher, & Meir, 2007).

Sediment δ^{15}N integrates a variety of nutrient cycling processes including the loss of inorganic N to the atmosphere through denitrification (McLauchlan, Lascu, Myrbo, & Leavitt, 2013; Robinson, 1991). Denitrification and the subsequent enrichment of δ^{15}N requires abundant available carbon, available nitrate, and anaerobic conditions (Seitzinger et al., 2006). Thus, wet, anoxic soils tend to have enriched values of $\delta^{15}N$. 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).

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 & 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 & 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 & Slater, 1960). C_3 subfamilies, including the Pooideae, are adapted to cool and moist conditions and 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. 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 (400–1,000x). The number of phytoliths counted varied from 101–320 per slide. The modern palm swamp is a monospecific stand of *Mauritia flexuosa* that produces globular echinate phytoliths but does not produce hat-shaped phytoliths characteristic of other 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 *Mauritia flexuosa* during the Middle and Late Holocene, phytolith percentages from globular echinate phytoliths were calculated using a separate sum. Percentages of non-*Mauritia* phytoliths were calculated on the basis of the total sum of phytoliths. Phytolith identification was made by comparison with modern plant reference collections curated at the University of Exeter Archaeobotany Lab. The classification of Poaceae implemented a three-partite morphological classification related to grass taxonomy (Panicoideae-Chloridoideae-Pooideae; Twiss, Suess, & Smith, 1969) and further developed in both North America (Fredlund & Tieszen, 1994) and the Neotropics (Bertoli de Pomar, 1971; Iriarte & Paz, 2009; Iriarte, 2003; Piperno & Pearsall, 1998; Piperno, 2005; Sendulsky & Labouriau, 1966; Söndahl & Labouriau, 1970; Teixeira da Silva & Labouriau, 1970; Zucol, 1996, 1998, 1999, 2000). The phytolith percentage diagrams were plotted using Tilia and Tilia Graphing software (Grimm, 1987).

Results

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

Zone 1: 14,500–11,500 cal yr BP Late Glacial

Arboreal taxa, grasses, and Asteraceae (opaque perforated platelets) phytoliths (Figure 5) dominated Late Glacial vegetation on Huanchaca Mesetta. 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 Late Glacial. The presence of C_3 Pooideae grasses is interpreted as cooler Late Glacial conditions compared to present. The Late Glacial vegetation community at Huanchaca Mesetta lacks a modern analogue plant community in NKMNP. The presence of both of 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 Late Glacial. The magnetic susceptibility and bulk density values were low and exhibit minimum variability compared to the rest of the record (Figure 6). Coupled with LOI organic values below 10%, the sediment lithology was summarized as a low-energy depositional environment with relatively low nutrient input. Organic matter deposited during the Late Glacial had $\delta^{13}C$ values of -16‰ (Figure 7), 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 & 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 Late Glacial, indicating relatively low amounts of organic matter in the system compared to those of today. The C:N ratio ranged from 20 to 30, indicating a terrestrial organic matter source. N concentrations were low from 0.1 to 0.2% and the $\delta^{15}N$ values were ca. 5‰ indicating minimal denitrification during the Late Glacial. The $\delta^{13}C$, % C_4 contribution, and high C:N values coupled with the phytolith data dominated by trees and grasses, suggest a predominantly terrestrial signal, characterized by open savanna grassland during the Late Glacial. The $\delta^{15}N$ values suggest that sediments within the swamp were drier than present creating aerobic conditions and low denitrification rates. Charcoal accumulation levels were low during the Late Glacial (14,500–12,000 cal yr BP). Fire return interval

(FRI) was 2 fire episodes per 1,000 years (Figure 8). 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 accumulation levels coupled with low magnitude charcoal peaks, suggest that the nonanalogue 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 accumulation coupled with low fire frequency suggest that the Late Glacial environment was likely fire-sensitive within the basin.

Zone 2: 11,500–9,000 cal yr BP Early Holocene

Decreased C_4 Panicoideae grasses and consistent C_3 Pooideae grasses, arboreal, and Asteraceae (opaque perforated platelets) phytoliths dominated the assemblage. The presence of C_3 grasses, and the absence of *M. flexuosa,* the dominant component of the modern basin vegetation, suggest temperatures cooler than present. The lithology, magnetic susceptibility, bulk density, and LOI values indicate minimal shift during the vegetation transition. Organic geochemistry reflected a change in organic matter source, with $\delta^{13}C$ values becoming more negative, indicating an increase in the contribution of C_3 vegetation ca. 11,000 cal yr BP The $\delta^{13}C$ contribution of C_4 grasses decreased dramatically from 60 to 20% during this period (Figure 9). 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 accumulation at Huanchaca Mesetta increased ca.11,200 cal yr BP coupled with an increase in the fire frequency to five episodes (periods of increased burning) per 1,000 years. The peak magnitude values indicated two substantial fire episodes (periods of increased burning) ca. 10,200 and 9,100 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 accumulation and fire episodes suggest that the Early Holocene vegetation community was becoming increasingly more fire dependent and vegetation was likely adapting to the increase in fire frequency associated with the period.

Zone 3: 8,000–3,750 cal yr BP Middle Holocene

Significant vegetation changes occur through the Middle Holocene. From 8,000 to 5,500 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. 7,000 cal yr BP and remain absent for the remainder of the record. Arboreal phytoliths reached the highest levels in the record at 8,000 cal yr BP followed by a slight decline to 3,500 cal yr BP. $\delta^{13}C$ values ranged between -24 and -22‰ from 7,900 cal yr BP to 5,100 cal yr BP. These values corresponded to a diminished C_4 contribution to organic matter (approximately 18%). Decreased C_4 grass phytoliths from 8,000 to 5,000 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 5,000 cal yr BP, C_4 Panicoideae grasses and C_4 Chloride (warm/dry) grasses gradually increased in the surrounding watershed, coupled with increased $\delta^{13}C$ values to -19‰. *Mauritia flexuosa* phytoliths first appeared at 5,000 cal yr BP and gradually increased to modern levels by 3,750 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 8,000 to 3,750 cal yr BP dominated the lithology that transitioned to black detrital peat ca. 3,750 cal yr BP associated with the establishment of *M. flexuosa.* After 4,000 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 8,000 to 3,750 cal yr BP ranging from 2 to 12‰, indicating repeated and extensive dry periods on the mesetta.

Increased charcoal accumulation ca. 8,000 cal yr BP was followed by an abrupt decrease to the lowest values during the record from ca. 7,900 to ca. 3,800 cal yr BP. Peak frequency reached the highest levels of six fire episodes (periods of increased burning) per 1,000 yrs. during the Middle Holocene. These data corresponded to the highest levels of $\delta^{15}N$ values, indicating extended dry periods that likely promoted frequent fires on the mesetta. The first evidence of grass charcoal appeared ca. 6,500 cal yr BP, suggesting a change in the fire ecology on the mesetta. From 5,000 to 3,750 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 3,900 cal yr BP, charcoal accumulation and fire frequency increased. Significant increases in grass charcoal reflected a change in the fuel composition in the watershed. Phytolith, isotope, and charcoal data suggest that after 3,900 cal yr 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.

Zone 4: 2,800 cal yr BP– Present: Late Holocene

During the Late Holocene, arboreal taxa were replaced by a pure stand of *M. flexuosa*. C_4 Panicoideae (warm, wet) grasses continued to dominate the surrounding watershed. *Mauritia flexuosa* values reached the highest levels during the Holocene from 2,000–1,200 cal yr BP. The hat shaped phytoliths indicate very low concentrations of other palms during this time. There was a gradual decrease in *M. flexuosa* towards present coupled with the highest levels of 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 consisted of black detrital peat ca. 2,450–2,050 cal yr BP associated with high LOI (ca. 22) and magnetic susceptibility values (ca. 1,000). After 2,500 cal yr BP the %C, %N, and $\delta^{15}N$ increased, suggesting moist, anoxic conditions that enabled moderate denitrification from the swamp. These lithological 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 2,800 cal yr BP, although values exhibit increased variability, fluctuating between -19 and -24‰ covarying with the

C_4 grass contribution between 10–20%. 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. 1,550 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, 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 near at present. The dramatic increases in both %C and %N were likely the result of in situ carbon cycling and nitrogen fixation.

Charcoal accumulation at Huanchaca Mesetta remained low, 2,800 to 1,800 cal yr BP with a FRI of five episodes (periods of increased burning) per 1,000 yrs. from 2,800 to 1,800 cal yr BP. Grass charcoal reached the highest continuous levels ca. 2,800 to 2,000, 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. Charcoal accumulation increased ca. 1,400 to 1,200 cal yr BP and 700 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 1,200 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 1,200; thus the values are also provided as log transformed. Peak frequency increased after ca. 400 cal yr BP to ca. four fire episodes (periods of increased burning) per 1,000 yrs. towards present. There was a decrease in grass charcoal indicating increased woody biomass burned. The increased charcoal accumulation coupled with low FRI and more woody charcoal was interpreted as fire episodes that infrequently penetrated the fire sensitive palm stand and burned the *M. flexuosa* woody biomass. The charcoal, phytolith, and isotope data collectively suggest that the vegetation surrounding the palm swamp was fire dependent and fire adapted, while the vegetation within the palm swamp was fire sensitive.

Discussion

First Order Control: Edaphic Constraints

Modern vegetation distribution of *cerrãdo* savannas are largely related to edaphic factors (Colgan et al., 2012; Killeen, 1998). Since the Late Glacial, the vegetation, soil geochemistry, and fire history indicate edaphic constraints were the first order of control on vegetation on Huanchaca Mesetta. Despite significant climate variability since the Late Glacial, the open savanna surrounding the basin was continuously dominated by fire adapted 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 covaried 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 vegetation to C_4 drought adapted grasses. Arboreal and palm vegetation was limited to the interfluvial depression basins where soil was sufficiently deep to support more complex vegetation communities.

Second Order Control: Climatological Drivers

Late Glacial Surazos Winds and Mauritia flexuosa

Nonanalogue Late Glacial vegetation communities are documented from low elevation sites including Laguna Chaplin (14°, 28'S, 61° 04'W, approximately 40 km west) and Laguna Bella Vista (13°, 37'S, 61°, 33W, 140 km northwest). The absence of *Ananedanthera*, a key indicator in deciduous and semideciduous 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 tree species (Burbridge et al., 2004). Similarly, the nonanalogue Late Glacial vegetation community at Huanchaca Mesetta is notable for the absence of *M. flexuosa*. *Mauritia flexuosa* can tolerate a broad precipitation gradient ranging from 1,500 mm to 3,500 mm annually in areas with annual temperature averages above 21 °C, roughly coinciding with the 1,000 m.a.s.l. contour line (Rull & 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 a.s.l.) during the Late Glacial (Burbridge et al., 2004), indicate conditions were sufficiently warm and with a locally wet habitat below the mesetta to support the palms despite an estimated 20% decrease in precipitation (Mayle, Beerling, Gosling, & Bush, 2004; Punyasena, 2008). Temperature was thus the likely a limiting factor for the establishment of *M. flexuosa* on the mesetta. However, temperature reconstructions of Late Glacial conditions from Laguna La Gaiba (ca. 500 km SE of Huanchaca Mesetta) indicate temperatures reached modern conditions (ca. 25 to 26.5 °C) around 19,500 cal yr BP and have remained relatively stable to present (Whitney et al., 2011). However, previous studies have suggested the increased frequency of *surazos* winds (Bush & 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 & Garcia, 1993; Latrubesse & 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 & Silman, 2004). Increased frequency of *surazos* would have had little effect on the absolute temperature minima but the mean monthly and annual temperature minima may have been ca. 5 °C lower (Bush & Silman, 2004). Based on a lapse rate of 6.4 °C/km (Glickman, 2000), the 400 m difference between the lowland sites (Laguna Chaplin and Laguna Bella Vista, ca. 250 m.a.s.l.) and Huanchaca Mesetta (ca. 650–800 m.a.s.l.) could have resulted in up to ca. 2.6 °C difference in average annual temperatures. Despite near modern annual temperatures ca. 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 °C for *M. flexuosa* (Rull & Montoya, 2014). Thus, during the Late Glacial, increased frequency of *surazos* likely resulted in increased biological stress on the vegetation community at Huanchaca Mesetta resulting in vegetation dominated by trees and grasses opposed to *M. flexuosa.*

Holocene Precipitation and Fuel Moisture and Fuel Availability

During the Middle Holocene the presence of dry forest taxa and increased charcoal accumulation at Laguna Chaplin and Laguna Bella Vista indicate a combination of seasonally flooded savannas and semideciduous dry forests (Mayle et al., 2004). At Laguna Orícore (13°20'44.02'S, 63°31'31.86"W, 335km NW), peaks in drought tolerant tree taxa, coupled with maximum charcoal concentrations, indicate drier and regionally more open vegetation (Carson et al., 2014). Laguna Granja (13°15'44" S, 63°, 42' 37" W) 350km 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 9), attributed to precipitation levels ca. 40% below present (Baker, Seltzer et al., 2001; Cross et al., 2000; D'Agostino, Seltzer, Baker, Fritz, & Dunbar, 2002). The spatial extent of the Middle Holocene dry period suggests a common mechanism affecting Amazonian moisture and precipitation. During this period, weakened SASM convective activity was attributed to an orbitally-driven minimum in January insolation at 15–10°S (Berger & Loutre, 1991). Reduced insolation would have restricted the southerly penetration of the ITCZ and deep cell convective activity over the Amazon Basin, thus decreasing the length of the summer rainy season resulting in longer, more severe dry seasons (Berger & Loutre, 1991).

The discrepancy in increased fire activity in the lowlands sites and decreased fire activity on the mesetta is attributed to fuel connectivity. In the lowland sites of Laguna Bella Vista, Laguna Chapin, and Laguna 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 (3,550 cal yr BP to present) 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). Additionally, Lake Titicaca reach modern water levels during this time (Rowe et al., 2003) indicating wetter regional conditions with less severe dry seasons. The rainforest–savanna ecotone is currently at its most southerly extent over at least the last 50,000 years (Burbridge et al. et al., 2004; Mayle et al. 2000; Mayle and Whitney, 2012). The progressive succession through the Holocene in the lowlands of NKMNP from savanna/semideciduous forest to semideciduous/evergreen forest to evergreen rainforest is part of a long-term unidirectional trend of climate-driven rainforest expansion associated with the regional increase in precipitation associated with a stronger South American Summer Monsoon (Mayle et al., 2004). The basin wide increase in mean annual precipitation and reduction in the length/severity of the dry season is attributed to increasing summer insolation at 10–15°S driven by the Milankovitch precessional forcing (Mayle & Whitney, 2012). The wet conditions of the Late Holocene created ideal waterlogged conditions for the establishment of the *M. flexuosa* palm swamp in the drainage basin. The asynchrony of charcoal records between the low elevation sites and Huanchaca Mesetta is attributed to fuel flammability. Increased precipitation led to different effects on fire frequency, with decreases in the lowlands and increases on Huanchaca Mesetta. Increased precipitation in the low elevation closed canopy rainforests decreased fuel flammability along with fire activity. Whereas increased precipitation resulted in the build up of fire-adapted 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 & Pivello, 2000). Increased precipitation would have been accompanied by increased incidence of lightning-caused fire, fueled by the abundance of fire adapted grass fuels in the surrounding watershed.

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

Human versus Natural Drivers on the Evolution of Mauritia Flexuosa

The development of *M flexuosa* swamps and increases in charcoal accumulation have been see in numerous paleoecological records from savanna ecosystems in Colombia (Behling & Hooghiemstra, 1998, 1999; Berrio, Hooghiemstra, Marchant, & Rangel, 2002), Venezuela (Montoya, Rull, Stansell., et al., 2011; Rull, 1999, 2009; Rull & Montoya, 2014) and Brazil (Da Silva Meneses et al., 2013). Previously two hypotheses have been proposed to account for the Late Holocene development of these *M. flexuosa* palm swamps. The first hypothesis suggests that the increase in *M. flexuosa* and charcoal accumulation is attributed to increased precipitation and wet season lightning fires driven by strengthened SASM activity (Kahn, 1987; Kahn & de Castro, 1985; Kahn & de Granville, 1992). The second hypothesis suggest that the simultaneous rise in *M. flexuosa* and charcoal was linked to intentional planting or semidomestication of *M. flexuosa* for human use (Behling & Hooghiemstra, 1998, 1999; Montoya, Rull, & Nogué, 2011; Rull & Montoya, 2014). Currently there is insufficient archaeological evidence from any of these savanna sites to support a robust anthropogenic signal (Rull & 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, Rushton, Carson, Iriarte, & Mayle, 2012), the reanalysis of pollen data from Laguna Bella Vista and Laguna Chaplin revealed *Zea mays* pollen was present around 1,700 to 940 cal yr BP, approximately 2,000 years after the initial increase in *M. flexuosa* at these sites (B. Whitney, personal communication, July 22, 2014). Although humans were present in NKMNP, there is no evidence that they drove regionally significant ecotonal changes in forest-savanna boundaries. The patterns of forest-savanna shifts exhibited at these sites are consistent with climate forcing (Burbridge et al., 2004). The absence of archaeological data on Huanchaca Mesetta dominated by nutrient poor, rocky soil, which 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.

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, 2002; Behling & Hooghiemstra, 1999; Berrio, Hooghiemstra, Behling, Botero, & Van der Borg, 2002; Hooghiemstra, Behling, & Jose, 1998; Ramos-Neto & Pivello, 2000; Rull & Montoya, 2014). The results from this study demonstrate that the continued presence of the savanna ecosystem at Huanchaca Mesetta is attributable to edaphic and climatic controls. The presence of fire in this system for the past 14,500 years indicates that naturally occurring, lightning-caused fire is an integral part of the ecology of the savanna ecosystem. Despite changes in floristic composition and tree density within the drainage basin, the savanna ecosystem has been resilient to major climatic changes in both temperature and precipitation since the Late Glacial period. These data suggest that savanna ecosystems will continue to be resilient to future climate change associated with global warming. The long history of ecosystem stability in the face of dramatic climate variability attests to the fact that the Huanchaca Mesetta savanna is one of the most floristically diverse savannas anywhere in the Neotropics (Da Silva Meneses & 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 predicted for the 21st century (IPCC, 2014), the future is optimistic for the conservation and preservation of biological diversity in the Huanchaca Mesetta savanna ecosystem.

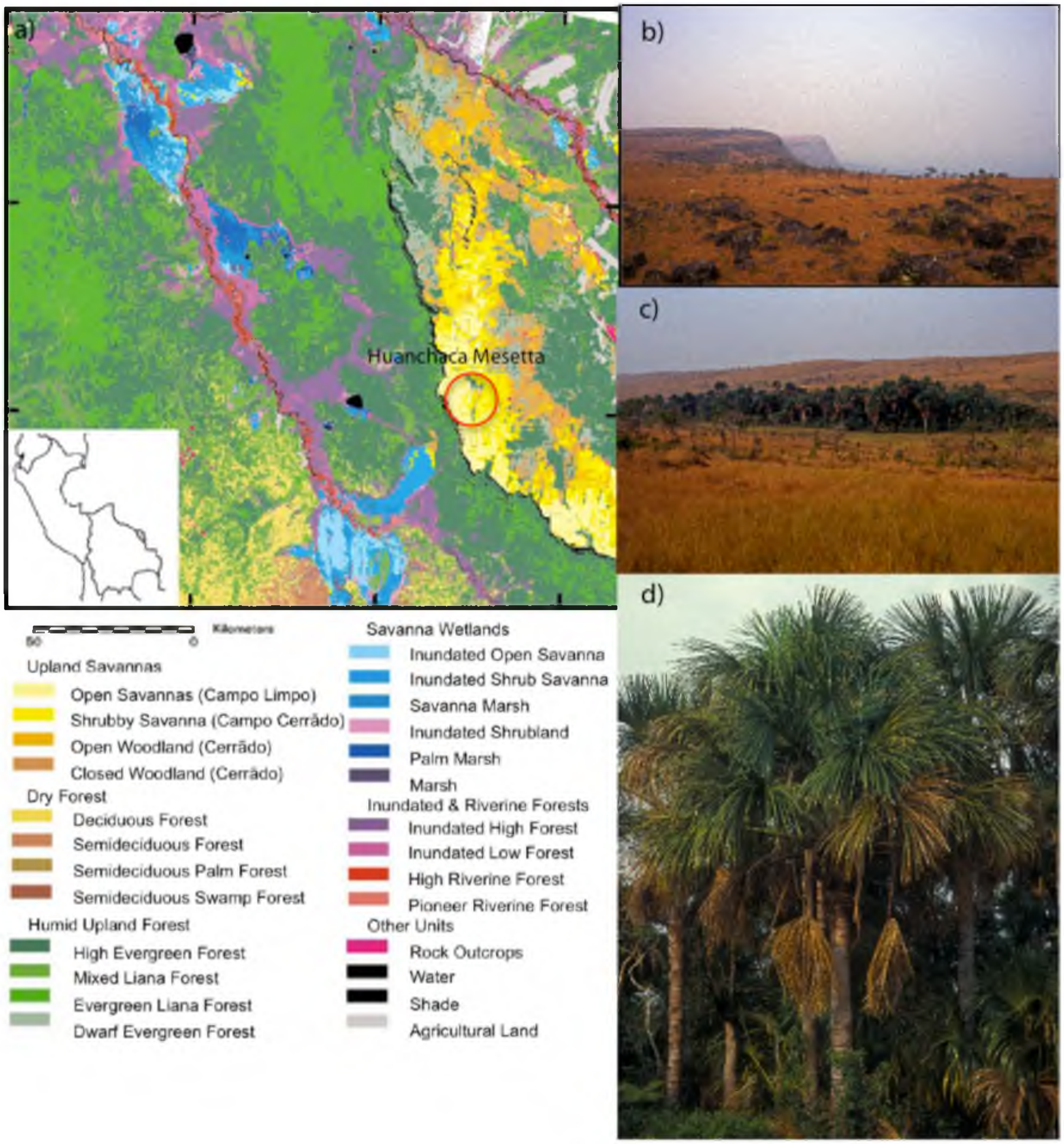
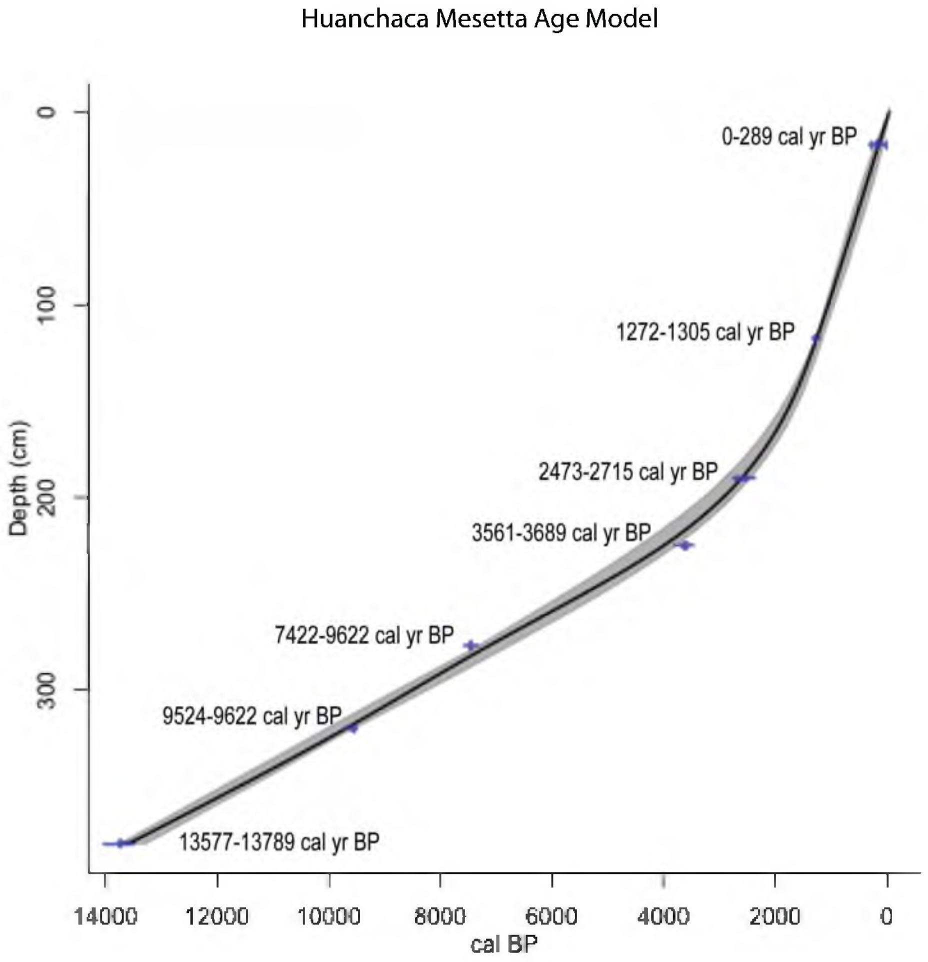


Figure 3 Huanchaca Mesetta study site a) Vegetation map of Noel Kempff Mercado National Park modified from Killeen, 1998, b) View from a top Huanchaca Mesetta, c) Huanchaca Mesetta palm swamp, d) Mono specific stand of Mauritia flexuosa. Photos by F. Mayle

Table 1 AMS Radiocarbon Dates from Huanchaca Mesetta

Lab Number	**Material**	**Depth (cm)**	**^{14}C age (yr BP)**	**δ^{13}C Ratio**	**Intcal 13 BP 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



Huanchaca Mesetta Age Model

Figure 4 Clam age-depth model for Huanchaca Mesetta

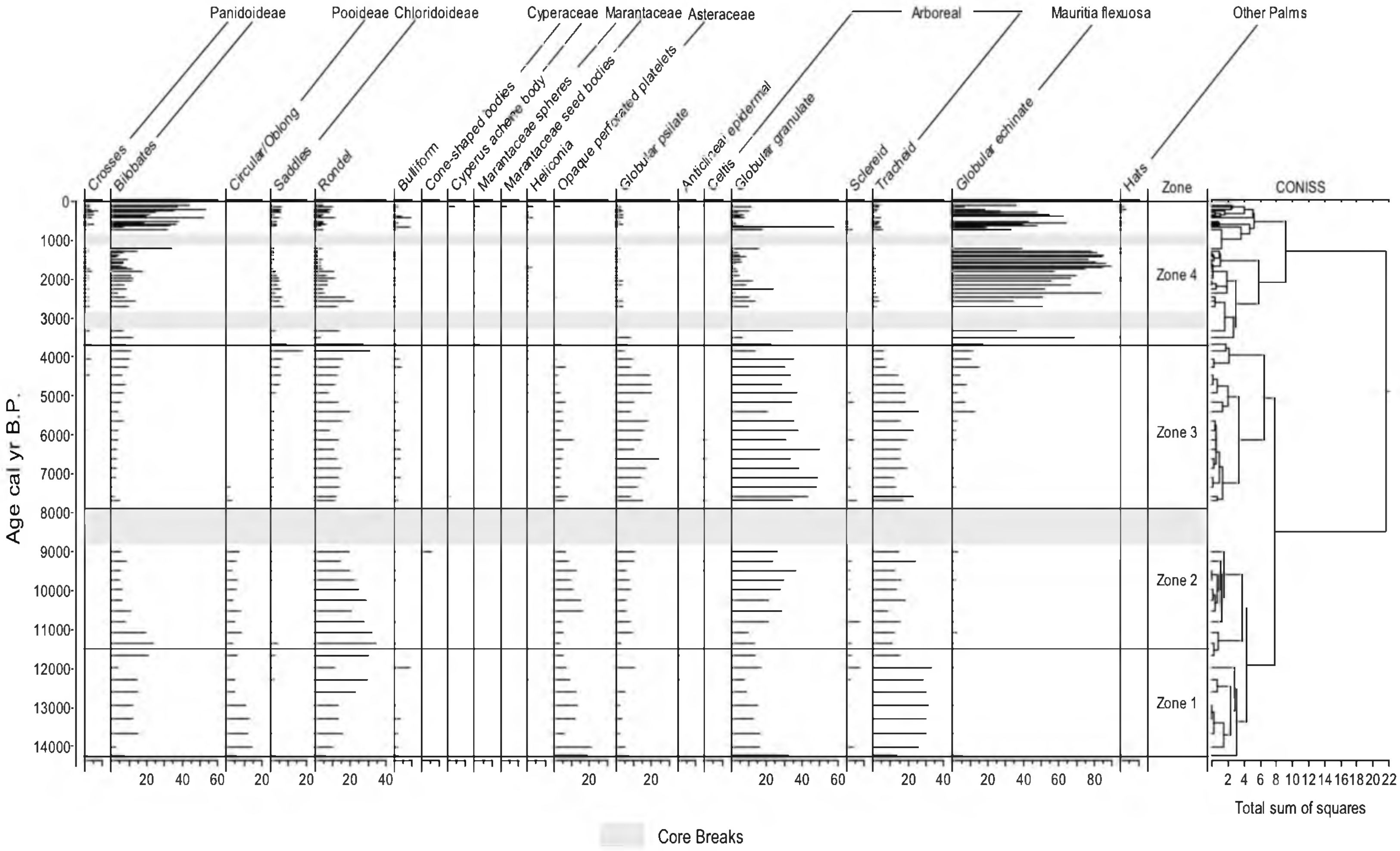


Figure 5 Huanchaca Mesetta phytolith data separated by zones created by constrained cluster analysis (CONISS). Grey bars indicate core breaks

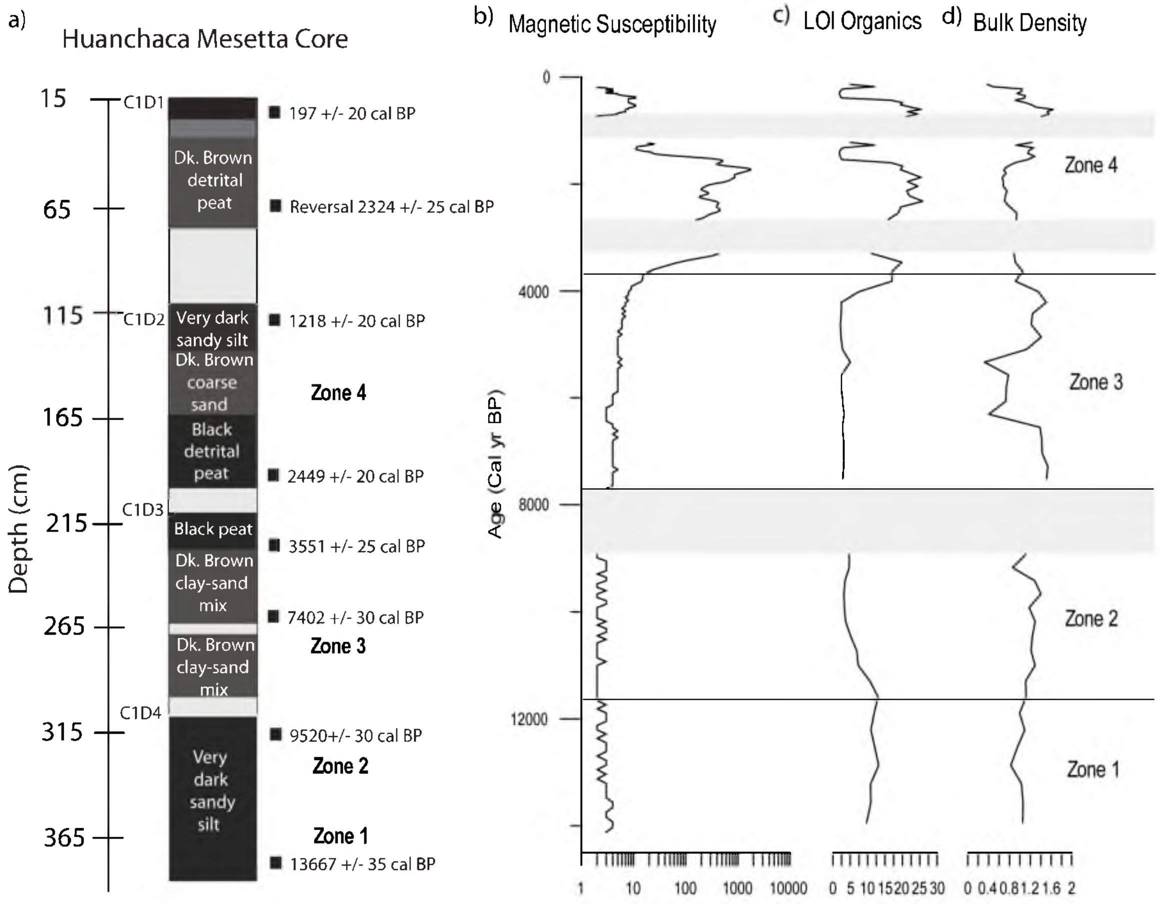


Figure 6 Huanchaca Mesetta lithology a) lithological description of the core profile, b) magnetic susceptibility, c) loss on ignition (LOI), d) bulk density. Grey bars represent core breaks.

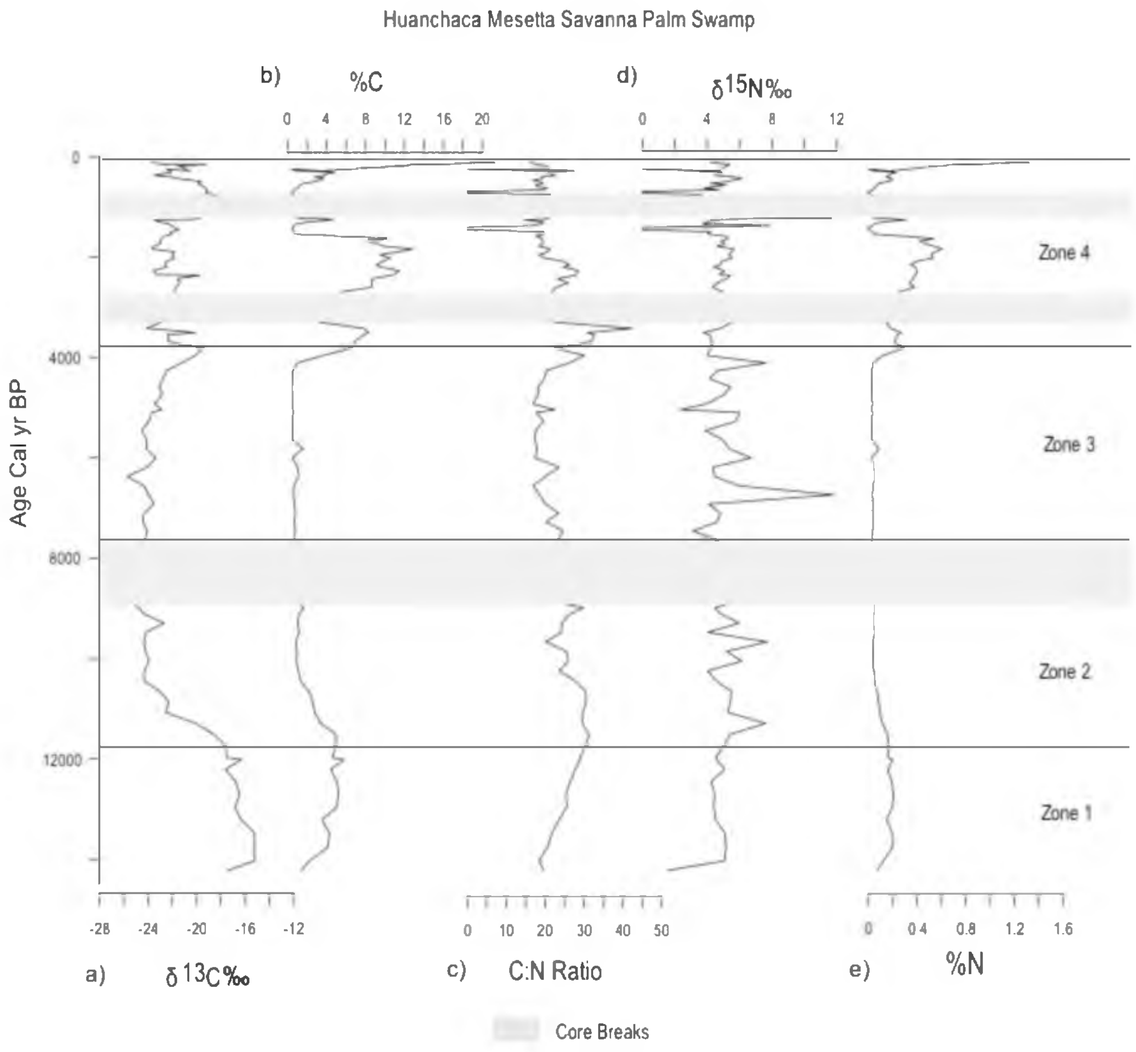


Figure 7 Huanchaca Mesetta stable isotope data: a) δ13C, b) % total carbon, c) carbon to nitrogen ratio, d) δ15N, e) total %N. Grey bars indicate core breaks.

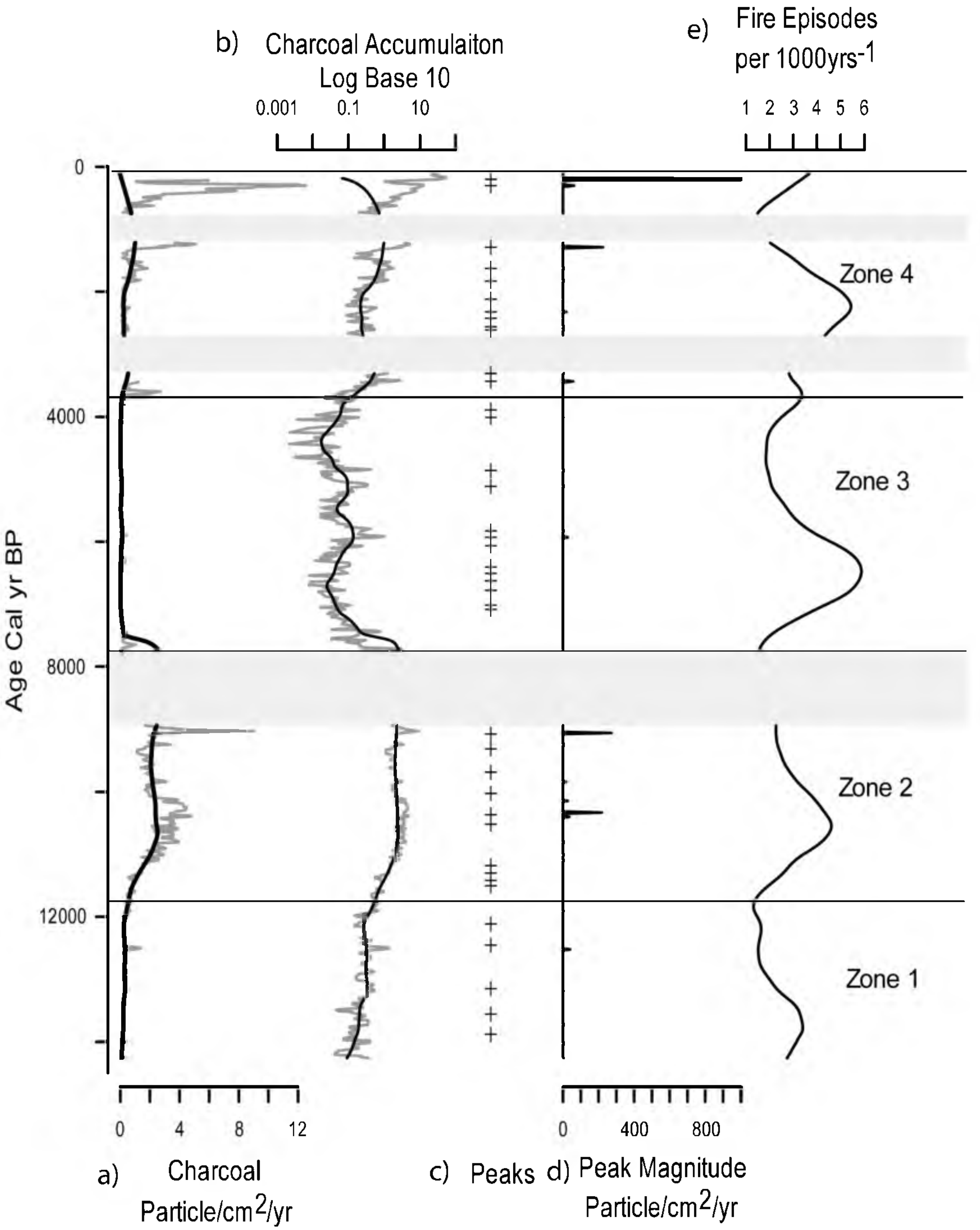


Figure 8 Huanchaca Mesetta charcoal data a) charcoal accumulation in grey, black background, b) charcoal accumulation log base 10 in grey, black background, c) peaks indicated by crosses, d) peak magnitude, e) fire episodes per 1,000 years. Grey bars indicate core breaks.

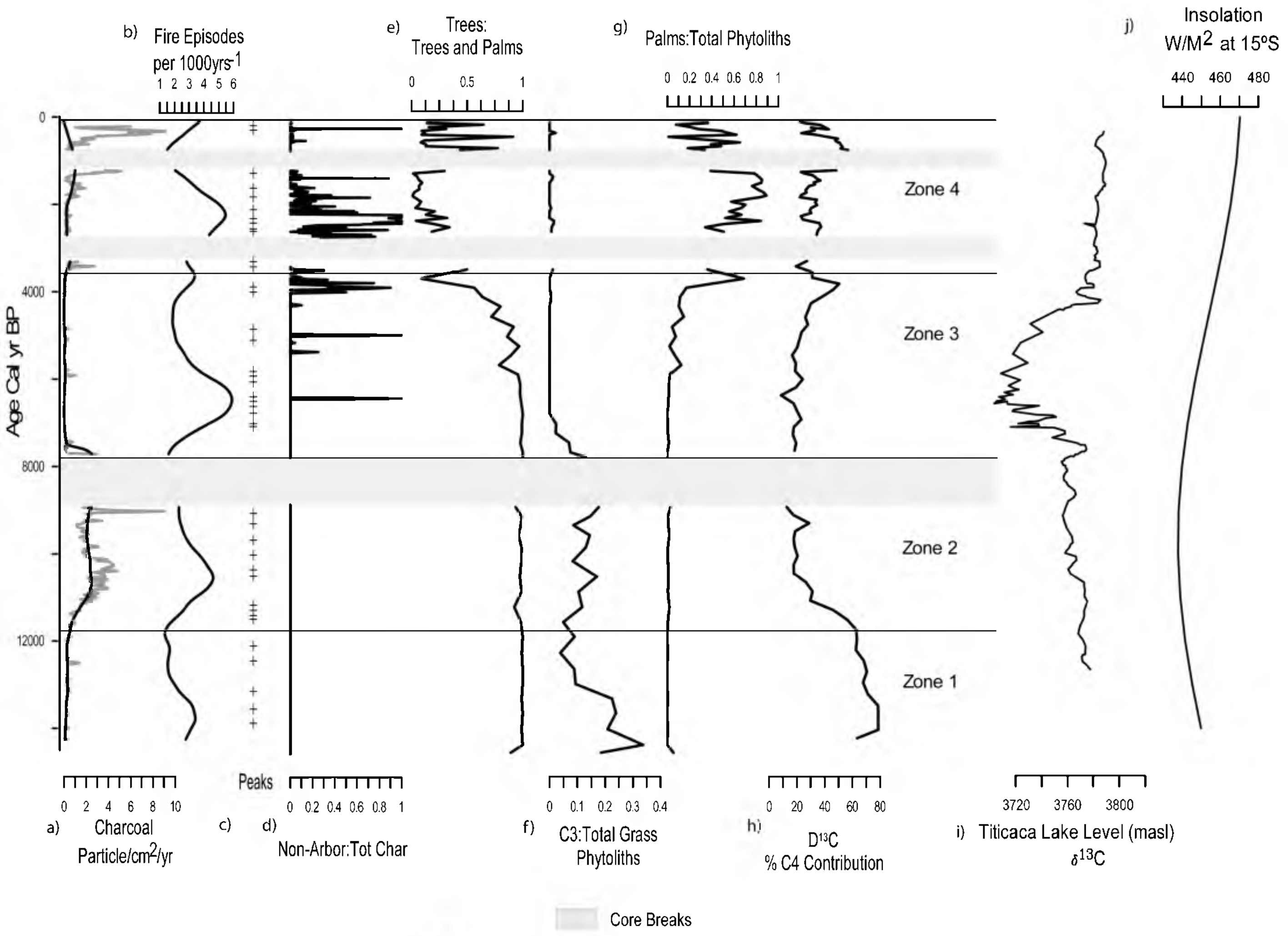


Figure 9 Huanchaca Mesetta summary figure a) charcoal accumulation in grey, black background, b) fire episodes per 1,000 years, c) peaks indicated by crosses, d) ratio of nonarboreal to total charcoal, e) ratio of trees to trees and palms, f) ratio of C3 to total grasses, g) ratio of palms to total phytoliths, h) % C4 contribution, i) lake level of Titicaca in meters above sea level, j) insolation at 15°S. Grey bars indicate core breaks.

CHAPTER 3

LAST GLACIAL MAXIMUM AND MIDDLE HOLOCENE FIRE ACTIVITY IN THE CUATRO VIENTOS PALM SWAMP, NE BOLIVIA

Introduction

Forest fires are growing in size and frequency across the Neotropics (Cochrane, 2003). Additionally, anthropogenic fire activity, deforestation for agriculture, changes in nutrient cycling and global warming create unprecedented challenges to Neotropical ecosystems (Lenton et al., 2008). The Amazon is one of the most significant terrestrial carbons sinks, playing an important role in global climate (Malhi et al., 2002). Net forest fire emissions may have released carbon equivalent to 41% of worldwide fossil fuels use in 1997–1998 (Cochrane, 2003). The global implications of accelerated Neotropical burning and the potential feedbacks between Neotropical deforestation in a warming climate necessitate a clearer understanding of ecosystem responses to past fire activity (Power et al., 2010).

Climate Variability and Fire Activity

Climate variability plays a dominant role in fire activity (Brown & Power, 2013; Marlon et al., 2013; Pyne, 2001). Changes in temperature and precipitation are the most important effects of climate on fire on synoptic climatological time scales (e.g. months to seasons to years). These factors govern net primary productivity (NPP), thus the abundance of available fuels (Marlon et al., 2013). On longer time scales, temperature is quantitatively the most important driver of changes in biomass burning (Daniau et al., 2012). Warmer temperatures are associated with increased burning through vegetation productivity and the occurrence of fire-promoting climatic conditions (Marlon et al., 2013).

The role of temperature can be mediated by precipitation (Brown & Power, 2013). Fire responds differently to increases in precipitation depending if fuel is initially abundant or limited in the ecosystem (Marlon et al., 2013). In arid and semiarid environments, increases in precipitation tend to increase fire, whereas increased precipitation in humid environments can reduce fire (Marlon et al., 2013). Today, fire activity in Neotropical rainforests are very rare in the absence of anthropogenic disturbance (Behling, 2001; Behling & da Costa, 2000; Behling, Keim, Irion, Junk, & Mello, 2001; Turcq et al., 1998). However, in strongly seasonal forests, there is approximately a 10 day window each year during the late stages of the dry season when natural fire is possible (Nepstad et al., 2004; van der Werf, Randerson, Giglio, Gobron, & Dolman, 2008).

Climate, Vegetation, Fire, and Nitrogen

To illustrate climate-vegetation-fire-nitrogen linkages, nitrogen is nested in a modified fire triangle (Pyne, 2001), illustrating multidirectional climate-vegetation-fire linkages (Figure 10). Climate can directly affect nitrogen with conditions that alter from wet (anaerobic) to dry (aerobic) conditions also enrich $\delta^{15}N$ values (Codron et al., 2005). Denitrification and the subsequent enrichment of $\delta^{15}N$ requires abundant available carbon and nitrate and anaerobic conditions (Seitzinger et al., 2006). Thus, wet, anoxic soils tend to have enriched values of $\delta^{15}N$. 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, soil and vegetation $\delta^{15}N$ increase through losses via volatilization, a process shown to preferentially release ^{14}N to the atmosphere (Prieto-Fernández, Carballas, & Carballas, 2004; Saito et al., 2007; Turekian, Macko, Ballentine, Swap, & Garstang, 1998).

Climate can also indirectly affect N by altering vegetation responsible for N fixation. N fixation is abundant in tropical environments due to well-adapted leguminous plants that have high rates of N fixation (Chapin, Chapin, Matson, & Vitousek, 2011). Extreme climatic conditions that limit the development of vegetation can decrease N fixation and the about of N available to other plants (Chapin et al., 2011). The strongest directly coupled feedback in N nutrient cycling is between vegetation and N. N is essential for vegetation growth and succession (Knicker, 2007). N fixation requires N fixing bacteria associated with leguminous plants. Vegetation uptake directly alters the amount of available N through nitrogen fixing bacteria (Chapin et al., 2011).

Fire can also directly affect N nutrient cycling (Dunnette et al., 2014; Knicker, 2007). There are a variety of mechanisms through which the fire event itself, the subsequent changes in vegetation or net primary productivity, or the altered soil properties can affect the N cycle (Knicker, 2007). Fire can build or diminish N stocks and availability depending on variability in fire frequency or severity and rates of N mineralization (unavailable N) and symbiotic N fixation (available N; Giesen, Perakis, & Cromack, 2008; Rustad et al., 2001; Yelenik, Perakis, & Hibbs, 2013). Fires can increase N availability through the release of stored N in biomass (Dunnette et al., 2014). Biological and nonbiological processes during and after burning transform organic N forms into available ammonium and nitrate (Prieto-Fernández et al., 2004). Nitrate requires nitrification and without prompt vegetation uptake, nitrate will be lost from the ecosystem by denitrification or leaching (Knicker, 2007). This N loss can cause a decrease in available N that can result in decreased above and belowground biomass, altered net primary productivity, and the amount of available fuel during a fire (Ojima, Schimel, Parton, & Owensby, 1994).

Modern ecological studies on fire and N cycling are complicated by the spatial and temporal heterogeneity of processes affecting N pools throughout forested landscapes (LeDuc, Rothstein, Yermakov, & Spaulding, 2013). Lake-sediment $\delta^{15}N$ integrates N cycle processes over space and time; thus this paleoecological proxy has the potential to address N cycling at the watershed scale (Dunnette et al., 2014). However, it is likely that there is at least two major mechanisms operating (direct climate and direct fire effects) that could complicate the interpretation of nitrogen data in sediment cores. Coupling N data with charcoal data and independent paleoclimate records may help to resolve past variability in N cycling.

Past Climatic Variability in the Neotropics

Considerable climatic variability has occurred in Neotropical South America since the Last Glacial period that provides information on past fire-climate linkages.

Temperature reconstructions from Laguna La Gaiba in the Pantanal wetlands (ca. 500 km SE of Cuatro Vientos) demonstrate full glacial temperatures were ca. 4 °C cooler than present. Temperatures rose ~4 °C immediately following the LGM at 19,500 yr BP reaching near modern levels (ca. 25 to 26.5 °C), and exhibiting a transitional period to 16,000 yr BP, by 15,900 yr BP (Whitney et al., 2011). Drier than present conditions during the Last Glacial were present in the interior continent of the Neotropical lowlands (Burbridge et al., 2004; Clapperton et al., 1997; Cordeiro et al., 2008; D'Apolito, Absy, & Latrubesse, 2013; Ledru, Bertaux, Sifeddine, & Suguio, 1998; Whitney et al., 2011). Regional climate models of the LGM simulate reduced moisture transport from cooler tropical Atlantic sea surface temperatures delayed the onset of the South American Summer Monsoon (SASM) and weakened the South American Low-Level jet (SALLJ) and the Chaco Low (Figure 11; Cook & Vizy, 2006; Vizy & Cook, 2007), resulting in decreased precipitation in the interior continent of South America.

During the middle Holocene Arid Phase (MHAP), paleobotanical (Burbridge et al., 2004; Carson et al., 2014; de Freitas et al., 2001; Mourguiart & Ledru, 2003; Whitney et al., 2011) and paleoclimatic (Baker, Rigsby et al., 2001; Cross et al., 2000; Cruz et al., 2005; D'Agostino et al., 2002; Thompson et al., 1995) archives suggest lower mean annual precipitation (<150 cm) and a longer dry season (>5 months with <100 cm; Burbridge et al., 2004; Mayle et al., 2000). The MHAP was attributed to an oribitally driven minimum in January insolation at 15–10°S (Berger & Loutre, 1991), which would have restricted moisture advection and deep cell convective activity over the Amazon Basin, reducing the length of the summer rainy season, resulting in longer and more severe droughts (Burbridge et al., 2004; Mayle et al., 2000). Previous data (Whitney et al.,

2011) suggest, however, that the aridity associated with the middle Holocene was not as severe as during the LGM.

During the Late Holocene (4,500 cal yr BP to present), there was a trend in increasing precipitation beginning ca. 4,500^{14}C y BP (4,972–5,312 cal yr BP) that was part of a wide spread phenomenon throughout southwestern Amazonia and the Altiplano (Baker, Seltzer et al., 2001; de Freitas et al., 2001; Mourguiart & Ledru, 2003; Thompson et al., 1998). The Late Holocene increase in precipitation reflects progressive increases in January insolation at 10–15°S and greater southerly penetration of the Intertropical Convergence Zone (ITCZ; Berger & Loutre, 1991). The movement of the ITCZ lengthened the rainy season and increased mean annual precipitation (Burbridge et al., 2004). Neotropical climate since the Last Glacial thus provides key climatic periods with varying intensities of dry conditions and annual temperatures to examine the response of local (1 m^2), meso (10^6 to 10^{10} m^2), and regional (>10^{10} m^2) biomass burning.

Paleofire Archives and Past Climatic Variability

A long-term perspective of fire response to climate can be gained from paleoecological analysis (Cronin, 2013). Local and regional charcoal records combined with paleoclimatic archives provide details on the role of climate on paleofire activity (Brown & Power, 2013). Previous sedimentary charcoal studies in the Neotropics suggest fire activity is associated with periods of high climate variability, including changes in moisture budgets and the intensification of seasonal droughts (Power et al., 2010). The variability of temperature, precipitation, and length of the dry season since the LGM likely extended the dry season, lengthening the amount of time suitable for fire activity.

However, extreme and/or extended dry periods associated with the middle Holocene may have limited the development of fuels, resulting in decreasing fire activity. Centennial-to-millennial-scale charcoal records provide evidence of ecosystem variability to a range of fire responses that can aid in understanding future climate-fire linkages in the Neotropics.

Objectives

This research presents a sedimentary charcoal and soil geochemical record dating to 25,000-years ago from Bahia Cuatro Vientos (14°31'18.5"S, 61° 7' 11.3"W). Cuatro Vientos is a small (<100 m diameter) palm swamp from Noel Kempff Mercado National Park (NKMNP), Bolivia. The aim of this research was to understand how climate variability impacts tropical fire activity and soil nutrient cycling on local scales (1 m^2 to 10^6 m^2) and how past fire activity varied on meso (10^6 to 10^{10} m^2) and regional ($>10^{10}$ m^2) scales. Cuatro Vientos provides one of the first local subcentennial, high-resolution records of charcoal, stable carbon, and nitrogen isotope data in the region. These high-resolution data were combined with existing sediment charcoal archives from eight nearby sites to capture meso and regional scale trends in fire activity since the Last Glacial period.

Cuatro Vientos is located near a climatically sensitive ecotone between humid evergreen rainforests to the north, semideciduous dry forests to the south, and upland *cerrãdo* savanna to the east (Burbridge et al., 2004; Killeen, 1998). Existing paleoecological records from NKMNP indicate climate was a dominant control on the southerly extent of the ecotonal vegetation boundary of the humid evergreen rainforest since the Last Glacial (Burbridge et al., 2004; Mayle et al., 2000). Cuatro Vientos is thus ideally located within this climatically sensitive ecotone to investigate the influence of key time periods of climatic variability in temperature and precipitation on fire activity and soil geochemistry.

Three hypotheses moving from local (1 m^2 to 10^6 m^2), meso (10^6 to 10^{10} m^2), and to regional scale ($>10^{10}$ m^2) were explored in this research: (1) climate is the first order control of local fire activity and soil geochemistry at Cuatro Vientos, (2) Fire activity at Cuatro Vientos follows patterns of biomass burning on meso and regional scales, and (3) periods of increased climatic variability result in increased regional fire activity.

Background

Study Site

Noel Kempff Mercado National Park (NKMNP) is a 15,230 km^2 biological reserve in northeastern Bolivia, and 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* (nonflooded) evergreen rainforest, riparian and seasonally-flooded humid evergreen forest, seasonally flooded savanna, wetlands, upland *cerrãdo* savannas, and semideciduous 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 12; Burn et al., 2010). Two major black-water rivers boarder NKMNP: the Río Iténez to the north and east (Brazilian Border) and the Río Paraguá to the west (Killeen & Schulenberg, 1998). Cuatro Vientos palm swamp

(14°31’18.5”S, 61° 7’ 11.3”W) is ca. 100 meters in diameter and ca. 184 m above sea level. It is located in the Bolivian lowland peneplain that is composed of Cenozoic alluvial sediments (Burbridge et al., 2004). The spatial distribution of the vegetation types is controlled by different geomorphic landscapes (Cochrane, 1985; Oliveira-Filho & Ratter, 1995); however, local edaphic, topographic, and hydrologic conditions can be a controlling factor (Burbridge et al., 2004). The alluvial sediments that dominate the peneplain support closed canopy *terra firme* evergreen rain forests (also referred to as tropical rain forest, tropical moist forest; Marchant et al., 2009).

Vegetation

Terra firme has the highest local species richness (*alpha* diversity) compared to the other ecosystems in NKMNP (Mayle et al. 2007). Plants with mesophyll leaves, occasional sclerophyllous plants, and palms dominate the vegetation of the *terra firme* (Mayle et al. 2007). The majority of the vegetation in the moist *terra firme* is not fire adapted. Common arboreal species include *Pseudolmedia laevis, Qualea paranensis, Erisma gracile, Apulei leiocarpa,* and Moronobea coccinea. The arboreal herbaceous plant *Phenakospermum guianense* is locally abundant and tends to form large dense colonies (Killeen, 1998). Common palms include *Astrocaryum aculeatum* and *Attalea maipa*. *Euterpe precatoria* and *Socratea exorrhiza* are more common in areas with poor drainage or high water tables (Killeen, 1998). Trees typical of secondary forests include *Cecropia* spp., *Schizolobium amazonicum, Apeiba tibourbou, Didymopanax morotoni, Cordia alliadora, Heliocarpus americanus, Casearia gossypiosperma, Erythrinam* spp., and *Zanthoxylum* spp. (Killeen, 1998).

Climate

The climate of NKMNP is characterized by a tropical wet and dry climate with intermediate rainfall between the wetter regions to the northwest and southwest and the drier areas to the northeast (Da Silva Meneses & Bates, 2002). The mean annual precipitation at NKMNP derived from nearby weather stations (Concepción, Magdalena, San Ignacio) indicate mean annual precipitation is ca. 1,400–1,500 mm per year, with a mean annual temperature between 25 and 26 °C (Hanagarth, 1993; Montes de Oca, 1982; Roche and Rocha, 1985). There is a 3 to 5 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 SASM and the ITCZ (Figure 11; Vuille et al., 2012). The SASM transports Atlantic moisture into the basin and corresponds to the southern extension of the ITCZ driven by seasonal variation in insolation (Bush & Silman, 2004; Vuille et al., 2012). During winter (June, July, August), cold, dry polar advections from Patagonia, locally known as *surazos*, can cause short-term cold temperatures to frequently decrease down to 10 °C for several days at a time (Latrubesse et al., 2012; Mayle & Whitney, 2012).

Methods

Sediment Core

A 3.09 meter-long sediment core from Cuatro Vientos palm swamp was collected in August 1995 using a Livingstone modified square-rod piston corer from the center of the swamp. The uppermost 150 cm was comprised of a floating sedge mat and underlying water of the swamp that was not recoverable. Cuatro Vientos sediment cores 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 paleoenvironmental data.

Chronology

The chronological framework for Cuatro Vientos was based on four AMS radiocarbon dates from noncalcareous bulk sediment analyzed at the University of Georgia Center for Applied Isotope Studies (Table 2; Figure 13). The uncalibrated radiometric ages are given in radiocarbon years before 1950 AD (years "before present," yr BP). The errors are quoted at 1 standard deviation and reflect both statistical and experimental errors. Radiocarbon ages were calibrated using CALIB 7.0 and the IntCal13 calibration dataset (McCormac et al., 2004). IntCal13 was selected in place of the SHcal13 calibration curve because of the latitudinal location (14°S) of Cuatro Vientos and the proximal hydrologic connection with the origin of the SASM in the northern hemisphere. The seasonal migration of the Intertropical Convergence Zone (ITCZ) is thought to introduce a northern hemisphere ^{14}C signal to the low latitude southern hemisphere (McCormac et al., 2004). This study area is located in the low latitudes (14°S) and within the range of the ITCZ influence; thus, the IntCal13 calibration curve was selected for the radiocarbon calibrations. Following calibration, the mean age value of the largest probability at 2 sigma was used to create the smoothing spline age model using classical age-depth modeling, in the package CLAM (Blaauw, 2010) within the open-source statistical software R.

Loss on Ignition

Percentage loss-on ignition (LOI) was conducted to determine organic content. 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. LOI was 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 1,000 ˚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).

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, evaporates, 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 Bartington 75 mm aperture. Organic content typically mirrors MS in lake sediments, increasing when MS decreases, and decreasing when MS increases. Thus, the MS and organic content of lake sediments can provide an indication of the relative importance of allogeneic sediment deposition versus authigenic processes in the basin at various times in the past.

Stable Isotopes

Stable carbon isotopes provide a proxy for changes in vegetation structure and composition. Carbon isotopic composition of terrestrial organic matter is determined based on plants' photosynthetic pathway (Malamud-Roam et al., 2006). Photosynthetic pathways differ for C_3 and C_4 plant species (Malamud-Roam et al., 2006). C_4 plants are more adapted to environments that experience water stress through concentrating CO_2 and efficiently photosynthesizing. C_3 plants dominate mesic habitats and are less adapted to water stress and lack the CO_2 concentrating mechanism (Malamud-Roam et al., 2006). $\delta^{13}C$ are used to distinguish the relative contribution of C_3 (ca. -27) and C_4 (-12%) 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 and the subsequent enrichment of $\delta^{15}N$ (McLauchlan et al., 2013; Robinson, 1991). Nitrogen isotopic compositions ($\delta^{15}N$) can help to identify sources of organic matter of lakes and to reconstruct post productivity rates. Additionally, disturbance-induced shifts in terrestrial N cycling can be detected from the natural abundance N stable isotope composition ($\delta^{15}N$) of bulk sediment in organic matter (McLauchlan, Craine, Oswald, Leavitt, & Likens, 2007). The isotopic difference among sources of nitrogen is roughly preserved in the $\delta^{15}N$ values of organic matter from algae ($+8.5^{0}/_{00}$) and from C_3 terrestrial plants ($+0.\ 5^{0}/_{00}$; Peterson & Howarth, 1987). % N can indicate the amount of available N (Pessenda et al., 1998).

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).

Charcoal

Sediment samples were analyzed for charcoal using a modified macroscopic sieving method (Whitlock & Larsen, 2001) to reconstruct the history of local and extra-local fires. The analysis of macroscopic charcoal was used to reconstruct local fire frequency, or charcoal accumulation rates, on a decadal to millennial scale (Brown & Power, 2013; Whitlock & Larsen, 2001). Enumeration is based on simple counts of particles greater than 125 μm. The charcoal samples were analyzed in contiguous 0.5 cm intervals for the entire length of the sediment core. From each 0.5 cm interval, 1 cm^3 of wet sediment was subsampled and disaggregated in 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) was counted in a gridded petri dish at 40× on a dissecting microscope.

Charcoal pieces were identified morphologically. Nonarboreal 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 nonarboreal and arboreal categories based on their morphology, which enabled the characterization of fuel sources in the charcoal record (Mueller et al., 2014). Nonarboreal/total charcoal fuel ratios were determined by dividing the sum of nonarboreal particles by the total charcoal count for each sample in the record. High ratios are interpreted as abundant nonarboreal (grass) type charcoal. Low-intensity surface fires episodes generally produce a high abundance of grass/shrub (nonarboreal) charcoal pieces (Enache & Cumming, 2009).

The resulting dataset was converted to charcoal concentration (number of charcoal particles cm^{-3}) and charcoal accumulation rates by dividing by the deposition time (yr cm^{-1}) using CharAnalysis statistical software (Higuera et al., 2009). Charcoal data were decomposed to identify distinct charcoal peaks based on a standard set of threshold criteria. Low frequency variation is considered background charcoal, which reflects 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.

Regional Charcoal Records

Charcoal records were complied from the Global Charcoal Database (GCD) and analyzed using the paleofire R package software (Blarquez et al., 2014). Charcoal records between 15 and 14°S and 60 to 62°W that had greater than 20 samples were included in this analysis. To facilitate the comparison between various existing data, records were pretreated using standard protocol (Marlon et al., 2008; Power et al., 2008) for transforming and standardizing of individual records that includes (1) transforming noninflux data (e.g., concentration particles/cm^3) to influx values (particle/cm^2/yr), (2) homogenizing the variance using the Box-Cox transformation with a base period of 200 years, (3) rescaling the values using a minimax transformation to allow comparisons among sites, and (4) rescaling the values once more to Z-scores. Sites were smoothed with a half width of 500-year smoothing window and a bootstrap of 100 years.

Results

Variability in the high-resolution stable isotope and charcoal data was used to identify three distinct zones: the Last Glacial Maximum (28,000–20,000 cal yr BP), the Late Glacial (19,000–14,500 cal yr BP), and the Holocene (7,000–3,800 cal yr BP). The Glacial and Holocene periods are discussed separately because of a sediment hiatus from ca. 14,500–7,000 cal yr BP.

Last Glacial (28,000–20,000 cal yr BP)

The lithology of the Last Glacial was characterized by inorganic greyish brown silty clay (Figure 14). The sedimentation rate was ca. 0.01cm/yr. Magnetic susceptibility gradually increased from 28,000 to 25,000 cal yr BP, averaging ca. 6 umt LOI values were <10%. $\delta^{13}C$ values ranged from -20 to -8 $^{0}/_{00}$ (average ca. -18 $^{0}/_{00}$). Less negative values indicate greater contribution of C_4 drought adapted grasses (Figure 15). Total %C values were near zero with a maximum value of ca. 30% at 23,000 cal yr BP. Prior to 23,000 C:N ratios, $\delta^{15}N$, and %N values were ca. zero, indicating C and N limitation was then followed by increasing variability. $\delta^{13}C$ values decreased from -8 to -24$^{0}/_{00}$, indicating a greater contribution of C_3 plants. Total %C and %N values remained <5% with a peak in %carbon to 30% ca. 23,500 cal yr BP. Charcoal accumulation was low and peak frequency ranged between 1 and 2 fire events per 1,000 yrs. (Figure 16). Fire "episodes" were interpreted as periods of increased fire activity versus an isolated fire event. The nonarboreal charcoal ratio indicated both woody and grass charcoal were sources of fuel. Charcoal data from Cuatro Vientos are compared to a network of previously published fire history records to investigate regional fire response to climatic variability. The influx data from Cuatro Vientos and Laguna Chaplin (10 km east) have the lowest charcoal values during the Last Glacial Maximum for the entire record. A limited number of charcoal samples during the Last Glacial from the existing charcoal records limit the comparison to regional biomass burning (Figure 17).

Late Glacial (19,000–14,500 cal yr BP)

Fire activity and soil geochemistry responded to abrupt deglacial warming in the Bolivian lowlands coupled with persistent dry conditions of the Late Glacial period. The lithology of the Late Glacial was dominated by grey silty clay with organic inclusions, and the sedimentation rate was ca. 0.01cm/yr. Magnetic susceptibility values average ca. 6 umt. LOI values were ca. 10%. $\delta^{13}C$ values decrease from -18 to -24 $^{0}/_{00}$, indicating less contribution of organic matter from C_4 plants. C:N ratios exhibited high amplitude variability, but averaged ca. 15.

Fire frequency increased from ca. 1 to 4 events per 1,000 yrs. and was accompanied by the largest peak magnitude values in the record ca. 16,000 cal yr BP. Increased nonarboreal charcoal ratios indicate grass was a dominant fuel source. After 16,000 cal yr BP, the fire regime changed, with a decrease in charcoal accumulation, a change to primarily grass charcoal, and an accompanying decrease in peak magnitude and fire frequency to near zero. There are limited high-resolution charcoal data from Laguna Chaplin during the Late Glacial. However, influx data show an increase in biomass burning after ca. 20,000 cal yr BP

Middle Holocene (8,000–3,800 cal yr BP)

Existing paleoclimate records indicate continued dry conditions associated with the Late Glacial, which is likely responsible for the sediment hiatus at Cuatro Vientos between the Last Glacial and Holocene (ca. 14,500 to 7,000 cal yr BP) and low sedimentation rate at Laguna Chaplin (ca. 9,000 to 6,000 yr BP [10,250–6,980 cal yr BP]; Burbridge et al., 2004). Following the sediment hiatus, the lithology of the middle

Holocene was characterized by black detrital peat. The sedimentation rate increased to ca. 0.03 cm/yr from 6,600 to 3,888 cal yr BP. Magnetic susceptibility values exhibit the lowest record values of ca. -1 while LOI values increased to ca. 90%, reaching the highest values. $\delta^{13}C$ values increased from -22 to -12 $^{0}/_{00}$ followed by a slight decrease towards present supporting a greater contribution of C_4 plants. Total %C values reached maximum values of ca. 50%, coupled with peak LOI values indicating increased organic matter likely associated with the peat layer. C:N values between 12 and 16 indicated a continued terrestrial signal. The $\delta^{15}N$ values show a minor increased from ca. -1 to 0 $^{0}/_{00}$. Lower $\delta^{15}N$ values are associated with peak levels of %C that likely limited denitrification during this period. Total %N values increased to ca. 5. Peak values in charcoal accumulation occurred at ca. 7,000 cal yr BP followed by decreasing values ca. 3,800 cal yr BP.

Fire frequency was ca. 2 events per 1,000 yrs. followed by peak fire frequency of ca. 10 events per 1,000 years around 4,000 cal yr BP. Increased grass and woody charcoal suggest an increase in grass fuels from 6,500 to 3,800 cal yr BP. Charcoal influx data from Laguna Chaplin exhibits a similar pattern of increased burning during the middle Holocene reaching peak charcoal values between ca. 7,000 to 3,000 cal yr BP with a decrease of ca. 4,000 cal yr BP. Regional charcoal summaries suggest biomass burning was low until the onset of the Holocene (ca. 10,000 cal yr BP). Biomass burning increased between ca. 10,000 to 8,000 cal yr BP, decreased until 6,700, and was followed by an increase that remained higher than present until ca. 3,000 cal yr BP.

Discussion

The aim of this research was to understand how climate variability impacts tropical fire activity and soil nutrient cycling on local scales (1 m^2 to 10^6 m^2) and how past fire activity varied on meso (10^6 to 10^{10} m^2) and regional ($>10^{10}$ m^2) scales. Three hypotheses moving from local, meso, and to regional scale were explored in this research: (1) Climate is the first order control of local fire activity and soil geochemistry at Cuatro Vientos, (2) fire activity at Cuatro Vientos follows patterns of biomass burning on meso and regional scales, and (3) periods of increased climatic variability result in increased regional fire activity.

Climate Controls on Fire Activity at Cuatro Vientos

Existing records from NKMNP have identified climatic variability since the Last Glacial as the dominant driver of paleoecological change (Burbridge et al., 2004; Mayle et al., 2000; Whitney et al., 2011). The existing record of Laguna Chaplin (10 km east) offers a 50,000 yr high-resolution pollen record as an analogue of vegetation composition and structure at Cuatro Vientos (Burbridge et al., 2004). Both sites have similar modern *terra firme* vegetation, geomorphic, edaphic, and climatic conditions. Laguna Chaplin thus provides the best approximation for past vegetation change for Cuatro Vientos. The extended drier-than-present conditions associated with the Last Glacial resulted in less negative $\delta^{13}C$ values (ca. -18 to -8), indicating increased contribution of C_4 drought adapted grasses. Presence of savanna vegetation at Laguna Chaplin during the Last Glacial in an area currently covered by humid rainforests indicate increased dry climatic conditions in the Bolivian lowlands (Burbridge et al., 2004). Cuatro Vientos and Laguna

Chaplin both have low charcoal influx levels during the Last Glacial period, likely as a result of the cool, dry Last Glacial conditions (Cruz et al., 2005; Thompson et al., 1998; Whitney et al., 2011) that suppressed fuel accumulation and decreased biomass burning.

Temperature reconstructions of Late Glacial conditions from Laguna La Gaiba demonstrate a transitional deglacial period (ca. 20,000 and 16,000 yr BP). Temperatures reached near modern levels (ca. 25 to 26.5 °C) by 19,500 yr BP and have remained relatively stable to the present (Whitney et al., 2011). The climate remained drier than present until ca. 12,800 BP when the onset of wetter conditions occurred (Whitney et al., 2011). $\delta^{15}N$ values from Cuatro Vientos exhibited the greatest variability from 23,000 to 15,000 cal yr BP ranging from 0 to 5, indicating increased denitrification. Environmental conditions that alter from wet (anaerobic) to dry (aerobic) conditions enrich $\delta^{15}N$ values (Codron et al., 2005). Increased denitrification was likely associated with the increased length of the dry season during the Last Glacial (Whitney et al., 2011). The warm, dry conditions of the Late Glacial likely created climate conditions conducive to fire as evidenced by increased charcoal accumulation and high peak magnitude at Cuatro Vientos.

The MHAP (Baker, Rigsby et al., 2001; Baker, Seltzer et al., 2001; Cruz et al., 2005; Thompson et al., 1998) was evidenced by the sediment hiatus at Cuatro Vientos from ca. 14,500 to 7,000 cal yr BP and decrease sedimentation at Laguna Chaplin (Burbridge et al., 2004). Charcoal values at the end of the sediment hiatus at Cuatro Vientos reach the highest values on record. As precipitation increased into the Late Holocene, there is a change from clay to organic rich peat dominated lithology starting ca. 6,500 cal yr BP coupled with peak %C, %N, and C:N values. These changes were accompanied by a greater contribution of C_4 drought and fire adapted grasses as indicated by the less negative $\delta^{13}C$ values (-18 to -12). This interpretation is supported by pollen data from Laguna Chaplin that indicated the continued presence of seasonally flooded dry forest-savanna vegetation (Burbridge et al., 2004). The presence of fire/drought-adapted vegetation coupled with increased fire activity corresponds to the longer dry seasons characteristic of the MHAP (Burbridge et al., 2004).

After 6,000 cal yr BP, precipitation began to increase in the Amazon potentially linked to precessional forcing (Baker, Seltzer et al., 2001). Increased charcoal accumulation, moderate peak magnitude values, and the highest fire frequency in the record coupled with abundant nonarboreal charcoal suggest frequent, low magnitude fires that were likely the result of precipitation driven increase in the development of fine fuels. Variability in stable carbon and nitrogen isotope and charcoal data from Cuatro Vientos support the interpretation of climate as the dominant driver, validating hypothesis number one.

Potential Climate-Vegetation-Fire-Nitrogen Interactions

There are very few studies exploring climate-fire-nitrogen interactions in the Neotropics (Lobo, Mozeto, & Aravena, 2001; Pessenda et al., 2010). Modern ecological studies demonstrate the importance in N nutrient cycling for the production of biomass, particularly following a fire (Knicker, 2007; Ojima et al., 1994). Both climate and fire can alter N. Climatic (precipitation variability and length of dry season) and can alter N as the result of changes in $\delta^{15}N$ values from denitrification (Codron et al., 2005). Additionally, studies on fire activity and nitrogen indicate fire and the release of nutrients in burned biomass can increase available N (Knicker, 2007). To investigate long-term N cycling dynamic, a combination of lithological, charcoal, stable isotope and vegetation data were used to explore climate-fire-nitrogen linkages in the Neotropics. Existing pollen data from Laguna Chaplin indicate that seasonally dry tropical forest and savanna vegetation were present in the region from the Last Glacial period to ca. 2,000 ^{14}C yr BP (ca. 1,861–2,070 cal yr BP). The continuity in the vegetation composition coupled with consistent lithological characteristics during the Last Glacial suggest that the increased fire activity ca. 15,900 cal yr BP likely released stored N into the sediment through biomass burning resulting increase % N (Figure 18).

During the middle Holocene, charcoal influx values, fire frequency, and %N are the highest in the record. The interpretation of N cycling was complicated by a change in the lithology from grey clay to organic rich peat. There is a similar lithological transition at Laguna Chaplin; however, the pollen data from Laguna Chaplin does not indicate any substantial changes in vegetation during this time. The increase in % N could be attributed to the release of stored N through the burning of existing biomass or the change in nitrogen sequestration associated with fixing bacteria on leguminous plants. The lack of synchroneity in charcoal influx and % N data suggest fire was not the controlling factor of N variability during the Holocene. Rather, the increase in precipitation likely drove the proliferation of leguminous plants and nitrogen fixing bacteria that increased atmospheric N sequestration. The increase in available N coupled with increased precipitation likely resulted in increased biomass accumulation and available fuels. These data correspond to the change in the lithology to organic rich sediments and increased in % C indicative of the production of in situ organic material. This interpretation is supported by increased abundance of seasonal dry forest taxa at Laguna Chaplin (ca. 10,000 to 6,400 cal yr BP) and increased charcoal accumulation that indicate more drought-tolerant/fire-adapted vegetation (Burbridge et al., 2004). These data indicate that Holocene climate controlled vegetation change that drove variability exhibited in % N.

Local, Meso, and Regional Scale Fire Activity

The neighboring site of Laguna Chaplin has a larger basin size (ca. 4–6 km) versus Cuatro Vientos (<100 m). Previous studies on charcoal taphonomy (Brown & Power, 2013; Whitlock & Anderson, 2003; Whitlock & Larsen, 2001) and charcoal morphology (Jensen et al., 2007; Mueller et al., 2014; Tweiten et al., 2009) suggest that the size of the charcoal particles and the proximity to the fire rather than the size of the basin play the most significant role in recording past fire activity.

The method used for charcoal analysis at Laguna Chaplin (Rhodes, 1998) and Cuatro Vientos (Whitlock & Larsen, 2001) followed slightly different sieving methodologies to determine the size class distribution of charcoal particles to obtain insights into differing charcoal source areas (e.g., local versus regional). The charcoal data from Laguna Chaplin includes size classes <53 μm) and >53 to <180 μm, representing regional charcoal and >180 μm to <250 μm, >250 μm to <500 μm, and >500 μm representing local charcoal (Burbridge et al., 2004; Rhodes, 1998). Thus the Laguna Chaplin charcoal data are ideally suited to investigate linkages between local, meso, and regional scale patterns of burning. For the purposes of this study, macrocharcoal (>180 μm) data from Laguna Chaplin was interpreted to represent local scale fire activity, and >125 μm was used as the threshold for local scale fire activity at

Cuatro Vientos. The local scale (>125 μm) charcoal influx data from Cuatro Vientos follows similar increases to the regional (<180 μm) and local (>180 μm) charcoal influx data from Laguna Chaplin ca. 15,900 cal yr BP and after 10,000 cal yr BP. The synchroneity in the charcoal data suggest similar patterns of local, meso, and regional scale biomass burning. These data are further supported by the synchroneity of charcoal influx data to regional charcoal summaries ca. 16,000 cal yr BP and ca. 8,000 cal yr BP. These charcoal data support the second hypothesis that fire activity at Cuatro Vientos follows patterns of biomass burning on meso and regional scales.

Increased Climatic Variability and Fire Activity

The synchronous patterns exhibited between local (Cuatro Vientos and Laguna Chaplin influx) coupled with the similar patterns of increased regional biomass burning suggest a common driver. Regional charcoal syntheses in North America (Marlon et al., 2009) indicated periods of abrupt climatic variability resulted in increases in broad-scale fire activity. Existing sedimentary charcoal records from the Neotropics also suggest fire activity is associated with periods of high climate variability, including changes in moisture budgets and the intensification of seasonal droughts (Power et al., 2010). Previous research testing for climatic controls on Holocene fire records (Gavin, Hu, Lertzman, & Corbett, 2006) indicate climatic controls on fire were stronger with increased climatic variability (Gavin et al., 2006).

Previous studies indicate temperature is quantitatively the most important driver of changes in fire activity (Daniau et al., 2012). Temperatures rose ~4 °C immediately following the LGM at 19,500 yr BP reaching near modern levels (ca. 25 to 26.5 °C), and exhibiting a transitional period to 16,000 yr BP, by 15,900 yr BP (Whitney et al., 2011). The climate remained drier than present until ca. 12,800 BP when the onset of wetter conditions occurred (Whitney et al., 2011). The increased local, meso, and regional fire activity ca. 16,000 cal yr BP corresponds with the transitional warming period ca. 20,000 and 16,000 yr (Whitney et al., 2011). The continued dry conditions that span this period suggest that the increased temperature variability was the dominant driver of increased fire activity. The dry Late Glacial conditions were likely a secondary control promoting increased burning through vegetation productivity and the occurrence of fire-promoting climatic conditions (Marlon et al., 2013).

Precipitation changes were the primary factor driving MHAP vegetation dynamics. Atmospheric CO_2 concentrations and temperature record limited variability through the Holocene (Indermühle, Stauffer, Stocker, Raynaud, & Barnola, 1999) relative to those of the LGM-Holocene transition (Monnin et al., 2001). The arid conditions of the MHAP resulted in a sediment hiatus at Cuatro Vientos and decreased sedimentation at Laguna Chaplin. The sediment hiatus at Cuatro Vientos terminates ca. 6,900 cal yr BP and is accompanied by record levels of charcoal accumulation. Pollen data from Laguna Chaplin indicate increased abundance of seasonal dry forest taxa and increased charcoal accumulation (ca. 10,000 to 6,400 cal yr BP), suggesting more drought-tolerant/fire-adapted vegetation associated with drier and/or more seasonal climate (Burbridge et al., 2004). Regional charcoal summaries suggest sustained high levels of fire activity during the dry early and middle Holocene that was likely not captured at Cuatro Vientos during the sediment hiatus.

The lack of significant change in temperatures during the middle Holocene suggests that changes in precipitation driven by increased seasonal variability was the dominant control on local, meso, and regional biomass burning. Drier than present conditions, coupled with increased seasonal variability likely drove the increased fire activity during the MHAP. At the end of the MHAP, increased precipitation associated with the Late Holocene (Baker, Seltzer et al., 2001) is attributed to the oribitally driven gradual increase in mean annual precipitation and reduction in the length/severity of the dry season (Berger & Loutre, 1991). Increased precipitation resulted in a biome shift from savanna vegetation to *terra firme* rainforest at Laguna Chaplin (Burbridge et al., 2004). This change in vegetation to less flammable rainforest vegetation coupled with increased precipitation likely drove the decrease in fire activity. These data support the third hypothesis that periods of increased climatic variability result in increased fire activity on local, meso, and regional scales.

Conclusions

Cuatro Vientos provides one of the first subcentennial resolution charcoal and stable carbon and nitrogen records in the Bolivian lowlands. The aim of this research was to understand how climate variability impacts tropical fire activity and soil nutrient cycling on local scales (1 m^2 to 10^6 m^2) and how past fire activity varied on meso (10^6 to 10^{10} m^2) and regional ($>10^{10}$ m^2) scales. These data suggest climate was the first order of control of fire activity at Cuatro Vientos. Climate-fire-vegetation-nitrogen linkages indicate N variability was controlled by climatic driven changes in vegetation, which increased the abundance of leguminous plants and nitrogen fixing bacteria. Charcoal influx data from Cuatro Vientos and Laguna Chaplin indicated similar millennial scale patterns of burning on local scale (1 m^2 to 10^6 m^2) and meso scale (10^6 to 10^{10} m^2) and regional (>10^{10} m^2) scale fire activity despite low sampling resolution from Laguna Chaplin during the Last Glacial period. This interpretation is further supported with the synthesis of regional charcoal records that exhibited similar patterns of biomass burning. The synchroneity of past biomass burning suggests that periods of increased climatic variability drove increased biomass burning on local, meso, and regional scales.

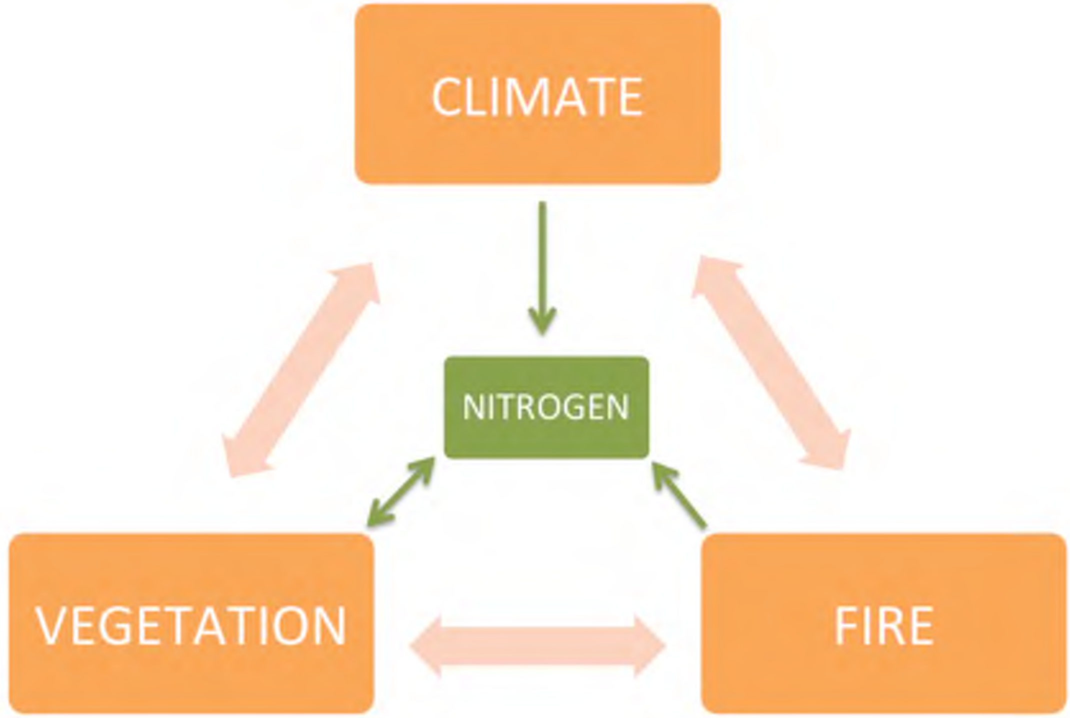


Figure 10 Climate, fire, vegetation, and nitrogen triangle. Beige arrows represent multidirectional interactions between climate, vegetation, and fire. The green arrows represent the multi- and unidirectional interactions between climate, vegetation, fire, and nitrogen.

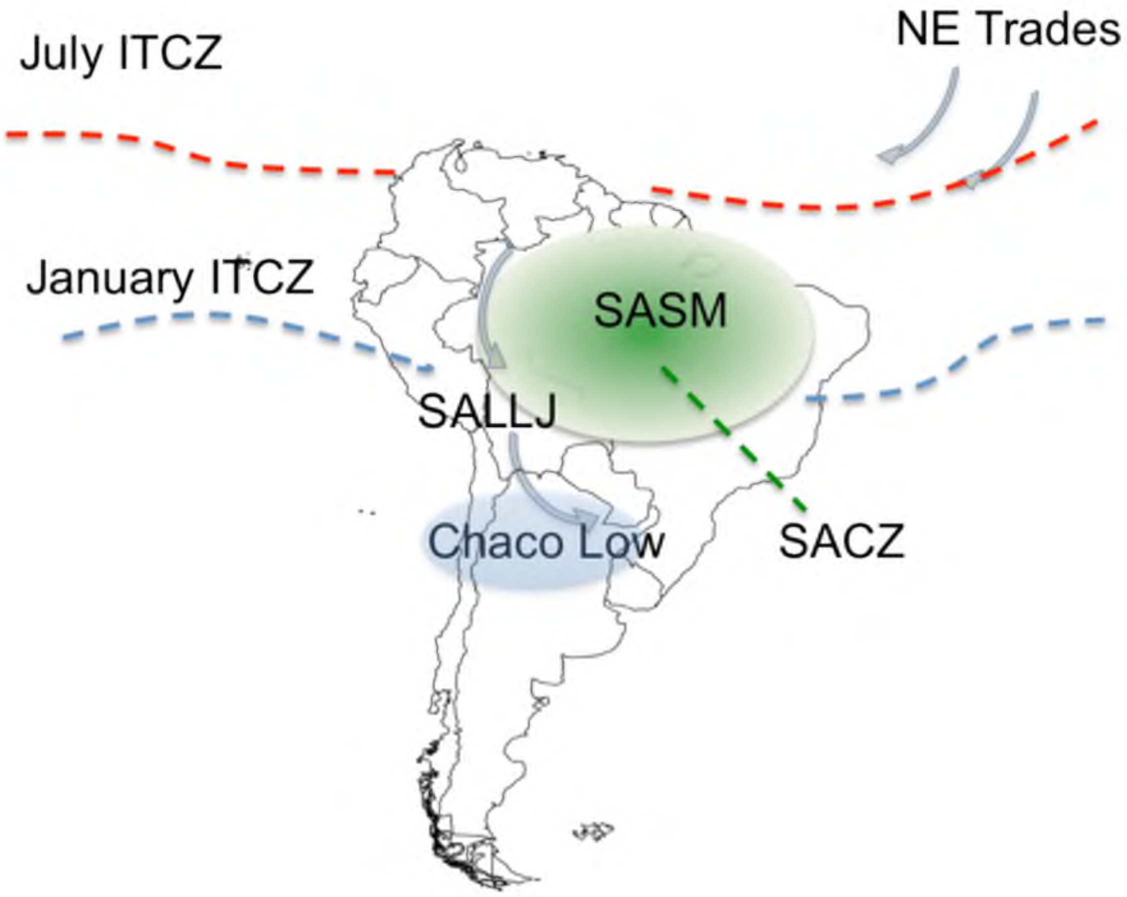


Figure 11 Climatic features of South America. Green circle represents South American Summer Monsoon (SASM), red dashed line represents July position of the Intertropical convergence zone (ITCZ), blue dashed line represents the January position of the ITCZ, green dashed line indicates the location of the South Atlantic Convergence Zone (SACZ), and blue arrows indicate the northeast trade winds (NE trades) and the South American low lever jet (SALLJ).

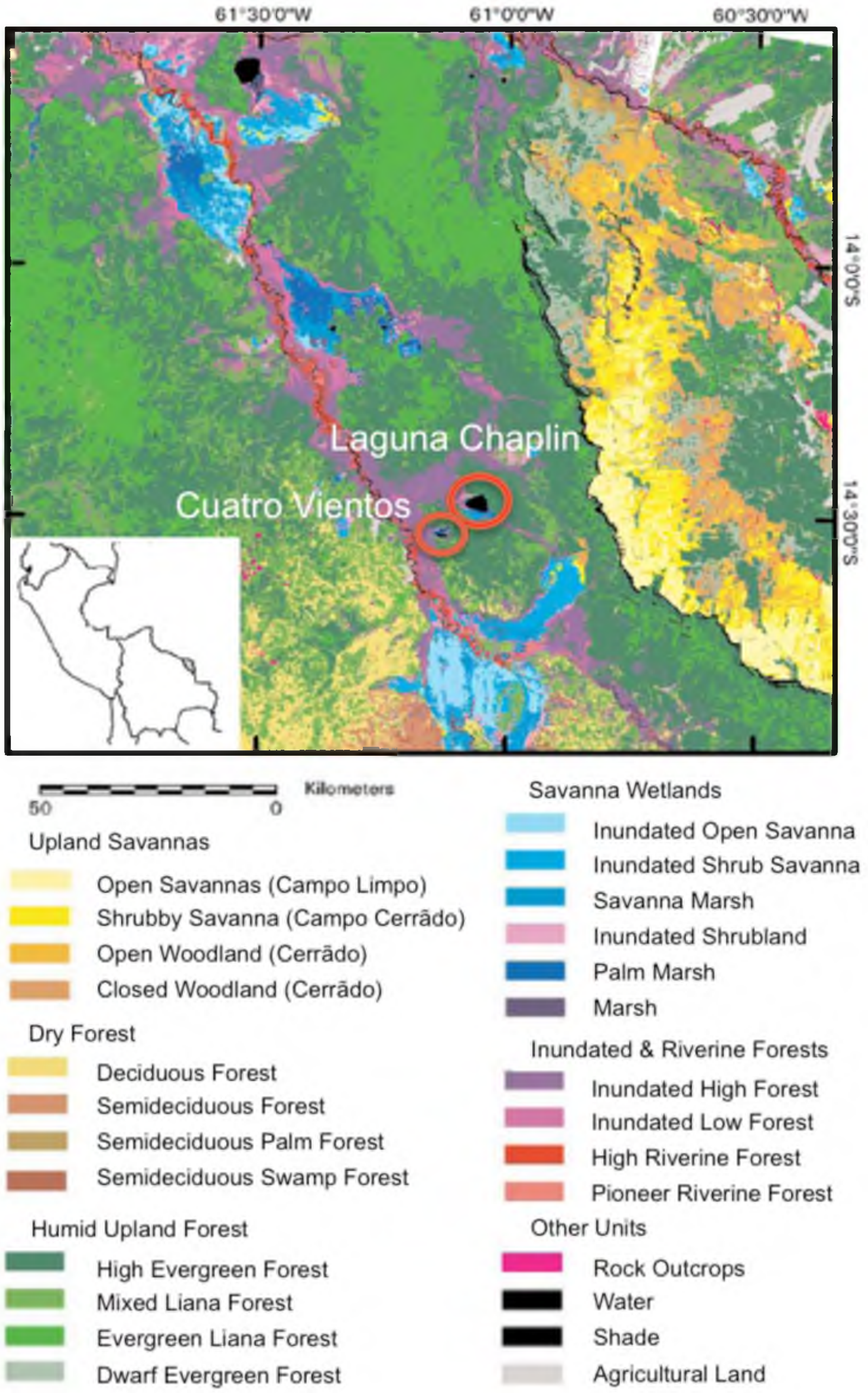


Figure 12 Cuatro Vientos study site with regional inset. Landsat vegetation map modified from Killeen et al. 1998, Cuatro Vientos, and Laguna Chaplin study sites highlighted with red circles.

Table 2 AMS Radiocarbon Dates from Cuatro Vientos

Lab Number	Material	Depth (cm)	^{14}C age (yr BP)	$\delta^{13}C$ Ratio	Intcal13 cal yr BP 2 sigma
UGAMS 13197	Bulk Sediment	161	3760 ± 25	-28.5	4077-4164
UGAMS 11809	Bulk Sediment	229	5750± 30	-26.5	6467-6639
UGAMS 15265	Bulk Sediment	260	16140± 40	-18.1	19295-19637
UGAMS 15157	Bulk Sediment	292	21070 ± 50	-17.4	24908-25508

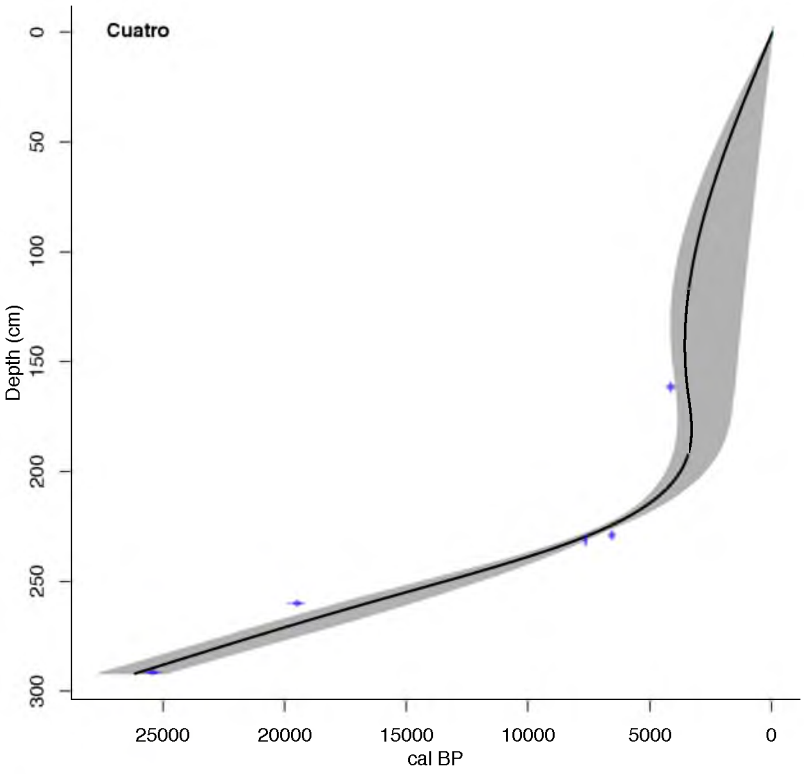


Figure 13 Clam age-depth model for Cuatro Vientos

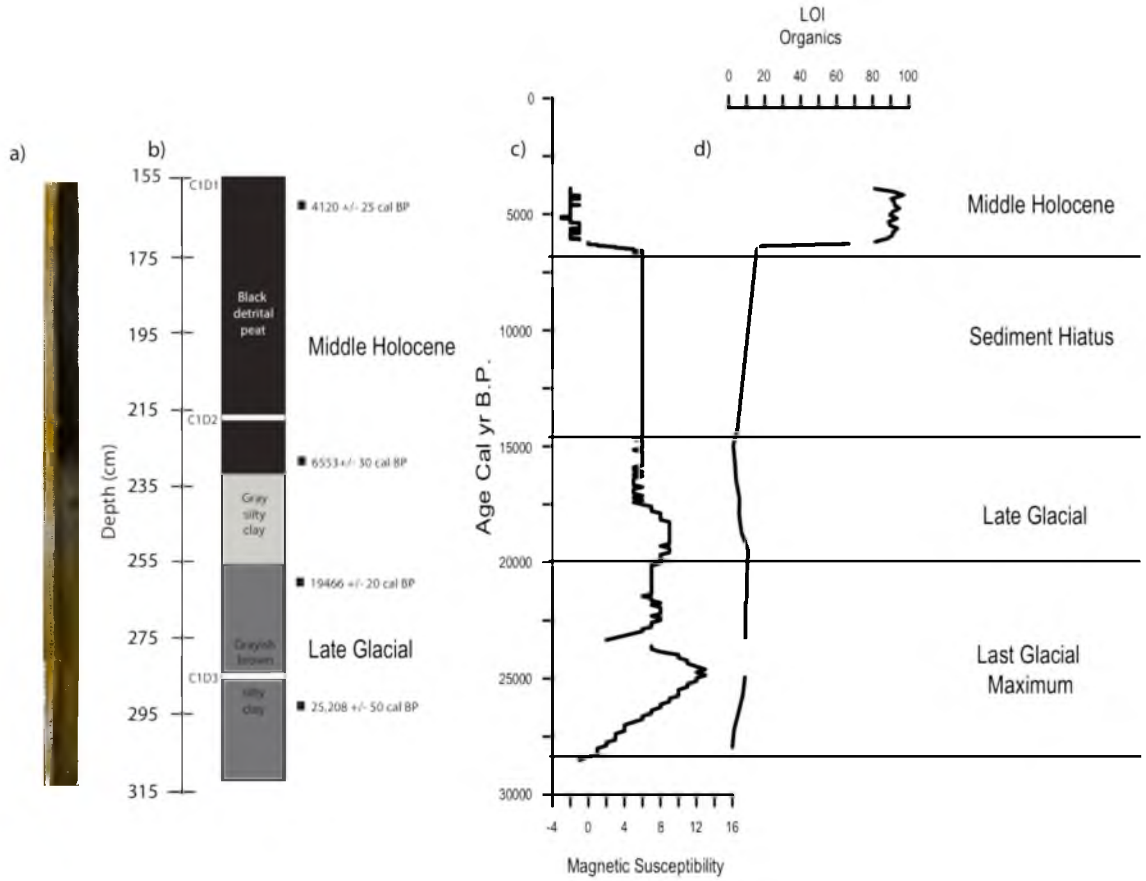


Figure 14 Cuatro Vientos lithology: a) core photo, b) core description, c) magnetic susceptibility, d) Loss on Ignition (LOI)

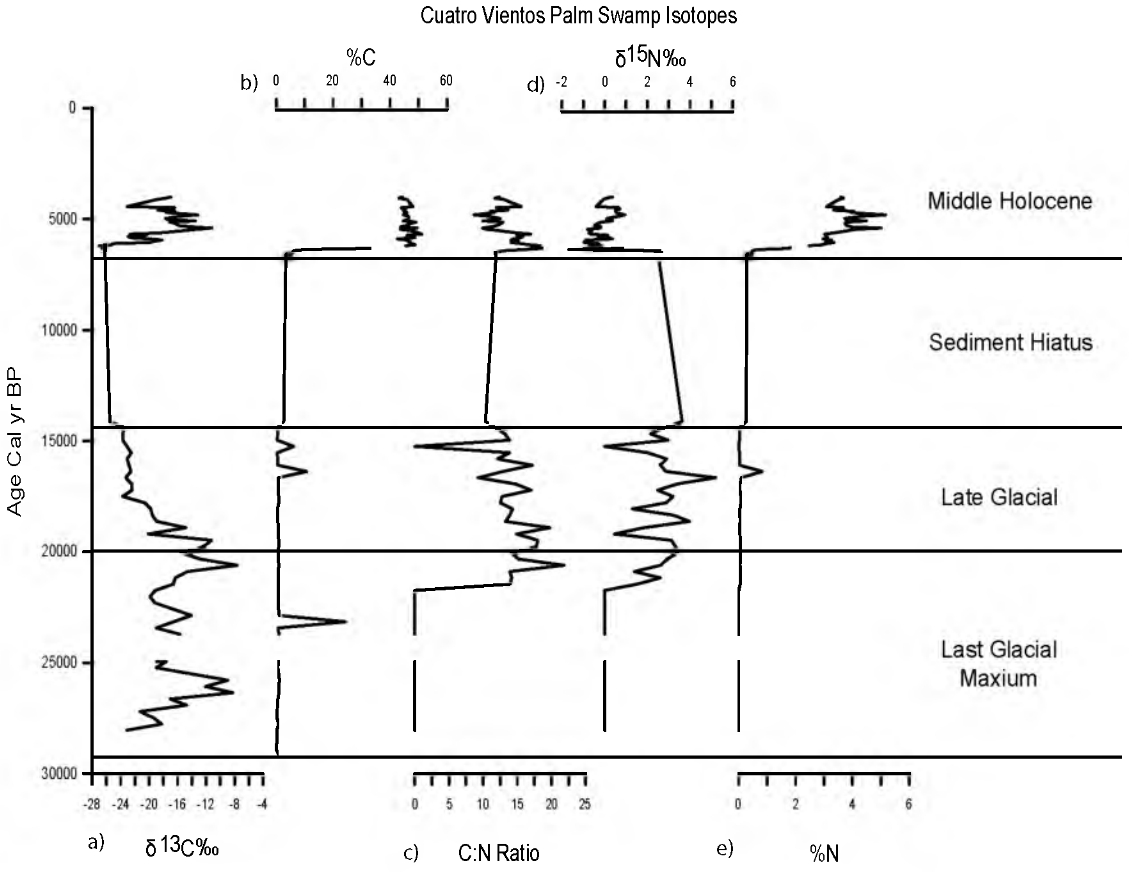


Figure 15 Cuatro Vientos stable carbon and nitrogen isotopes: a) δ13C $^{0}/_{00}$, b) % C, c) C:N ratio, d) δ15N$^{0}/_{00}$, and e) % N

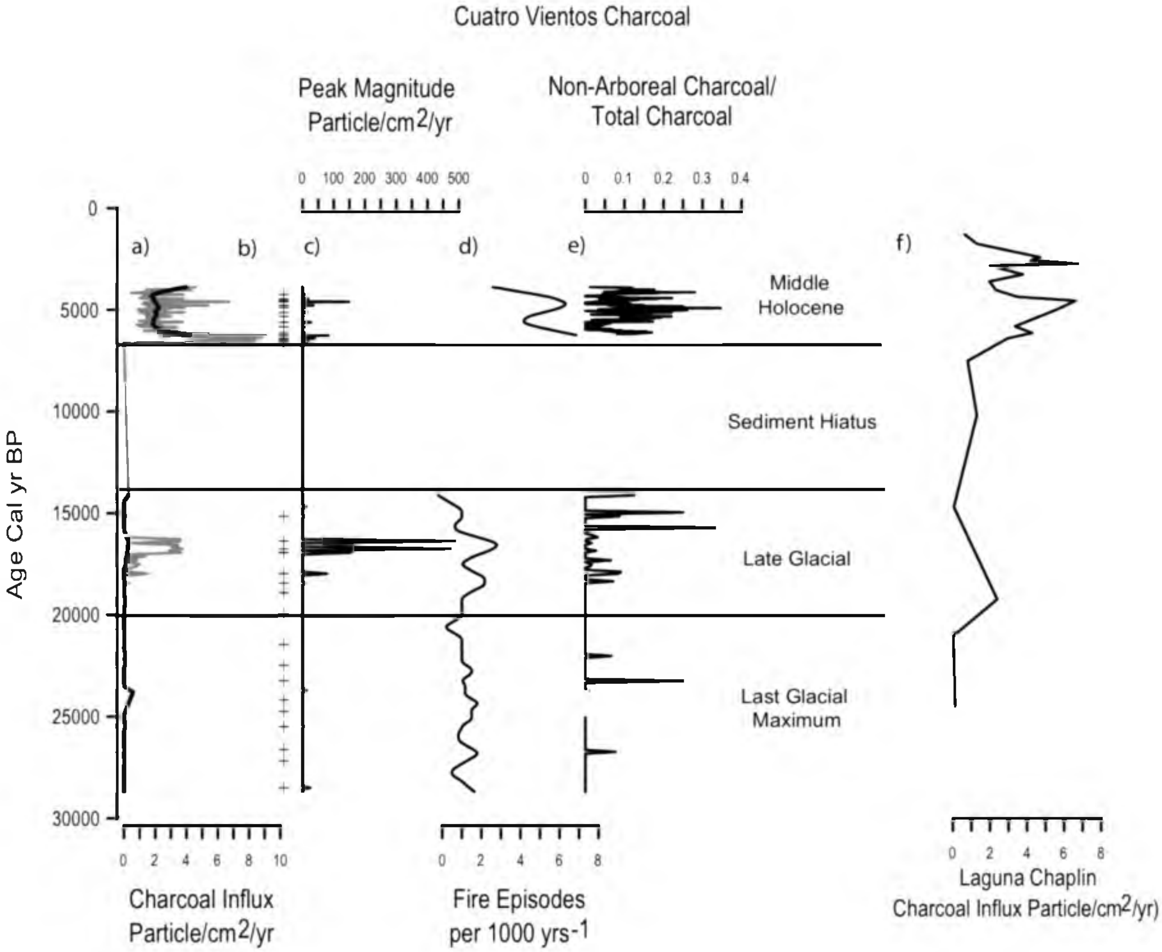


Figure 16 Cuatro Vientos and Laguna Chaplin charcoal data: a) charcoal influx, b) peaks, c) peak magnitude, d) fire frequency, e) nonarboreal charcoal, f) Laguna Chaplin charcoal influx

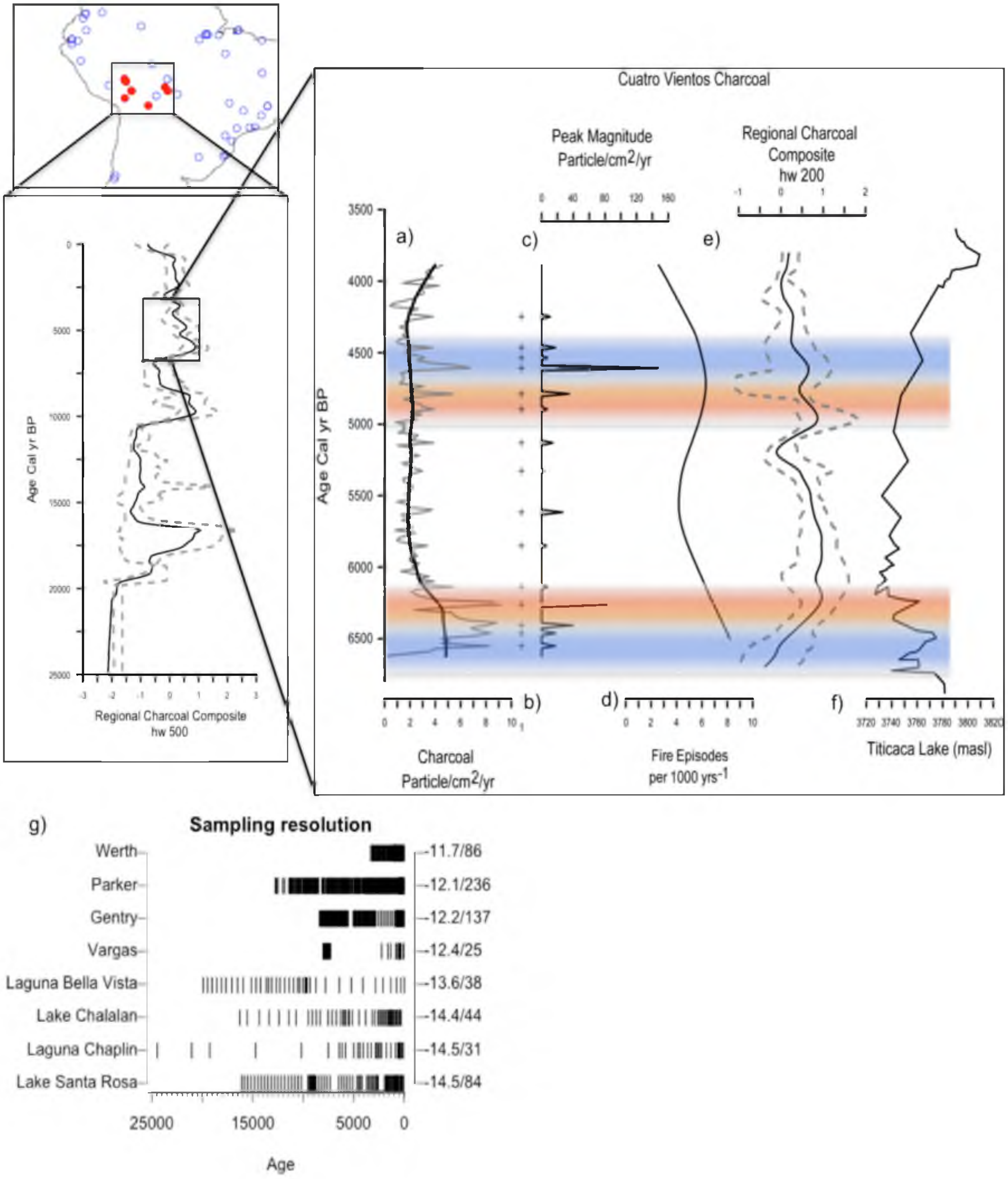


Figure 17 Regional Holocene charcoal data a) charcoal influx, b) peaks, c) peak magnitude, d) fire frequency, e) regional charcoal composite, f) Titicaca lake level, g) site list and sample resolution

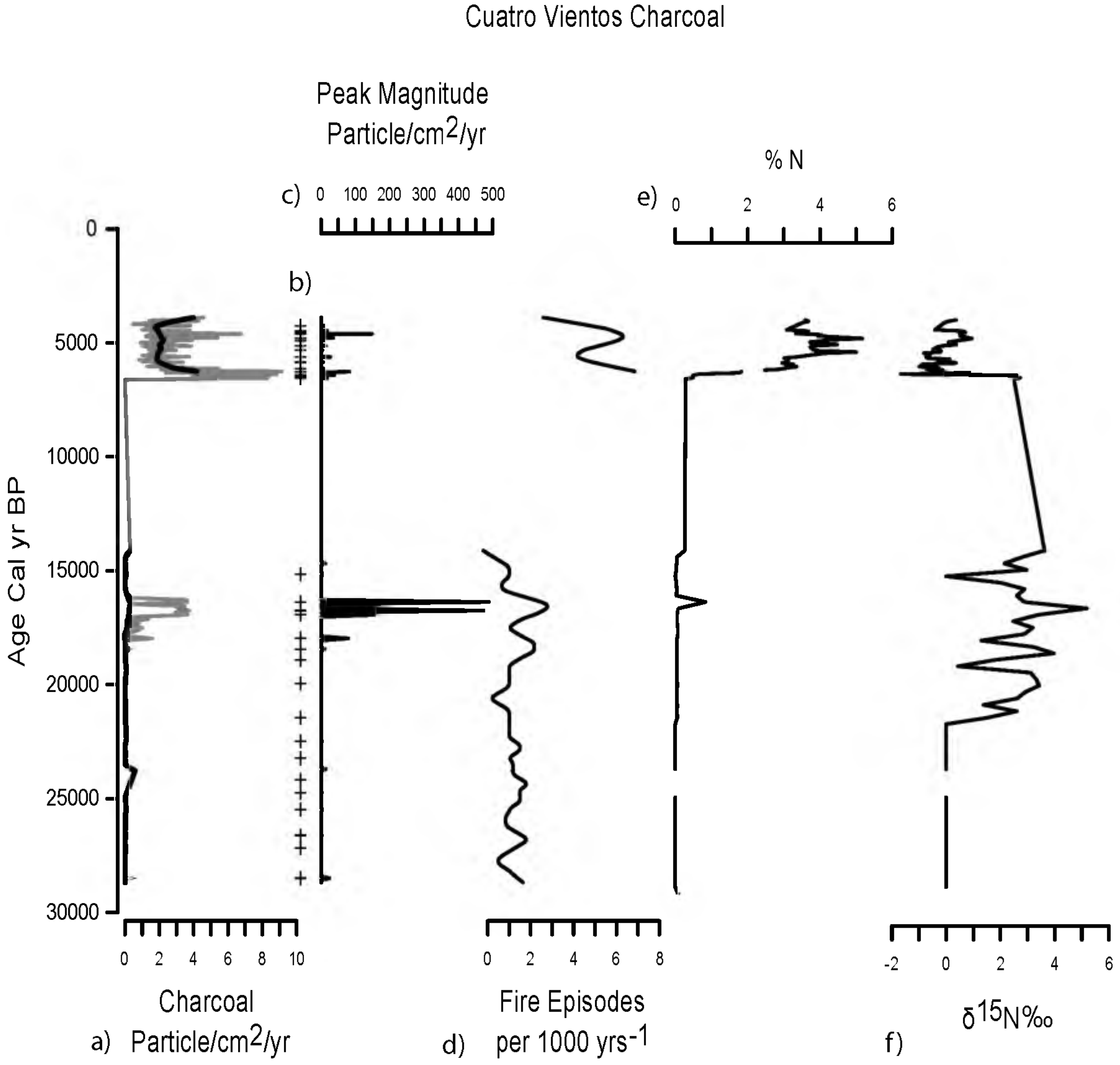


Figure 18 Cuatro Vientos charcoal and nitrogen data: a) charcoal influx, b) peaks indicated by plus signs, c) peak magnitude, d) fire frequency, e) % nitrogen, f) δ^{15}N

CHAPTER 4

INVESTIGATING SYSTEMS THEORY IN PALEOECOLOGICAL ANALYSIS: IDENTIFYING VEGETATION TIPPING POINTS IN FOSSIL POLLEN DATA

Introduction

Vegetation change can occur gradually and abruptly. Abrupt change can result in exceeding ecosystem tipping points that result in alternative vegetation states (Scheffer, Carpenter, Foley, Folke, & Walker, 2001). Vegetation succession tends to be linear; however, the Rate of Change (R.O.C.) may accelerate and decelerate through time (Wang, Wang, & Lee, 2007). Abrupt events can interrupt gradual succession by drastic, even catastrophic shifts in the R.O.C. that can result in either accelerated vegetation succession or a switch to an alternative steady state ecosystem (Shuman, Newby, & Donnelly, 2009). A tipping point is a critical threshold at which an ecosystem shifts abruptly from one state to another (Scheffer et al., 2001; Scheffer et al., 2009). Ecosystems are resilient to daily and seasonal variation; however, novel or particularly severe directional perturbations decrease the systems resiliency, causing an unstable equilibrium (Willis, Bailey, Bhagwat, & Birks, 2010). The degree of resiliency defines how ecosystems respond to these perturbations, by either shifting back to the original state (higher resiliency) or being pushed beyond the tipping point (lower resiliency) into an alternative steady state (Figure 19; Willis et al., 2010).

The resiliency of the Amazon rainforest is of particular interest as anthropogenic processes, e.g., global warming, deforestation for agriculture, anthropogenic fire activity, and global warming, introduce severe directional perturbations that will likely exceed tipping point thresholds (Lenton et al., 2008). In addition, decreased forest resilience is predicted as a result of anthropogenic deforestation and decreasing evapotranspiration (Hirota, Holmgren, Van Nes, & Scheffer, 2011). Up to 75% of precipitation in the Amazon in recycled through convective evapotranspiration (Zeng, Dickinson, & Zeng, 1996). Global vegetation and climate models indicate rainforest deforestation will cause large reductions in evapotranspiration and result in decreased precipitation ca. 20–30%, consequently lengthening the dry season and increasing summer temperatures (Lenton et al., 2008; Zeng et al., 1996). Overall, future climatic conditions, amplified by forest fragmentation due to human activity, will likely increase ecosystem instability and potentially exceed ecosystem tipping point thresholds, resulting in rainforest dieback (Lenton et al., 2008).

However, the projected extent of rainforest dieback remains uncertain (Betts et al., 2004; Cook & Vizy, 2008; Cox et al., 2004; Li, Fu, & Dickinson, 2006; White, Cannell, & Friend, 1999). A better understanding of long-term ecosystem resiliency will aid in decreasing uncertainty in future model projections (Gil-Romera et al., 2010). Long-term ecological changes are typically not detectable in modern ecological studies, which span years to decades (Mayle & Whitney, 2012). Paleoecological archives provide evidence of long-term biotic response (via pollen, phytoliths, and stable isotopes) and the dynamics of species interactions with climatic change (Willis et al., 2010). These records can help determine the rate and nature of biodiversity response to climate change, identify climate processes responsible for ecological thresholds, and identify ecological resiliency to climate change (Willis et al. 2010).

Previous studies have used various statistical methods on pollen metadata to explore vegetation resiliency and response to climatic change (Cañellas-Boltà, Rull, Vigo, & Mercadé, 2009; Gil-Romera et al., 2010; Gosling, Mayle, Tate, & Killeen, 2005; Kuneš et al., 2008; Mazier, Galop, Brun, & Buttler, 2006; Pelánková & Chytrý, 2009; Sugita, 2007). Multiproxy approaches are used to evaluate linkages among human, climate, and landscape processes to identify threshold responses and alternative steady states in past ecosystems (Dearing et al., 2008; Virah-Sawmy, 2009). Detrended correspondence analysis (DCA) and rarefaction biodiversity indices have been used to identify climatic perturbations that altered resiliency responses in ecosystems functioning, diversity, and landscape structure (Gil-Romera et al., 2010). Large changes in DCA scores indicated perturbations acting as catalysts for abrupt vegetation change, ultimately leading to new steady states (Gil-Romera et al., 2010).

Additionally, dissimilarity analysis of fossil pollen samples using square-chord distances (SCDs) has been used to detect rapid change events in regional vegetation history (Shuman et al., 2009). The SCD method coupled with independent paleoclimatic records enabled the detection of both long-term gradual and abrupt ecosystem changes (Shuman et al., 2009). In temperate latitudes, plant populations respond rapidly (<50-yr lags) to multidecadal to century-scale climatic change (Birks & Ammann, 2000; Tinner & Lotter, 2001; Williams & Jackson, 2007); thus it is possible to examine centennial and longer changes in climatic conditions via differences in vegetation from one time period to another (Shuman, Bartlein, & Webb III, 2005).

SCD assumes vegetation change is forced by slow climate trends undetectable at submillennial scales because of small magnitude changes over short intervals relative to the longevity of tree species (Shuman et al., 2009). In a previous study in the northeastern U.S., average SCDs values taken over 5,000-yr intervals ranged from 0.8 to 0.1 (0.01 at 500 yr intervals; Shuman et al., 2005). SCDs >0.15 represent dissimilarities that exceed the range of those found among pollen spectra within individual biomes today (Anderson, Bartlein, Brubaker, Gajewski, & Ritchie, 1991; Overpeck, Webb III, & Prentice, 1985). Large SCDs between two pollen samples (>0.15) indicate they were derived from significantly different vegetation types (Shuman et al., 2005). Past climate changes can thus be inferred from large SCD values, with the larger values inferring greater change (Shuman et al., 2005).

Three idealized types of change can occur in the late Quaternary paleoclimate records (Bartlein, 1997; Bradley, 1999): (1) long-term progressive change, (2) abrupt steps or "mode shifts," and (3) short-lived "events" or oscillations." Each of these three types can produce a characteristic signal in the dissimilarity data (Figure 20; Shuman et al., 2005). Long-term progressive change is reflected on dissimilarity plots as an increase in the general magnitude of dissimilarities as progressively longer time intervals are considered. The R.O.C. of long-term progressive change is slow and virtually undetectable across short time steps. Thus the shape of the SCD analysis can be used to interpret the type of past vegetation changes in Neotropical pollen data.

The detection of variability in the R.O.C. that accompany periods of extreme, rapid ecological transitions in paleoecological record require high-resolution sampling coupled with well-dated age models (Liu, Brewer, Booth, Minckley, & Jackson, 2012). Previous research on the effects of temporal sampling density on stratigraphic and chronological placement of an event horizon indicate that pollen sampling density has a critical impact of the stratigraphic placement of an event (Liu et al., 2012). Thus, a criterion for the adequate sampling density (f_a) for age estimation of the salient features of an event was established (Liu et al., 2012). Sites must have a time minimum resolution during the event period that is $\leq 1/f_a$. Records should be sampled by applying a sampling density f, which satisfies $f \leq f_a$. To avoid the aliasing (distortion) phenomena, a sampling rate higher than the Nyquist rate (twice the highest frequency contained in the original signal) is required (Shannon, 1949). Combined with the SCD methodology of pollen metadata from the Amazon Basin, the adequate sampling resolution to detect rapid change (abrupt succession or a tipping points) needs to be twice every 500 years (the amount of time used to indicate slow vegetation response; Shuman et al., 2009). For this study, the sampling resolution of existing pollen records from the Neotropics limited the detection of abrupt events that occurred at a scale finer than 500-year intervals.

Objectives

In this study, the SCD method was selected to examine past vegetation changes because it is easier to use with multiple sites opposed to DCA. SCDs were calculated on a dataset of 26 pollen sequences to explore the long-term variability in the R.O.C. of ecosystem response to climate in the Amazon. The purpose of this research was to identify abrupt changes at pollen sites within a defined spatial area, to look for periods of accelerated regional change, and to link these periods to drivers that may influence ecosystems at a regional scale. Three hypotheses were explored in this research:

(1) Variability in the R.O.C. was not constant over time

(2) Patterns of variability in the R.O.C. exhibited similar regional patterns

(3) Periods of nonrandom change were linked to regional drivers (e.g., climate, humans).

Methods

Site Selection

Twenty-four pollen records from lake sediments in Amazonia were compiled from the Latin American Pollen Database (LAPD), Neotoma, and from datasets provided from coauthor contributors (Figure 21). Sites were selected between -80°W,-30°S, -35°E, and 10°N that occurred below 2,000 m.a.s.l. The sites were assigned to one of four geographic regions to aid in the spatial analysis of past vegetation change. Calendar year BP chronologies used here are based on the available radiocarbon dates and are the same as those used for the original publication of the site. There have been no additional changes to the chronologies (Figure 22; Table 3).

Selected Pollen Taxa

SCDs were calculated based on the relative abundance of pollen types included in the pollen sum of existing records (Table 4). Calendar-year chronologies used here are based on available radiocarbon dates and intersite correlation of regional pollen stratigraphic events.

Square Chord Distance Analysis

Square-chord distance (SCD) was used to estimate dissimilarity between adjacent fossil pollen spectra in individual records (Jacobson, Webb III, & Grimm, 1987; Overpeck, Bartlein, & Webb III, 1991; Shuman et al., 2005). SCDs provide a measure of the multivariate distance (dissimilarity) between two pollen spectra (Overpeck et al., 1985) and are used here to represent rate of change. As the amount of change between any two samples will also be affected by the amount of time elapsed, the abundance values were binned into time windows of set width, then calculated the SCD values between adjacent bins. SCDs were omitted from a bin if a site lacked pollen samples in a given window. Following Shuman et al. (2009), the 20th percentile of SCD values for each site were calculated and used as a threshold to indicate periods at a site when the R.O.C. was greater than normal. The proportion of sites exhibiting high rates of change was then complied for all time periods, providing a landscape-to-regional scale record of change.

Randomization Test

High rates of change may occur at a given site because of local conditions. The significance of the proportion of sites with high SCD values was tested at each time period using randomization. One thousand iterations of a permutation test were used (Obbard, Harris, & Pannell, 2006), in which the periods of high R.O.C. were randomly resampled within each site, and the proportion of sites with high R.O.C. were calculated. The observed proportion of sites with high SCDs was considered significant if it was greater than 90% of all randomized differences.

Results

Individual SCD were calculated for each site (Figure 23). The 20th percentile was indicated for each figure. Randomization analysis was used to identify significant periods of change (>90% of randomized differences; Figure 24). Key time periods when SCD values exceeded this threshold occurred at 14,500, 12,500, 10,500, 9,500, 3,500, and after 1,500 cal yr BP.

Late Glacial (20,000–13,000 cal yr BP)

During the Late Glacial increased vegetation change occurred ca. 14,500–13,000 cal yr BP. There are 12 records located in the northwest, southwest, and southeast that span the vegetation change ca. 14,500–13,000 cal yr BP, including Cambara do Sol, Laguna El Pinal, Lago Pires, Lagoa Campestre de Salitre, Lagoa Patas, Laguna Chaplin, Laguna La Gaiba, Morro de Itapeva, Paramo de Miranda, and Boa Vista (Figure 25). During this period seven (ca. 30%) of these records, including Lagoa Campestre de Salitre, Lagoa das Patas, Laguna Chaplin, Morro de Itapeva, Paramo de Miranda, Serra da Boa Vista, and Valle Laguna Victoria, have SCD values above the 20th percentile.

Glacial-Interglacial Transition (12,000–9,000 cal yr BP)

During the Glacial-Interglacial Transition there was increased vegetation change ca. 12,000, 10,500, and 9,500 cal yr BP. There are 14 records from the northwest, southwest, and southeast that extend to 12,000 cal yr BP, including Cambara do Sul, Laguna El Pinal, Lagoa Campestre de Salitre, Lagoa Patas, Laguna Chaplin, Laguna La Gaiba, Laguna Bella Vista, Morro de Itapeva, Paramo de Miranda, Laguna Sardinas, Serra Campos Gerais, Boa Vista, Serra do Rio Rastro, and Laguna Victoria. Ca. 45% of the sites have SCD values >20th percentile during this period.

There are 15 records from the northwest, southwest, and southeast that span the period of increased vegetation from ca. 10,500 cal yr BP: Cambara do Sul, Laguna El Pinal, Lagoa Campestre de Salitre, Lagoa Patas, Laguna Chaplin, Laguna La Gaiba, Laguna Bella Vista, Pantano Monica, Morro de Itapeva, Paramo de Miranda, Laguna, Sardinas, Serra Campos Gerais, Boa Vista, Serra do Rio Rastro, and Laguna Victoria. Ca. 40% of the sites have SCD values >20th percentile.

Twenty-one records from all four geographic regions in the northwest, northeast, southwest, and southeast span the period of increased vegetation change ca. 9,500 cal yr BP: Laguna Angel, Lago Caldo, Cambara do Sul, Laguna El Pinal, Lago do Pires, Lagoa Campestre de Salitre, Rio Curua, Lagoa Patas, Laguna Bella Vista, Laguna Chaplin, Laguna La Gaiba, Laguna Loma Linda, Patano Monica, Morro da Igreja, Morro de Itapeva, Paramo de Miranda, Laguna Sardinas, Serra Campos Gerais, Boa Vista, Serra do Rio Rastro, and Laguna Victoria. Ca. 48% of the sites had SCD values > 20th percentile.

Late Holocene (3,500 cal yr BP–Present)

All 24 records from all four geographic regions span the period of vegetation change ca. 3,500 cal yr BP: Laguna Angel, Lago Calado, Cambara do Sul, Lago Cayambe, Lago Crispum, Laguna El Pinal, Lago do Pires, Lagoa Campestre de Salitre, Rio Curua, Lagoa Patas, Laguna Chaplin, Laguna La Gaiba, Laguna Bella Vista, Laguna Loma Linda, Patano Monica, Morro da Igreja, Morro de Itapeva, Paramo de Miranda, Poco Grande, Laguna Sardinas, Serra Campos Gerais, Serra da Boa Vista, Serra do Rio

Rastro, and Laguna Victoria. Ca. 30% of the sites had SCD values >20th percentile. All 24 records from all four regions span the past 1,500 cal yr BP. This period exhibits the highest proportion of sites changing with ca. 60% of the sites with SCD values 20th percentile.

Discussion

The purpose of this research was to identify abrupt changes at pollen sites within a defined spatial area, to look for periods of accelerated regional change, and to link these periods to drivers that may influence ecosystems at a regional scale. There were three hypotheses tested in this research: (1) variability in the R.O.C. was not constant over time, (2) regional patterns of variability in the R.O.C. exhibited similar patterns, (3) periods of non-random change were linked to regional drivers (e.g. climate, humans).

Detecting Variability in R.O.C. and Past Ecosystem Resiliency

The SCD values indicate considerable variability in the R.O.C. of vegetation data through time, supporting the first hypothesis that variability in the R.O.C. was not constant over time. If the SCD analysis had been detecting noise in the pollen data, changes in SCD values would be random, lacking synchronous temporal patterns. The patterns of vegetation change detected by SCD dissimilarity analysis identify periods of abrupt change where ca. 30–60% of the study sites exhibited vegetation change greater than the 20th percentile.

During the six abrupt changes detected in the SCD analysis, there were consistent spatial patterns in the variability in the R.O.C. At 14,500, 12,000, 10,500 cal yr BP, vegetation was changing in the northwest, northeast, and southwest. All four geographical regions responded to abrupt change at 9,500 cal yr BP. There was greater spatial heterogeneity of vegetation response at 3,500 cal yr BP. During the last 1,500 cal yr BP the northeast, southwest, and southeast were antiphased with the northwest. These data support the second hypothesis that regional patterns of variability exhibited similar patterns in the R.O.C. However, there are only three records in the Northwest region. Future research to improve the site density in the Northeastern region will facilitate regional vegetation comparisons. Additionally, further analysis on a site-by-site basis may help to clarify the unique spatial variability exhibited in vegetation response in the northeast during the last 1,500 years.

Randomization analysis using >90% confidence interval indicated that abrupt, nonrandom regional vegetation change occurred at least six times over the past 25,000 years, mainly concentrated around the end of the last glacial period and the past 1,500 years. In addition, low SCD values occurred during the last glacial (ca. 25,000–17,500 cal yr BP), indicating a period of limited vegetation change. These data suggest greater stability and higher resiliency. The interpretation of higher resiliency could be attributed to few records present in this time period. However, if the number of sites included in the analysis overemphasized resiliency during this period, it is likely that all SCD values would remain low until more samples were added to the analysis. There are ca. 7 records included during the period of high resiliency (SCD values ca. 0). There are ca. 8 records present in the first period of abrupt change (ca. 30% of the sites are changing). These data suggest that the SCD values are reflective of actual variability in the resiliency of the vegetation communities.

Higher frequency change has been interpreted as increased regional instability and lower ecosystem resiliency (Shuman et al., 2005). The higher proportion of sites changing during the glacial interglacial transition (14,500–10,000 cal yr BP) and the Late Holocene (1,500 cal yr BP to present) indicate greater instability and lower resiliency in the northeast, southwest and southeast, and high stability in the northwest.

Detecting Types of Vegetation Response to Abrupt Change

Distinguishing between accelerated succession and ecological tipping points is difficult due to the temporal resolution of most pollen data. Both accelerated succession and tipping points are associated with periods of abrupt vegetation change (defined here as an event between two time periods of 500-year windows). However, tipping points are unique in that the abrupt vegetation change results in the shift from one ecosystem state to another. These state changes are not limited to the patterns of successional vegetation trajectories and can result in unpredicted vegetation communities.

Implementing the model of idealized types of change (Figure 20; Shuman et al., 2005), the structure of the SCDs were used to identify different types of vegetation change in the records. Progressive changes exhibit smooth curves or arch in the SCD data. Cambara do Sul, Laguna El Pinal, Lagoa do Curuaa, Lagoa das Patas, Laguna Chaplin, Laguna La Gaiba, Morro da Itapeva, Poco Grande, Laguna da Boa Vista, and Laguna Victoria exhibit progressive change during a portion of the record. Step changes produce a broad peak in dissimilarity at the time of the change, representing either successional changes or tipping points. Laguna Angel, Cambara do Sul, Laguna Bella Vista, Laguna Chaplin, Morro de Itapeva, Serra do Rio Rastro, and Valle Laguna

Victoria exhibit step changes at least once in the record. Short-lived events appear as two peaks in dissimilarity analysis, representing short-lived perturbations on the vegetation communities. Laguna Angel, Lagoa Calado, Lago Cayambe, Lago Crispum, El Pinal, Lagoa Campestre de Salitre, Rio Currua, Lagoa Patas, Laguna Bella Vista, Laguna Chaplin, Laguna La Gaiba, Laguna Loma Linda, Lagoa Monica, Paramo de Miranda, Laguna Sardinas, Serra Campos Gerais, Serra da Boa Vista, Serra do Rio Rastro, and Valle Laguna Victoria exhibit an event change at least once during the record.

As the focus of the current study is to investigate past variability in regional ecosystem resiliency, this analysis does not go further here in interpreting the nature of these events. Future analysis on a site-specific basis will be used to examine the nature of these abrupt changes to clarify if these changes were identifying periods of accelerated succession or ecosystem tipping points. Both would appear as a step change as vegetation change is characterized in distinct changes in both scenarios. To further clarify the nature of these changes, SCD values compared at each interval through the step change to vegetation communities before and after the change can aid in understanding how vegetation composition was responding to the abrupt change. The vegetation community before and after the state change can help distinguish the nature of the vegetation change. Accelerated succession would follow linear successional patterns, whereas tipping points would result in nonlinear vegetation change with distinct ecological states. Additionally the identification of changes in ecosystem function based on pollen data may help to inform the nature of the vegetation change.

Further analysis on the nature of vegetation response to abrupt change in the Neotropics may help to inform changes in past ecosystem resiliency. If frequent events occurred in the record but the vegetation returned to its original state and floristic composition, it suggests the ecosystem was more resilient to perturbation. Conversely if isolated or infrequent events occur that result in the change in the vegetation composition, it suggests decreased resiliency. Distinguishing past spatial and temporal ecological resiliency across a variety of ecosystems will inform the understanding of modern ecological resiliency in the Neotropics.

Drivers of Regional Variability in the R.O.C.

The similar patterns in the spatial and temporal variability in the R.O.C. in the vegetation data suggest a common driving mechanism. The periods of accelerated change, indicated by the SCD values >20th percentile, correspond to periods of well-documented climatic variability in the Neotropics. Recent studies suggest that the glacial-interglacial transition was characterized by a highly variable precipitation regime (Metcalfe et al., 2014). Existing records from intercontinental tropical South America indicate between 12,200–11,800 cal yr BP there is a period of high variability alternating between wet and dry periods perhaps driven by changes in seasonality, followed by increasing wet conditions to 10,000 cal yr BP (Metcalfe et al., 2014). A similar pattern of glacial-interglacial variability is exhibited from the Cariaco Basin (Lea, Pak, Peterson, & Hughen, 2003), Lake Caco, Brazil (Sifeddine et al., 2003), the Gulf of Mexico (Flower, Hastings, Hill, & Quinn, 2004), and coastal Peru (Rein et al., 2005). The increased climatic variability between 12,200–10,000 cal yr BP is associated with the glacial-interglacial transition corresponds to three abrupt changes occurring at 30–50% of the sites, indicating decreased resiliency.

The middle Holocene arid phase (MHAP) is well documented in tropical South America (Baker, Seltzer et al., 2001; Cross et al., 2000; Cruz et al., 2005; D'Agostino et al., 2002). During this period, weakened SASM convective activity was attributed to an orbitally-driven minimum in January insolation at 15–10°S (Berger & Loutre, 1991). Reduced insolation restricted the southerly extent of the ITCZ and deep cell convective activity over the Amazon Basin, thus decreasing the length of the summer rainy season, resulting in longer, more severe dry seasons (Baker, Seltzer et al., 2001). The onset of the MHAP corresponds with abrupt vegetation change at ca. 50% of sites, indicting decreased ecosystem resiliency.

During the Late Holocene (ca. 3,500 cal yr BP to present) there has been a basin wide increase in mean annual precipitation and reduction in the length/severity of the dry season. This is attributed to the strengthening of the South American Summer Monsoon (SASM) in response to increasing summer insolation at 10–15°S driven by the Milankovitch precessional forcing (Mayle & Whitney, 2012). This period also corresponds to a time of increasing evidence for anthropogenic disturbance (Behling & Hooghiemstra, 1998; Behling & Lima da Costa, 2001; Behling, Pillar, Orlóci, & Bauermann, 2004). These combined pressures are associated with change at 30% of the sites at ca. 3,500 cal yr BP and 60% ca. 1,500 cal yr BP, the highest proportion of sites experiencing abrupt change over the last 25,000 years.

Periods of reduced resiliency in the vegetation could have resulted from either change in vegetation that altered resiliency or from changes in the drivers (e.g., climate and/or humans) that in turn affected resiliency. Vegetation change can affect resiliency through plant physiological adaptations. Vegetation succession may result in decreased resiliency to disturbance. Climate can affect vegetation resiliency through increased physiological stress on the vegetation. Experimental studies of plant response to increased climatic variability found that plant water relations are very vulnerable to climatic extremes driven by changes in temperature and precipitation and that changing heat waves and flooding have stronger impacts on physiological processes than changing mean climate (Reyer et al., 2013). The highly variable glacial-interglacial climate, the shift to dry conditions during the MHAP, and the combined climatic and anthropogenic factors in the past 1,500 years likely drove the increased variability in vegetation and the decrease in ecosystem resiliency. These data support the third hypothesis that periods of nonrandom change were linked to regional drivers such as climate variability and human disturbance.

Management Applications of Ecosystem Thresholds

Identifying variability in past ecosystem resiliency has significant management applications for the 21st century. The data presented in this study suggest that the combined pressures of modern climatic change and anthropogenic forcing lower ecosystem resiliency and increase the threat of tipping points in Amazonian ecosystems.

The analysis of tipping point thresholds in management policy is complicated by nonlinear dynamics and by multiple factor controls that operate at diverse spatial and temporal scales (Groffman et al., 2006). A better understanding of the conditions under which tipping point thresholds are likely to be crossed and what mechanisms underlie threshold behavior is critical (Schreiber, Bearlin, Nicol, & Todd, 2004). The long-term paleoecological perspective provided in this chapter lays the foundation for future research into tipping point threshold dynamics and individual species response to past ecological disturbance in the Neotropics.

As Neotropical ecosystems reorganize in response to global change, realistic conservation and management goals should be instituted to minimize the loss of biodiversity and maximize ecosystem-buffering capacity (Jørgensen, 2002). The application of the ecological threshold concept has increased with the implementation of “adaptive management” as a tool for approaching environmental management issues (Figure 26; Bearlin, Schreiber, Nicol, Starfield, & Todd, 2002; Groffman et al., 2006). In an adaptive management model, solutions to problems are proposed and implemented, but prescriptions are constantly re-evaluated based on actual ecosystem response to management (Holling, 1978; Schreiber et al., 2004; Walters, 1986). The most successful outcomes of an adaptive management approach have involved a series of formalized, structured steps within the adaptive management cycle, including (i) extensive interdisciplinary collaboration of people involved in, or affected by management; (ii) modeling both the system being managed and alternative management scenarios; (iii) simulations of monitoring in relation to objectives; (iv) making decisions between a range of management options; (v) implementing, monitoring, and evaluating alternative management options; and (vi) assessing the outcomes of management in relation to specific initial goals (Schreiber et al., 2004).

An example of an adaptive management scenario in the Neotropics could incorporate ecosystem thresholds of non-fire-adapted rainforests, fire-adapted savannas, and agricultural lands experiencing different climate scenarios (e.g., warmer-wetter, warmer-drier). Feasible conservation goals that incorporate key biogeographic components, including preservation of species biodiversity, functional diversity, genetic diversity, community and ecosystem diversity, habitat diversity (Alho & Sabino, 2011; Lomolino, Riddle, Whittaker, & Brown, 2010), and the creation of various biological reserve models (e.g., the SLOSS debate (MacArthur & Wilson 1967)) should be incorporated into the adaptive management model. The application of an adaptive ecosystems perspective (Groffman et al., 2006) will aid in the development of robust, flexible, and adaptable Neotropical ecosystem management policy in the 21st century.

The data presented in this research can inform the adaptive management model by improving the existing knowledge of variability in past ecosystem resiliency on a regional scale. Over the past 25,000 years, periods of increased climatic variability resulted in decreased ecosystem resilience in all geographic regions in Neotropical South America. Combined anthropogenic and climatic pressures place unprecedented stress on Neotropical vegetation communities and should be accounted for in the formation of conservation goals. Additionally, it is likely that vegetation will experience abrupt change in the 21st century that alternative management options could address by focusing on ecotonal regions and biological corridors.

Conclusions

The purpose of this research was to identify abrupt changes at pollen sites within a defined spatial area, look for periods of accelerated regional change, and to link these periods to drivers that may influence ecosystems at a regional scale. The SCD dissimilarity analysis was selected, as it is more suitable to handle multiple sites than a DCA. The SCD analysis examined the rate of change (R.O.C.) of past Neotropical ecosystems. The data indicated 30–60 % of the sites exceeded vegetation thresholds since the last Glacial period. Using a randomization analysis to verify these thresholds were not coincidental, these data suggest that the study sites included in this analysis have responded to abrupt changes a minimum of six times since the last Glacial period. High regional variability occurred during the glacial-interglacial transition and during the Late Holocene (3,500 cal yr BP to present). The periods of increased R.O.C. were associated with climatic transitions for a majority of the record. Combined climatic and anthropogenic pressures in the last 1,500 years resulted in the highest level of regional vegetation change and the lowest ecosystem resiliency in the past 25,000 years. The unprecedented rate of anthropogenic climate change and deforestation in the 21st century suggest that Neotropical ecosystems will likely experience tipping points (IPCC, 2014). Implementing an adaptive management model to respond to various ecosystem responses will aid in creating effective management models for changing Neotropical ecosystems.

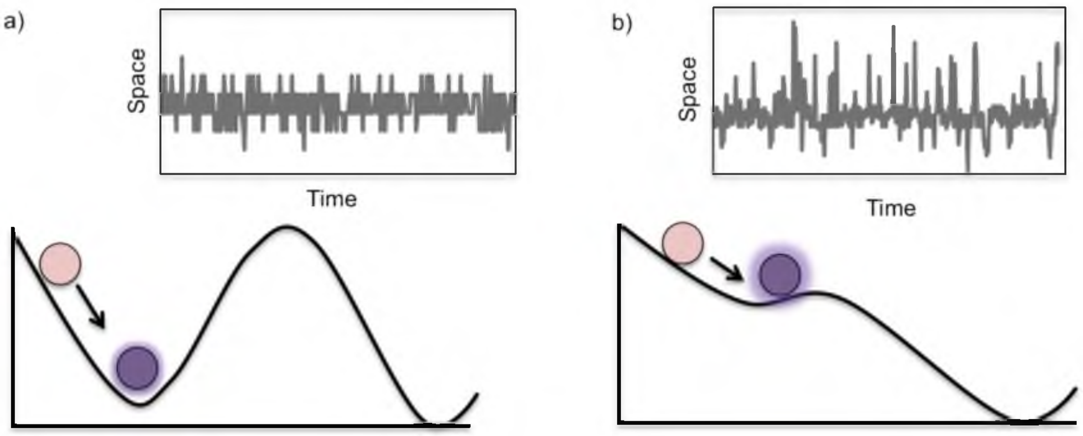


Figure 19 Idealized tipping point model a) low risk f transition: high resiliency, b) high risk of transition: low resilience. Modified from (Scheffer, 2010)

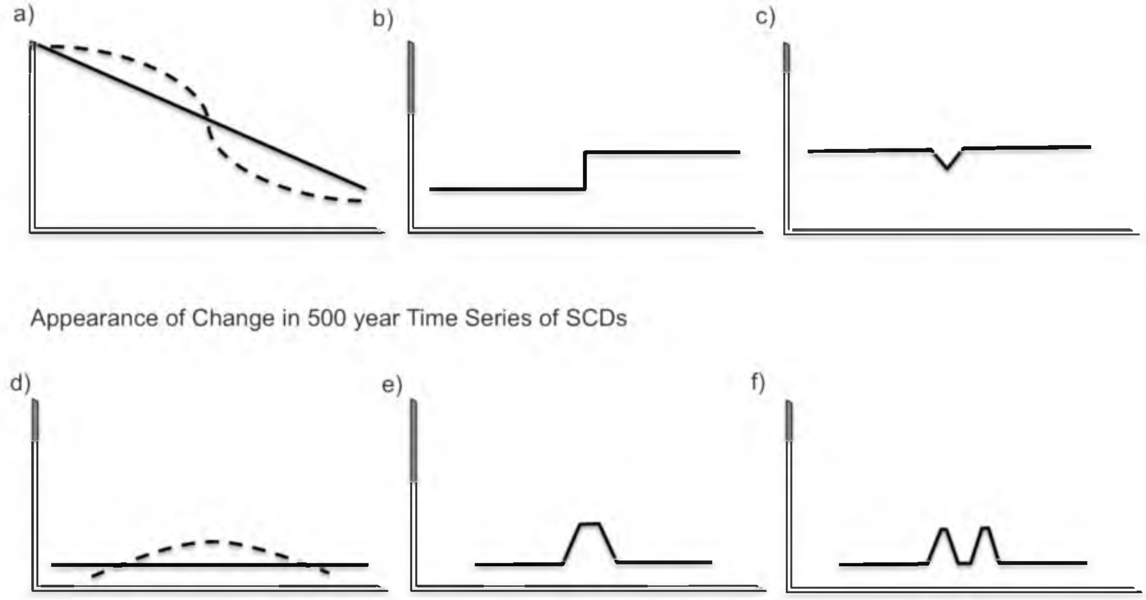


Figure 20 Idealized climate change and accompanying (SCD) measurements: a) progressive long-term change, b) a step change or “mode shift,” c) a short-lived “event,” d) SCD progressive change, e) SCD step change, f) SCD event change

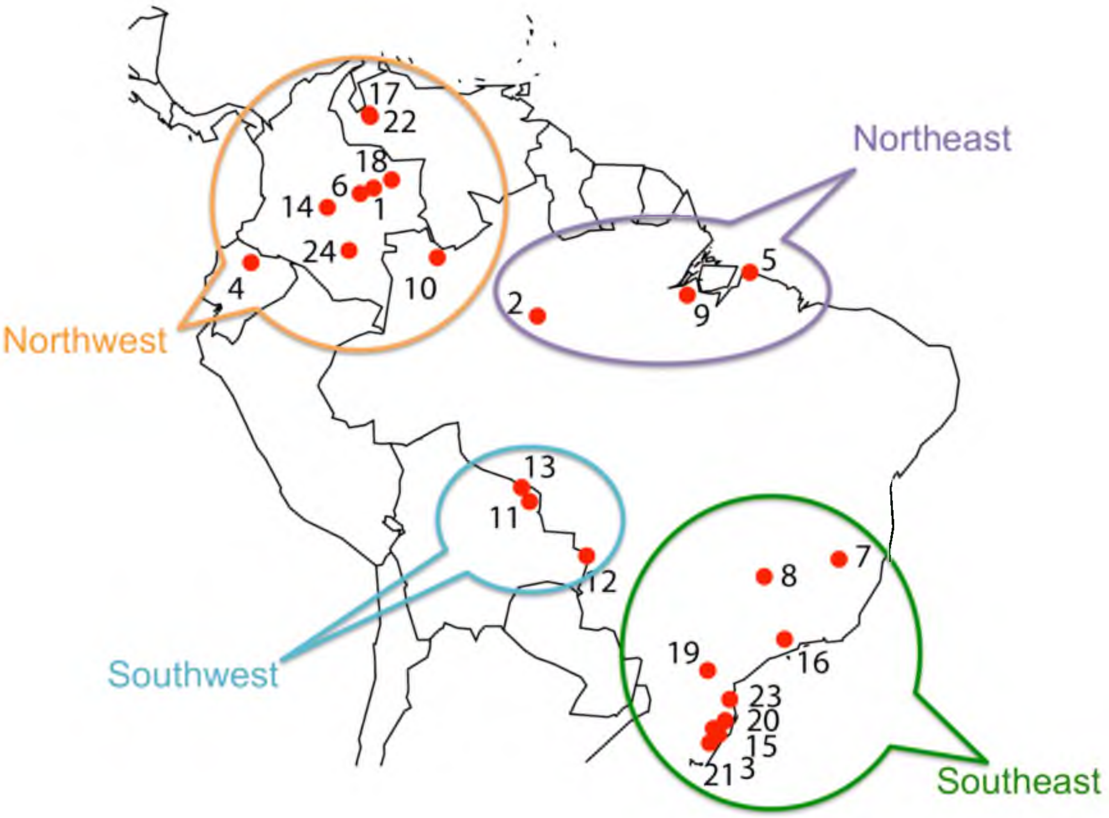


Figure 21 Regional map of pollen site distribution. Pollen records are indicated by red dot. Numbers correspond to sites listed in Table 3. Four primary geographic regions are depicted: northwest in orange, southwest in blue, northeast in purple, and southeast in green.

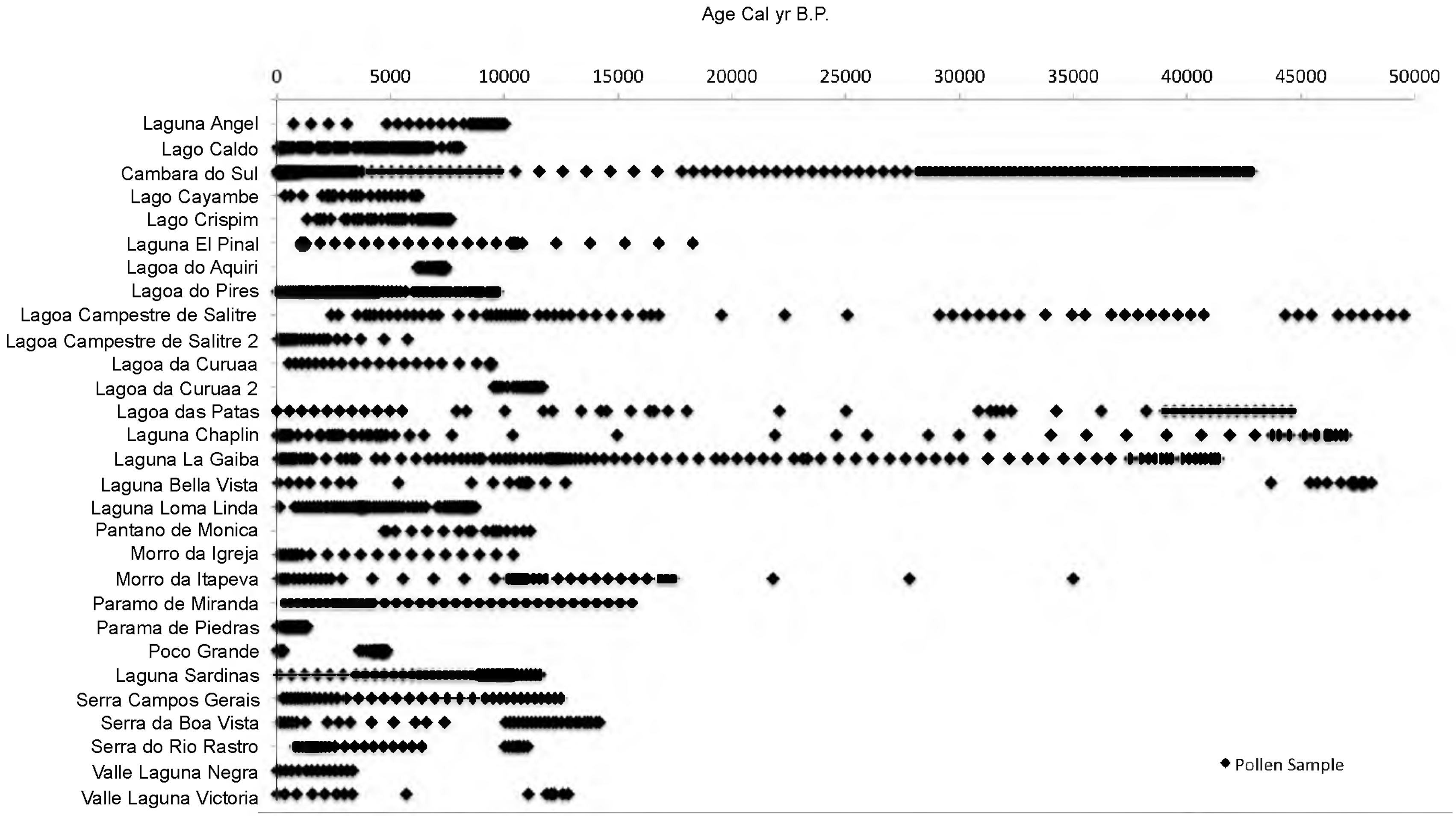


Figure 22 Site list and pollen chronologies: based on Neotoma age to depth profiles and sample frequency

Table 3 Site location and information

Site #	Site Name	Latitude	Longitude	Elevation m.a.s.l.	Basal Age	# of samples	# of samples/kyr	Source
1	Laguna Angel	4º, 28'N	70º, 34'W	200	12,880 ±80 ^{14}C	27	2.1	(Behling & Hooghiemstra, 1998)
2	Lago Calado	3º,16'S	60º,35'W	23	8330±50 ^{14}C	88	10.51	(Behling et al., 2001)
3	Cambara do Sul	29º,03'S	50º,06'W	1040	42,840 ±984 ^{14}C	189	4.4	(Behling et al., 2004)
4	Lago Cayambe	0º,02'S	78º,02'W	4350	5100^{14}C	21	4.11	(Graf, 1989)
5	Lago Crispim	0º, 46'S	47º, 51'W	2	7640±80 ^{14}C	39	5.11	(Behling & Lima da Costa, 2001)
6	Laguna El Pinal	4º, 08'N	70º,23'W	180	18,290 ±90^{14}C	35	1.9	(Behling & Hooghiemstra, 1999)
7	Lago do Pires	17º,57'S	42º,13'W	390	9720 ±110^{14}C	76	7.8	(Behling, 1995a)
8	Lagoa Camp. Salitre	19º,0'S	46º,46'W	1050	50,000 ±110^{14}C	77	1.5	(Ledru, 1993)
9	Rio-da-Curuca	1º,44'S	51º,27'W	2	6343±33^{14}C	24	3.8	(Behling & da Costa, 2000)
10	Lagoa-das-Patas	0º,16'N	66º,41'W	350	42,010 ±1200^{14}C	48	1.1	(Colinvaux et al.1996)
11	Laguna Chaplin	14º,28'S	61º,04'W	250	38,100±1,000^{14}C	61	1.6	(Burbridge et al., 2004)
12	Laguna La Gaiba	17º,45'S	57º,35' W	120	32,717±564^{14}C	102	3.1	(Whitney et al., 2012)
13	Laguna Bella Vista	12º,37'S	61º,33'W	250	50,850 ^{14}C	37	.7	(Burbridge et al., 2004)
14	Laguna Loma Linda	3º,18'N	73º, 23'W	310	8690±50^{14}C	66	7.6	(Behling & Hooghiemstra, 2000)
15	Morro-da-Igreja	28º,11'S	49º52'W	1800	10,200±275^{14}C	22	2.2	(Behling, 1995b)
16	Morro-de-Itapeva	22º47'S	45º,32'W	1850	29,000±1840^{14}C	42	1.5	(Behling, 1997a)
17	Paramo-de-Miranda	8º,55'N	70º,50'W	3290	11,400^{14}C	36	3.2	(Salgado-Labouriau, 1991)
18	Laguna Sardinas	4º, 58'N	69º,28'W	80	11,570±70 yr ^{14}C	46	4	(Behling & Hooghiemstra, 1998)
19	Serra-Campos-Gerais	24º,40'S	50º,13'W	1200	12,500 ±120^{14}C	36	2.9	(Behling, 1997b)
20	Serra-da-Boa-Vista	26º,42'S	49º,09'W	1160	13,905±295^{14}C	37	2.7	(Behling, 1995b)
21	Serra-do-Rio-Rastro	28º,23'S	49º,33'W	1420	11,210±385^{14}C	29	2.6	(Behling, 1995b)
22	Valle-Laguna-Victoria	8º,48N	70º,47'W	3250	12,100^{14}C	14	1.2	(Rull et al. 1987)
23	Poco Grande	26º,25' S	48º,52'	10	4680 ±120^{14}C	40	8.6	(Belhing 1995b)

Table 4 Pollen types selected for the analysis that occurred at more than four of the sites include the following.

Acalypha	Cyperaceae	Myrtaceae
Alchornea	Didymopanax	Piperaceae
Apiaceae undiff.	Ericaceae	*Plantago*
Araucaria	Fabaceae	Poaceae
Arecaceae	*Hedyosmum*	*Podocarpus*
Asteraceae	*Ilex*	Solanaceae
Cecropia	Mimosaceae undiff.	Urticaceae/Moraceae
Celtis	*Myrsine*	*Weinmannia*
Combretaceae/Melastomataceae		

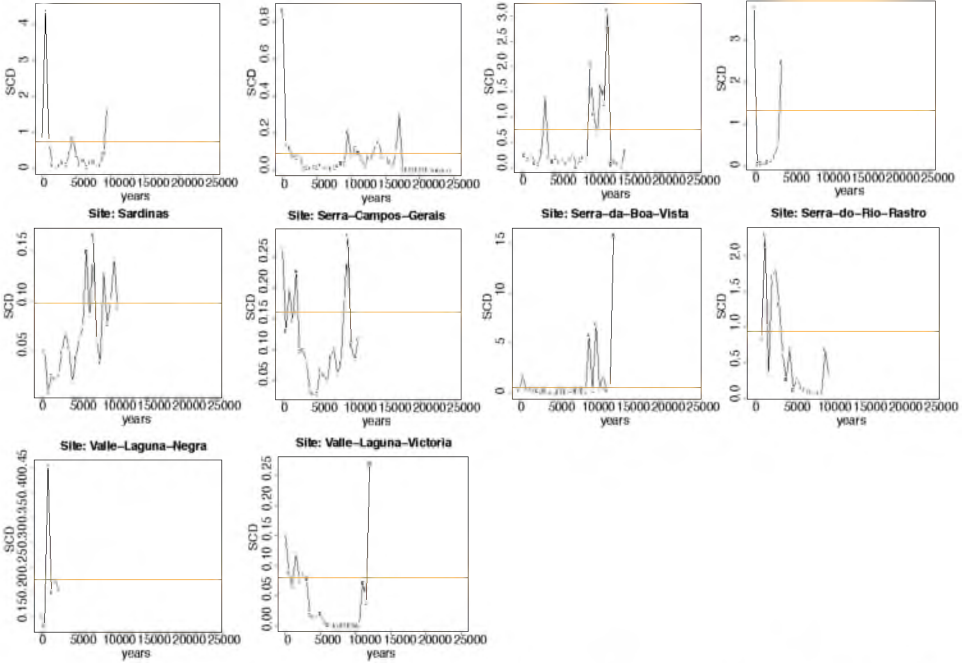
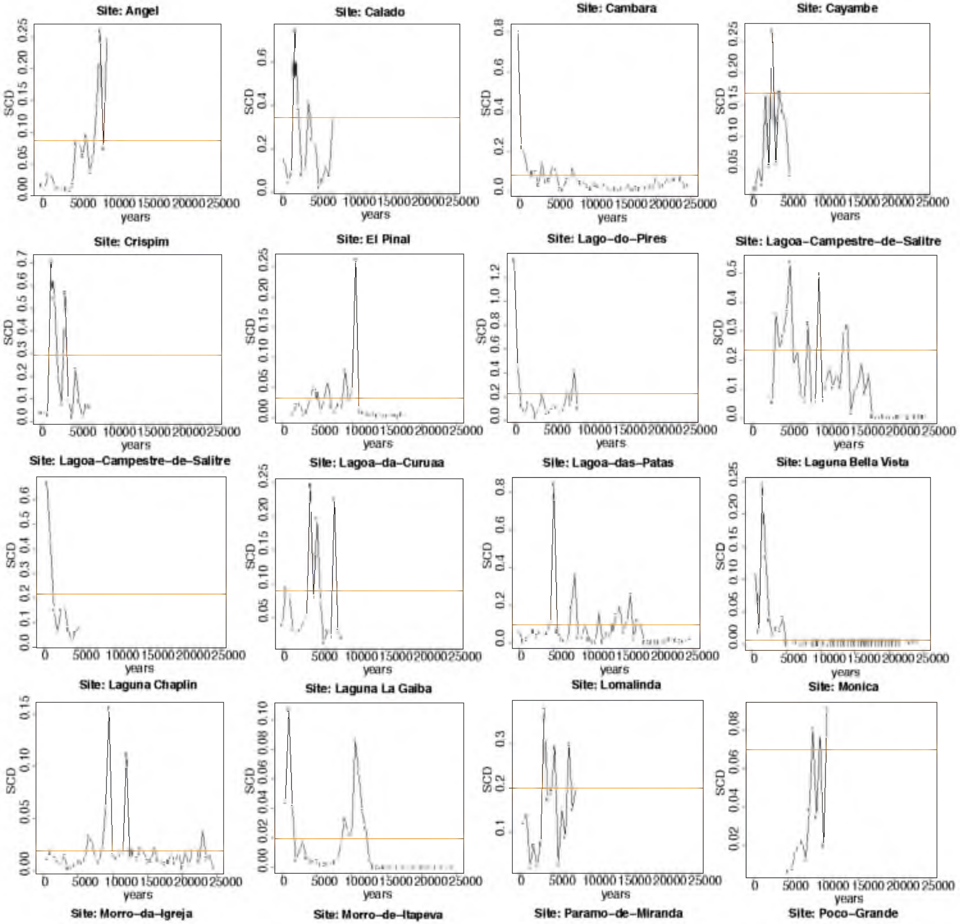


Figure 23 SCD values by individual site. Orange dashed line indicates 20th percentile.


Site: Angel
Site: Calado
Site: Cambara
Site: Cayambe
Site: Crispim
Site: El Pinal
Site: Lago–do–Pires
Site: Lagoa–Campestre–de–Salitre
Site: Lagoa–Campestre–de–Salitre
Site: Lagoa–da–Curuaa
Site: Lagoa–das–Patas
Site: Laguna Bella Vista
Site: Laguna Chaplin
Site: Laguna La Gaiba
Site: Lomalinda
Site: Monica
Site: Morro–da–Igreja
Site: Morro–de–Itapeva
Site: Paramo–de–Miranda
Site: Poco–Grande
SCD
years
0
5000
10000
15000
20000
25000

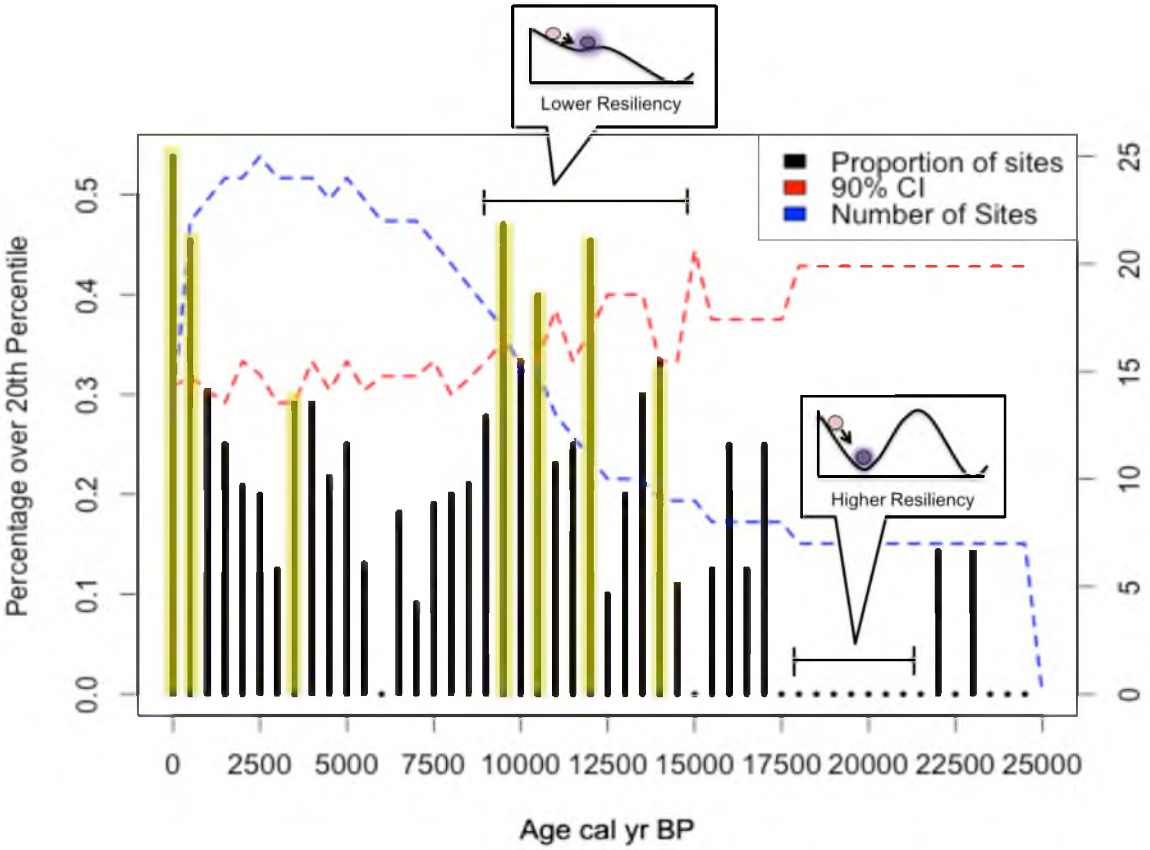
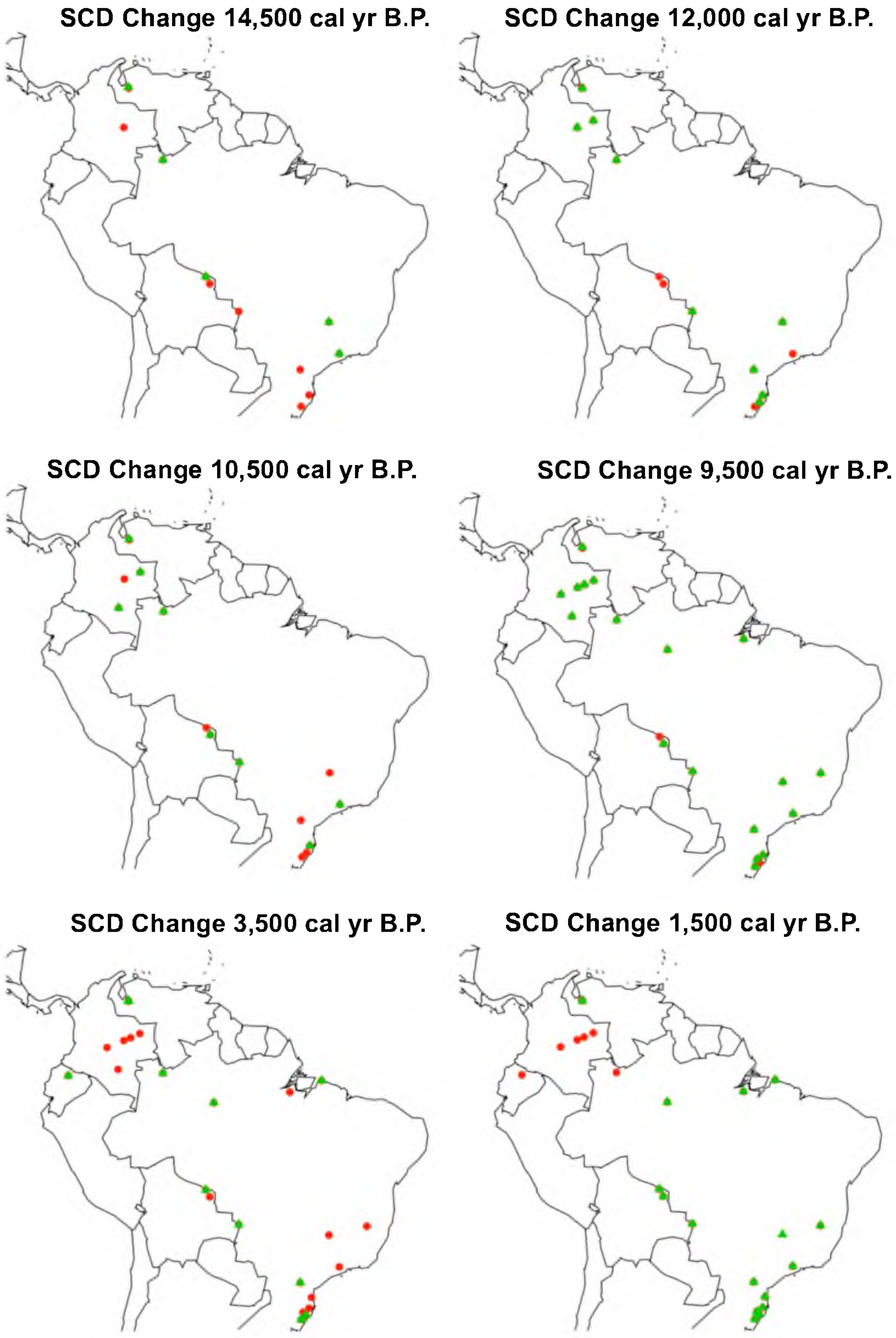


Figure 24 Randomization and resiliency: black bars proportion of sites with SCD values greater than the 20th percentile. Red dashed line indicates 90% confidence interval. Blue dashed line indicates the number of sites. Yellow bars highlight periods of abrupt vegetation change.



SCD Change 14,500 cal yr B.P.

SCD Change 12,000 cal yr B.P.

SCD Change 10,500 cal yr B.P.

SCD Change 9,500 cal yr B.P.

SCD Change 3,500 cal yr B.P.

SCD Change 1,500 cal yr B.P.

Figure 25 Pollen site distributions based on time intervals: red dots indicate no change and green triangles indicate sites with SCD values above the 20th percentile.

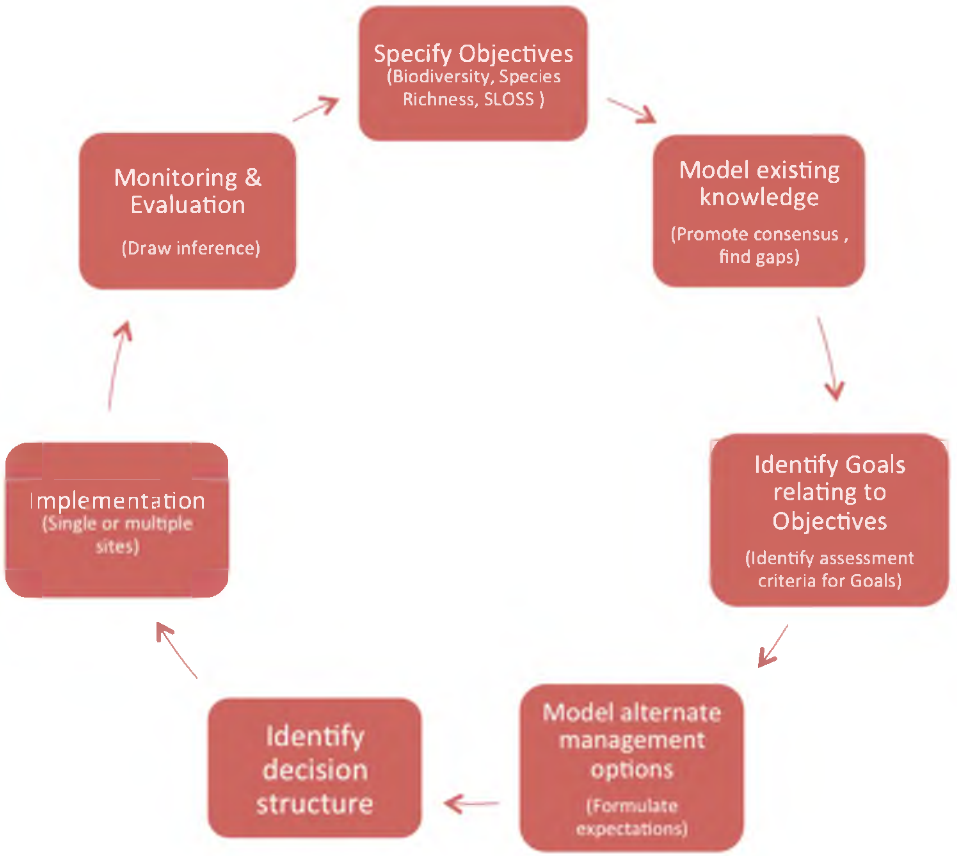


Figure 26 The adaptive management process. Modified from Bearlin et al. (2002).

CHAPTER 5

SUMMARY

Long-term records of climate, fire, and vegetation dynamics in eastern Bolivia provide a novel perspective on ecosystem process. Research findings from this dissertation extend the temporal scale of paleoecological change in nonanthropogenically disturbed *cerrãdo* savanna and *terra firme* rainforests in eastern Bolivia, identify controls on Neotropical local-meso-regional scale fire activity, and suggest drivers of variability in ecosystem resiliency in Neotropical ecosystems. Extending the spatial-temporal range of paleoecological data provides valuable insights into the legacy of past disturbance on the resiliency of modern Neotropical ecosystems. These data have important management applications and aid in making informed policy decisions on sustainable Amazonia futures across a range of ecosystems in the Neotropical South America.

The purpose of this research study was to reconstruct fire, vegetation, and soil geochemical histories from nonanthropogenically disturbed ecosystems to advance the understanding of ecological variability on subcentennial to multimillennial temporal scales and local, meso, and regional spatial scales. This dissertation had three primary research objectives: (1) provide subcentennial resolution control sites in savanna and rainforests ecosystems, (2) evaluate the climate-fire relationship on local, meso, and regional scales, and (3) synthesize regional pollen data to identifying potential ecosystem thresholds.

To address the first research objective on control sites, sediment cores collected from Huanchaca Mesetta and Cuatro Vientos in NKMNP, Bolivia, were analyzed at subcentennial resolution for charcoal, phytoliths, and stable isotopes. To date, evidence suggests negligible anthropogenic impact in the ecosystems in NKMNP (Burbridge et al., 2004; Mayle et al., 2000). Thus these study sites provide control records of natural controls on fire, vegetation, and soil geochemistry. These data indicate strong climate-fire-soil geochemistry feedbacks in both *cerrădo* savanna and *terra firme* rainforest ecosystems. These records can aid in clarifying the current debate on the extent of pre-Columbian disturbance in the Neotropics (Carson et al., 2014; Denevan, 2012; Erickson, 2010; Meggers, 1954) by providing baseline records of natural paleoecological change since the Last Glacial period.

To evaluate the second research objective on past climate-fire relationships on various spatial and temporal scales, macro charcoal influx data was compared to macro and micro charcoal influx data from Laguna Chaplin (10 km to the east). These data indicate similar patterns in local and meso scale fire activity. To explore regional patterns of biomass burning, the charcoal influx data from Cuatro Vientos were compared to regional charcoal records from eight sites in the region. These data suggest similar patterns of biomass burning on local and regional scales since the Last Glacial period that were likely linked to periods of increased climatic variability.

To investigate the third research objective on past ecosystem thresholds, pollen sites from across Amazonia were analyzed using SCD method to identify periods of abrupt vegetation change. These data indicate variability in past ecosystem resiliency on different temporal and spatial patterns. Ecosystem thresholds that exhibited a high degree of variability were clustered around the glacial-interglacial transition and the Late Holocene. This research lays the foundation for future investigation of past paleoecological tipping points in Amazonia. These three research objectives were presented as independent manuscripts for publication. The hypotheses, major findings, and management applications of these research objectives are summarized below.

A Paleoecological Assessment of the Huanchaca Mesetta *Cerrãdo* Savanna Ecosystem

Chapter 2 analyzed fire and vegetation change from Huanchaca Mesetta palm swamp located in the *cerrãdo* savanna of NKMNP. The objective of this chapter was to investigate the natural controls of fire and vegetation in *cerrãdo* savanna ecosystems. Three hypotheses were tested in this research: (1) edaphic conditions were the dominant control on the presence of savanna versus forest vegetation on the Huanchaca Mesetta, (2) climate was the dominant control on savanna structure and floristic composition, and (3) the Late Holocene rise in *Mauritia flexuosa* was driven by climate rather than a change in human land-use practices.

Major Findings from Huanchaca Mesetta

There were three major findings from the analysis of the Huanchaca Mesetta sediment cores. The first major finding was that edaphic constraints were the first order of control of vegetation, fire, and soil geochemistry on the Huanchaca Mesetta plateau. Despite significant climate variability since the Late Glacial, the vegetation on the highly weathered quartzite plateau was limited to drought and fire tolerant C_4 grasses as indicated by the continued presence of C_4 Panicoideae grass phytoliths that covaried with the $\delta^{13}C$ values. These data support hypothesis number one: irrespective of changes in temperature, precipitation, and fire activity over the past 14,500 years, edaphic conditions on the mesetta were the dominant control on savanna vegetation.

The second significant finding confirmed climate as the second order control on vegetation, fire, and soil geochemistry at Huanchaca Mesetta. During the Last Glacial period, nonanalogue vegetation communities were present, characterized by the absence of *Mauritia flexuosa*. The absence of *M. flexuosa* was attributed to the increased frequency of *surazo* winds during the Last Glacial period (Bush & Silman, 2004). Increased frequency of *surazos* would have had little effect on the absolute temperature minima, but the mean monthly and annual temperature minima may have been ca. 5 °C lower (Bush & Silman, 2004). Despite near modern annual temperatures ca. 19,500 cal yr BP (Whitney et al., 2011), the elevational lapse rate (6.4 °C/km (Glickman, 2000)) coupled with lower mean monthly and annual temperature minima from more frequent *surazos* likely resulted in climatic conditions below the thermal optimum of 21 °C for *M. flexuosa* (Rull & Montoya, 2014) on Huanchaca Mesetta.

Climate driven controls were also exhibited on the spatial variability of fire activity between the lowland sites and Huanchaca Mesetta. During the Middle Holocene (8,000–4,000 cal yr BP), increased fire activity in the lowlands sites and decreased fire activity on the mesetta were attributed to fuel availability. In lowland sites, dry forest-savanna vegetation combined with increased seasonality resulted in increased fire activity (Burbridge et al., 2004; Carson et al., 2014). Atop the edaphically constrained mesetta, lower annual moisture combined with greater seasonality during the MHAP resulted in limited grass fuel availability and decreased fire activity. During the Late Holocene (3,550 cal yr BP to present), increased annual precipitation and decreased seasonality resulted in the establishment of rainforest vegetation and decreased fire activity in the lowlands (Burbridge et al., 2004; Burn et al., 2010; Carson et al., 2014). Conversely, increased precipitation resulted in the accumulation of fire-adapted C_4 grasses on the mesetta. The increased precipitation was likely associated with an increased incidence of lightning-caused fires, fueled by the abundance of fire-adapted grass fuels, resulting in increased fire activity at Huanchaca Mesetta. These data support the second hypothesis that climate was the second order control on vegetation, fire, and soil geochemistry the mesetta.

The third major finding from Huanchaca Mesetta identified climate opposed to anthropogenic land-use practices as the dominant driver in the Late Holocene rise of *M. flexuosa*. These data suggest natural drivers controlled the continued presence of savanna vegetation and fire activity on the Huanchaca Mesetta for the past 14,500 years, supporting the third hypothesis, that the expansion of *M. flexuosa* was largely controlled by natural drivers (edaphic, climate, caused fires) as opposed to anthropogenic drivers.

A Paleoecological Assessment of Cuatro Vientos *Terra Firme* Rainforest Ecosystem

Chapter 3 identified controls on local, meso, and regional scale fire activity from Cuarto Vientos palm swamp from the *terra firme* rainforest in NKMNP and from existing charcoal records in the Neotropical lowlands. The objective of this chapter was to investigate subcentennial fire and soil geochemistry histories devoid of significant human impact since the Last Glacial period. To extend the spatial-temporal scale of past fire activity, charcoal data from Cuatro Vientos (subcentennial, local scale) were compared to existing charcoal records within NKMNP (centennial-millennial, meso scale) and to regional charcoal records (centennial-multimillennial, regional scale). These data were interpreted with existing paleoclimate data (Cross et al., 2000; Cruz et al., 2005; Rowe et al., 2003; Thompson et al., 1998) to assess the response of fire to long-term climatic variations. To explore fire-climate linkages on varying spatial-temporal scales, three hypotheses were tested: (1) climate was the first order control of fire activity and soil geochemistry at Cuatro Vientos, (2) fire activity at Cuatro Vientos follows patterns of meso and regional scale biomass burning, and (3) periods of increased climatic variability result in increased regional fire activity.

Major Findings from Cuatro Vientos

There were three major findings from the analysis of the Cuatro Vientos sediment cores and regional charcoal composite comparisons. The first major finding was that climate was the first order control on fire activity and soil geochemistry at Cuatro Vientos. Variability in stable isotopes and charcoal data exhibit similar trends to temperature reconstructions from Laguna La Gaiba, (ca. 500 km SE of Cuatro Vientos). Temperatures rose ca. 4 °C immediately following the LGM ca. 19,500 yr BP and reached near modern levels (ca. 25 to 26.5 °C) by 19,500 yr BP (Whitney et al., 2011). The $\delta^{15}N$ values exhibited the greatest variability from 23,000 to 15,000 cal yr BP, indicating increased denitrification likely associated with the increased length of the dry season during the Last Glacial (Berger & Loutre, 1991). The dry Late Glacial conditions created fire-promoting climatic conditions evidenced by the increase in charcoal accumulation and highest peak magnitude values at Cuatro Vientos.

The Middle Holocene Arid Phase (MHAP) ca. 8,000 to 5,400 cal yr BP (Baker, Rigsby et al., 2001; Baker, Seltzer et al., 2001; Cruz et al., 2005; Thompson et al., 1998) was evidenced by the sediment hiatus at Cuatro Vientos from ca. 14,500 to 7,000 cal yr BP. The presence of fire/drought-adapted C_4 vegetation indicated by the $\delta^{13}C$ values, coupled with increased fire activity, corresponds to longer dry seasons characteristic of the MHAP. After 6,000 cal yr BP, precipitation began to increase in the Amazon driven by orbital forcing (Baker, Seltzer et al., 2001). Increased charcoal accumulation, moderate peak magnitude values, the highest fire frequency and abundant nonarboreal charcoal indicate frequent, low magnitude fires associated with a precipitation-driven increase in the development of fine C_4 grass fuels. These data support the first hypothesis that climate was the first order control of fire activity and soil geochemistry at Cuatro Vientos for the past 25,000 years.

The second major finding was that local-scale fire activity at Cuatro Vientos exhibited similar patterns of burning to meso and regional scale fire activity. Charcoal influx data from Cuatro Vientos and the neighboring site of Laguna Chaplin (10 km east) indicate periods of increased biomass burning between 16,000–15,000 cal yr BP and after 8,000 cal yr BP. On the regional scale, there was increased biomass burning ca. 6,600 cal yr BP and again between ca. 5,000 and 4,500 cal yr BP. These data suggest Cuatro Vientos was representative of regional fire regimes. These charcoal data support the second hypothesis that fire activity at Cuatro Vientos followed similar patterns of meso and regional-scale biomass burning.

The third major finding was that periods of increased climatic variability were associated with increased biomass burning on local to regional scales. Previous analysis of existing sedimentary charcoal records from the Neotropics suggest fire activity was associated with periods of high climate variability, including changes in moisture budgets and the intensification of seasonal droughts (Power et al., 2010). Recent research on climate-fire drivers indicate temperature as quantitatively the most important driver of changes in fire activity (Daniau et al., 2012). Temperatures rose ~4 °C immediately following the LGM at 19,500 yr BP reaching near modern levels (ca. 25 to 26.5 °C), and exhibiting a transitional period to 16,000 yr BP, by 15,900 yr BP (Whitney et al., 2011). Dry conditions persisted until ca. 12,500 cal yr BP (Whitney et al., 2011). Regional charcoal composites show increased transformed charcoal influx, suggesting increased temperature variability was the dominant climatic driver of increased fire activity on local, meso, and regional scales. The dry conditions of the Late Glacial were likely a secondary control promoting increased burning through vegetation productivity and the occurrence of fire-promoting climatic conditions (Marlon et al., 2013).

The regional ($>10^{10}$ m^2) charcoal composite demonstrates an increase in biomass burning during the Middle Holocene Arid Phase (MHAP). The MHAP was characterized by decreased precipitation (Baker, Rigsby et al., 2001; Baker, Seltzer et al., 2001; Cruz et al., 2005; Thompson et al., 1998) and longer dry seasons (Berger & Loutre, 1991). Precipitation changes were the primary factor being observed in Holocene vegetation (and subsequent fire dynamics) because atmospheric CO_2 concentrations and temperature exhibited only minor fluctuations through the Holocene (Indermühle et al., 1999). In arid and semiarid environments, increases in precipitation tend to increase fire, whereas increased precipitation in humid environments can reduce fire (Marlon et al., 2013). The onset of drier-than present climates likely promoted the initial increase in fire activity during the Early–Middle Holocene either directly by reducing humidity, lowering fuel moisture and drying soils or indirectly by favoring more flammable vegetation (Power et al., 2010). These data support the third hypothesis that periods of increased climatic variability result in increased regional fire activity.

Assessing the Application of Neotropical Pollen Data in Threshold Detection

Chapter 4 identified drivers of regional variability in vegetation change. The purpose of this research was to identify abrupt changes at pollen sites within a defined spatial area, to look for periods of accelerated regional change, and to link these periods to drivers that may influence ecosystems at a regional scale. Three hypotheses were addressed in this chapter: (1) variability in the R.O.C. was not constant over time, (2) regional patterns of variability in the R.O.C. were synchronous, and (3) periods of nonrandom variability were linked to regional drivers (e.g., climate, humans).

Major Findings from Neotropical Pollen Data Synthesis

There were three major findings from Chapter 4. The first major finding was that the use of SCD dissimilarity analysis was able to detect variability in the R.O.C. Variability was concentrated around the glacial-interglacial transition and during the Late Holocene (ca. 1,500 years to present). These data support the first hypothesis that variability in the R.O.C. was not constant over time.

The second major finding in this analysis implemented randomization analysis to confirm that the variability exhibited in the R.O.C. was nonrandom. There were six periods of abrupt change (defined here as <1,000 years) since the last Glacial period where 30–60% of the sites changed: 14,500, 12,500, 10,500, 9,500, 3,500, and after 1,500 cal yr BP. Increased variability in vegetation suggests increased instability and lowered resiliency. These data support the second hypotheses that regional patterns of variability in the R.O.C. were synchronous.

The third major finding identified regional drivers of past vegetation change. Climatic variability associated with the glacial-interglacial transition, the drier MHAP, and the wetter Late Holocene were likely a dominant control on regional vegetation change. Anthropogenic disturbance during the Late Holocene was the highest in the 25,000 year record. The combined climatic and anthropogenic pressures in the last 1,500 years are associated with the highest proportion of sites (60%) changing in the record. These data suggest that these combined pressures drove vegetation change resulting in greater instability and lower resiliency. These data support the third hypothesis that periods of nonrandom variability were linked to regional drivers, including climate change and human disturbance.

Managing Savanna Ecosystems in the 21st Century

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. The results from this study demonstrate that the continued presence of the savanna ecosystem can be attributed primarily to edaphic and climatic controls. The presence of fire in this system since the Last Glacial indicates that naturally occurring, lightning-caused fire is an integral part of the ecology of the *cerrãdo* savanna ecosystem that needs to be incorporated into a sustainable savanna fire management policy. The Huanchaca Mesetta savanna ecosystem has been resilient to major climatic changes in both temperature and precipitation since the Late Glacial period. These data suggest that savanna ecosystems will continue to be resilient to future climate change associated with global warming.

Managing Rainforest Ecosystems in the 21st Century

Data from this chapter indicate fire activity is climatically driven at local, meso, and regional scales in the Neotropics. Periods of increased climatic variability (both temperature and precipitation) since the Last Glacial period were associated with increased fire activity. Global climate models predict unprecedented temperature increases and potentially longer dry seasons as a result of anthropogenic climate change (IPCC, 2014). The increased variability in future climate change will likely result in increased fire activity that will likely be exacerbated with positive feedbacks accompanying disturbed Neotropical ecosystems. The 2010 fire season evidences the need to improve fire-fighting infrastructure, resource allocation and response time to manage fires in Bolivia to meet conservation goals and to protect increasing human populations living in these increasingly fire prone ecosystems.

Adaptive Management Strategies of Neotropical Ecosystems

The successful detection of past ecosystem thresholds through a regional pollen synthesis has significant management applications for the 21st century. Abrupt climate driven ecological change have occurred on a regional scale in the Neotropical lowlands a minimum of six times since the Last Glacial Maximum. Vegetation change for the past 25,000 years was driven by oribitally paced climatic changes that altered both temperature and precipitation. In the last 1,500 years combined climatic and anthropogenic pressures resulted in the highest proportion of regional sites changing, indicating lowered ecosystem resiliency. These data support the interpretation that the unprecedented rate of global climate change, coupled with increased anthropogenic disturbance and positive feedbacks, will result in lowered ecosystem resiliency and likely lead to tipping points in Amazonian ecosystems (IPCC, 2014).

The application of the ecological threshold concept has increased with the implementation of "adaptive management" as a tool for approaching environmental management issues (Groffman et al., 2006). In an adaptive management model, solutions to problems are proposed and implemented, but prescriptions are constantly re-evaluated based on actual ecosystem response to management (Holling, 1978; Schreiber et al., 2004; Walters, 1986). As Neotropical ecosystems reorganize in response to climate change, realistic conservation and management models should aim to preserve species biodiversity, functional diversity, genetic diversity, community and ecosystem diversity, and habitat diversity (Alho & Sabino, 2011; Lomolino et al., 2010). Various biological reserve models (e.g., the SLOSS debate (MacArthur & Wilson, 1967)) should also be included in the adaptive models. The application of a complex, adaptive ecosystems perspective (Groffman et al., 2006) will aid in the development of robust, flexible, and adaptable Neotropical ecosystem management policy in the 21st century.

Future Research Perspectives

The research conducted in this dissertation provides a foundation for future research on the legacy of human disturbance in Neotropical ecosystems. Future research questions include (1) how can pollen data be used to distinguish tipping points from accelerated succession in the paleoecological record?, (2) how can the frequency of disturbance alter the resiliency of modern Neotropical ecosystems?, and (3) what is the human legacy on Neotropical ecosystems during the past 2,000 years? As the increasing impacts of anthropogenic climate change and human disturbance surpass ecological thresholds, long-term paleoecological research will continue to provide a valuable insights for management and policy toward maximizing the preservation of biodiversity in *cerrădo*, savanna, and rainforest communities in lowland Bolivia.

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