The Central American Isthmus:

Ecological Dynamics of the

Middle-Late Holocene

Word Count: *c.*60,000

Thesis submitted for the degree of Doctor of Philosophy,

University of Oxford

March 2019

William James Harvey

St Edmund Hall

Department of Zoology

To my parents

Ian James Harvey & Nancy Lynn Harvey

"So we beat on, boats against the current, borne back ceaselessly into the past."

F. Scott Fitzgerald

THESIS ABSTRACT

An ever-increasing demand for agriculture while conserving biodiversity, maintaining livelihoods, and providing critical ecosystem services is one of the largest challenges for tropical land management across the Central American Isthmus today. Climatic and anthropogenic drivers currently provide the largest threats to changes in the vegetation cover and composition for this region therefore understanding the dynamics of these systems, their variability across space and through time is important for discerning current and future responses.

I utilised a number of palaeoecological proxies (fossil pollen, macroscopic charcoal, microscopic charcoal, *Sporormiella*, and diatoms) extracted from lake sediment cores, to explore the past drivers of vegetation dynamics across the Central American Isthmus with a focus on two of the most threatened forest biomes: (i) the mixed coniferous forests of upland Guatemala; and (ii) the dry broadleaf forests of lowland Nicaragua. I explored the role of fire and Pre-Columbian civilization in the mixed coniferous forests of upland Guatemala spanning the last 6000 years., followed by the impact of European contact from c.1500C.E. through to 2015C.E.; and in lowland Nicaragua I investigated the vulnerability and resilience of the dry tropical forests to known climatic and anthropogenic perturbations over the past *c.*1200-years.

My results demonstrate the state of knowledge for climate, burning, the spread of agrarian practices and the impacts these drivers have had upon the structure, composition and resilience of vegetation across space and through time. I found that while there were several homogenous climatic shifts most changes in precipitation were spatially and temporally heterogeneous. Increases in burning from 10000 – 2000B.C.E. are largely associated with climate, particularly between 7000-4000B.C.E. The relationship between climate and fire decoupled between 3000 – 2500B.C.E. as humans increasingly impacted land use through agrarian practices and lime production. I present evidence for the anthropogenic use of fire as the dominant driver of structure and compositional change in the mixed pine-oak forests of Guatemala during the Pre-Columbian Era, while domestic bovid grazing and logging was found to have suppressed hard-wood forest taxa recovery and regeneration since European contact. In the dry tropical forests of Nicaragua climate appears to have driven local fire; however, regular disturbance to this vegetation type appears to have made it very resilient against both climatic and anthropogenic disturbance through time, both pre and post European contact.

This thesis provides new information on the past ecological responses of two Central American forest types to climatic and anthropogenic disturbances spanning the Middle to Late and Late Holocene 4000B.C.E. – 2015C.E. Changes to the structure and composition of these forests in the past represent a globally important and largely understudied region, for which my thesis offers fundamental insights into its ecology and history.

ACKNOWLEDGEMENTS

The concept of this thesis would never have been conceived without the celebrations and discussions held at the wedding of Luis Arizaleta Coro and Veronica E. Gomez Lacayo back in June 2012: “Why are you studying lakes in Mexico, come to Nicaragua: The land of lakes and volcanoes.” The outcome of these conversations led to a journey of adventure and wonder with multiple field expeditions to Nicaragua over the subsequent years.

My journey to complete a DPhil at the University of Oxford, has been subject to many challenges and life lessons. I would like to give thanks to Katherine J. Willis, Sandra Nogué Bosch, and Nathan D. Stansell for their academic supervision and support. Kathy, you have inspired me to be resilient. Sandra, your positivity and encouragement brightened my darkest days. Nathan, your logistical excellence and tenacity in the field made this research possible. It has been my privilege to have you all as role models and mentors in my work and in my life.

I would like to thank my colleagues from the Oxford Long-Term Ecology Laboratory: Andrew C. Martin, Gillian Petrokofsky[3], Carole Adolf, Peter R. Long, David Benz, Catherine E. A. Gresty, Georgia M. Hole, Nichola Kühn, Hernrik J. N. Hannemann, Herizo T. Andrianandrasana, Eva Herreros Moya, Danielle Sinclair and Beccy Wilebore for their camaraderie and support.

Field work in Nicaragua would not have been possible without the backing and encouragement of Julio B. Gomez Martinez, Veronica Lacayo de Gomez, Julio B. Gomez Lacayo., Manuel Roman Lacayo, Craig Vandersluys-Seers, Nidi Tapoulal, Stephen Perdziola, and Maurice Hodgson.

I would like to extend my deepest gratitude to Sarah J. Davies and Ian P. Matthews for setting me on this path of discovery and for indulging my studies in Central American for my undergraduate and master’s dissertations.

To my dearest friends Zafar Khurshid, Beatrice E. Tyrrell, and Grace S. Lievesley, you have all been by my side to support me through this journey, at home and abroad, and I am truly grateful to have had you all in my life. I would also like to thank Yilin Tim Chen, Fran Read, Ceren Zor, Kate Maffei, Pip Coore, and Kathryn T. Hutchinson who made my time at St Edmund Hall extra special.

I will be forever indebted to my family for their enduring support and encouragement. To my parents: Ian J. Harvey and Nancy L. Harvey; my brothers: Maximillian J. Harvey and Francis S. Harvey; and my grandparents: Katherine Harvey, Michael J. Harvey (1930-2013), Bruce Wertheimer, and Naomi Wertheimer (1928-2016). Without your lessons and morals, I would not have developed into the person I am today.

CONTENTS

List of Tables

List of Figures

List of Abbreviations and Acronyms

B.P. – Before Present

B.C.E. – Before the Common Era

CADC – Central American Dry Coridor

Cal – Calibrated

CCA – Canonical Correspondence Analysis

C.E. – Common Era

CF – Cloud Forests

DTF – Dry Tropical Forests

ESF – Early Successional Formation

FF – Fallow Field

IAS – Intra American Sea

ITCZ – Inter Tropical Convergence Zone

LIA – Little Ice Age

M.A.S.L. – Meters Above Sea Level

MCA – Medieval Climate Anomaly

MHWF – Mountain Hard Wood Forests

MPOF – Mountain Pine Oak Forests

MSF – Mid Successional Formation

MTF – Mountain Tropical Forests

NAO – North Atlantic Oscillation

OF – Oak Forests

PCA – Principal Component Analysis

PF – Pine Forests

POF – Pine Oak Forests

POLF – Pine Oak Liquidambar Forests

SHR – Shrubland

SI – Supplementary Information

SST – Sea Surface Temperature

Yrs – Years

1. INTRODUCTION

The largest challenge for tropical land management across the Central American Isthmus is to meet the ever-growing demand for agriculture while conserving biodiversity, maintaining livelihoods, and providing critical ecosystem services (Harvey et al. 2008). Climatic and anthropogenic drivers currently provide the largest threats to changes in the vegetation cover and composition of this region. Understanding the dynamics of these systems, their variability across space and through time, and their impacts to vegetation, is therefore important for discerning current and future responses. Such information is of value especially for risk mitigation, planning and conservation purposes (Chiabai, 2015).

Agricultural intensification has been accompanied by substantial reductions in tree cover, habitat diversity, and forest connectivity in recent years (Redo et al. 2012), with around 80% of the region's vegetation having been converted into agriculture (Harvey et al. 2008). In addition to human-driven land-use change, identifying the potential changes in available water resources in response to climate change is another top priority of the IPCC and policy makers throughout the Americas (IPCC, 2014). At present, future drought is difficult to predict, as current projections for tropical circulation changes under a range of warming scenarios remain highly uncertain (DiNezio et al., 2010). However, the impacts of droughts are now being seen. For example, a deficit in precipitation at the beginning of the *primera* cropping cycle in 2015C.E. caused significant losses in food production rendering an estimated 2.2 million people at risk of moderate or severe food insecurity (World Food Programme, 2016). The habitat loss driven by human activity and climate change is leading to increased fragmentation of the remaining forests and loss of biodiversity. For example, according to the IUCN Red List over 300 of the region's endemic species of flora and fauna are currently threatened with extinction of which 107 are critically endangered (CI, 2018).

Research examining the drivers and responses of different vegetation types to climatic and anthropogenic influences across the Central American Isthmus predominantly focuses on anthropogenic impacts spanning the last 50 years (Chiabai, 2015). Yet many of the processes associated with forest change occur on timescales much longer than this. It is also unclear how much of the present landscape was already impacted by these drivers before 50 years ago and its true 'natural' baseline. An understanding of the vegetation dynamics of this region through time is currently limited yet it is essential for understanding current patterns of change, particularly in regard to: (i) water availability; (ii) anthropogenic land management and agrarian practices; (iii) resource utilization; and (iv) response to environmental hazards (Stansell, 2013; and Adomat & Gischler, 2017). Examination of biotic (e.g. pollen, diatoms, and *Sporormiella*) and abiotic proxies (e.g. $\delta^{18}O$, $CaCO_3$ and magnetic susceptibility) extracted from environmental archives can provide evidence for these longer-term changes in vegetation and the drives such as changes in precipitation, buring, herbivory, and human activities.

This thesis therefore sets out to determine what is known about the drivers, the responses and the resilience of Central American vegetation over time. First, I will provide a brief overview of the current status of vegetation, and its drivers of change. Through doing this, I aim to introduce the region, the key drivers and the knowledge gaps that have led to the body or research outlined in this thesis. The second part of this chapter will then introduce the four research papers that form the main body of this thesis.

Current vegetation

The distribution of the flora and fauna across the Central America Isthmus can be broadly described under the six terrestrial biome types: (i) moist broadleaf forests; (ii) dry broadleaf forests; (iii) coniferous forests; (iv) grasslands, savannas and shrublands; (v) xeric shrublands; and (vi) mangroves (Figure 1.1).

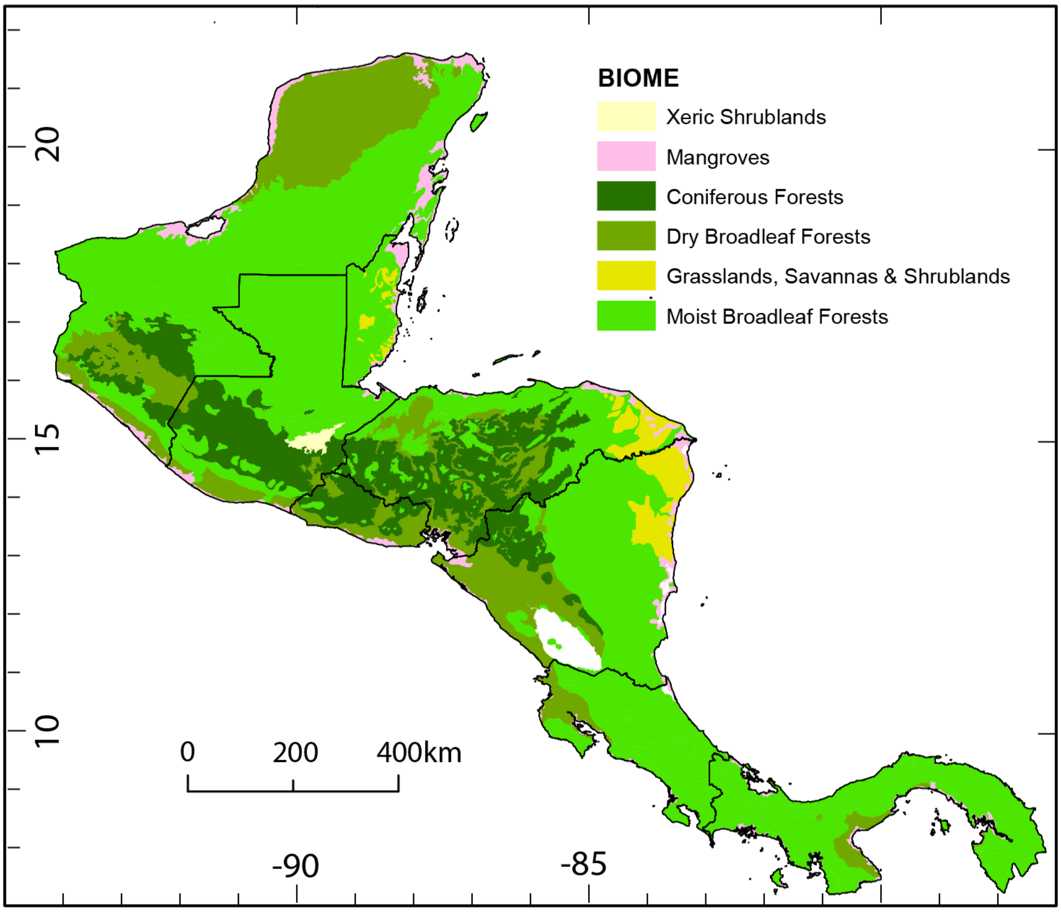


Figure 1.1: Biomes of the Central American Isthmus. Based on Dinerstein et al. (2017).

The moist broadleaf forests are dominated by semi-evergreen and evergreen deciduous tree genra, such as *Alnus*, *Cassipourea*, and *Hevea* (Pither & Kellman, 2002) and contain the highest tree species diversity of all the terrestrial biomes (Chibai, 2015). This biome can be further subdivided by ecoregions according to their altitudinal distribution, grouping them into lowland (<1000m) and upland (>1000m) areas (Dinerstein et al. 2017). The lowland moist broadleaf forests are distributed in continuous strips (e.g. the Petén-Veracruz moist forests and Central American Atlantic moist forests) while the montane moist broadleaf forest ecoregions are naturally fragmented by elevation (e.g. the Central American montane forests. The main drivers of land use change in this biome are agricultural and infrastructure expansion (Geist & Lambin, 2001; and Corrales et al. 2015).

The dry broadleaf forests were originally thought to have covered the north of the Yucatan peninsula and extended in a continuous strip from the Pacific Coast of southern Chiapas, to north-western Costa Rica (Figure 1.1). These forests now only cover 1% of this area. This drastic reduction in size is thought to have been due to increasing human settlement and extensive agrarian practices (Janzen, 1988). Rearing of cattle and conditions conducive to shifting cultivation make this region anthropogenically desirable and thus densely populated (Sabogal, 1992). These forests are usually composed of two strata, a higher story of deciduous trees, such as *Brosimum*, *Bursera* and *Cordia* (Griscom & Ashton, 2010); and a lower story of evergreen species, such as *Diospyros*, *Mimosa* and Bignoniaceae (Gillespie et al. 2000).

Coniferous forests are mainly distributed across the uplands of the Sierra de Madre de Chiapas, Mexico/Guatemala through the Sierra del Merendón, Guatemala/Honduras and south into northern Nicaragua (Figure 1.1). The most outstanding characteristic of this biome is the diversity of pine (>150 *Pinus spp.*) and oak (>150 *Quercus spp.*) species (Muller, 1942; Kappelle, 2006), which are well adapted to variable climatic conditions and natural fires (Corrales et al. 2015). These pine-oak forest formations often form intricate mosaics and complex successional interactions extending up into broad leaved cloud forests at higher altitudes (Kappelle, 2006; Rzedowski, 2006). This biome is currently threatened by agricultural expansion, logging, firewood extraction, forest fires, and pests (Veblen, 1978).

Grasslands, savannahs and shrublands can be found on the east coasts of Honduras and Nicaragua and in Belize (Figure 1.1). They predominantly comprise one species of pine, *Pinus carribaea,* and expansive grass fields. This ecosystem has poor soils and is subject to frequent burning (Parson, 1955).

Xeric shrublands are restricted to one ecoregion on the Guatemalan-Honduras boarder (Figure 1.1). The Motagia Valley comprises two main vegetation types: (i) thorn scrubland, comprised of cacti, such as *Opuntia*; and (ii) dry forests comprised mainly of shrubby Leguminosae; however, there is a high diversity of tree communities in riparian habitats (Corrales et al. 2015). Most of this region has been converted into irrigated agricultural fields (Najera, 2006).

Mangroves grow along the coastal regions of Central America (Figure 1.1). Tree species are red mangrove (*Rhizophora mangle*), yellow mangrove (*Rhizophora harrisonii*), white mangrove (*Laguncularia racemosa*), and black mangrove (*Terminalia erectus*). Residential and commercial anthropogenic expansion into these areas is threatening biodiversity and soil stability (Young, 2008).

Previous summaries of vegetation dynamics through time across Central America have focussed upon the regional expansion of mesic forests in the Early-Middle Holocene (e.g. Piperno et al. 1990; 1991) and the regional impacts of anthropogenic activities, particularly agriculture in the Maya lowlands, during the Pre-Classic 2000B.C.E. – 250C.E., Classic 250 – 950C.E. and Post-Classic 950 – 1500C.E. Maya periods (e.g. Neff et al. 2006; Ford & Nigh, 2009; Piperno et al. 2006; 2011; Islebe et al. 2018).

Driver: Climate

Today, precipitation across the Central American Isthmus (Figure 1.2) is principally driven by topography (Alfaro, 2000), as well as the complex interactions of factors influencing the Inter Tropical Convergence Zone (ITCZ) (Metcalfe et al. 2015). These include the North Atlantic Oscillation (NAO) and the El Niño Southern Oscillation (ENSO) (Giannini et al. 2001). Modern rainfall has a bimodal seasonal regime with high levels of precipitation between May-November and drier conditions between December-April (Enfield & Alfaro, 1999; GARDAWORLD, 2018). Modest shifts in either eastern tropical Pacific or Atlantic sea surface temperature (SST) drive circulation changes over the region that potentially lead to widespread drought. During the summer of 2014C.E., Central America suffered major shortages in rainfall and one of the worst drought years in decades as a result of shifting SST in the tropical Pacific (World Food Programme, 2016).

There are a number of palaeo-climatic reviews which present syntheses of past climate and precipitation for this region (e.g. Metcalfe et al. 2000; 2015; Beach et al. 2015; Douglas et al. 2016). These suggest spatial patterns of changes during select periods including (i) the onset into the Holocene 10000 – 7000B.C.E., (ii) the Middle Holocene 7000 – 2000B.C.E.; (iii) the Medieval Climate Anomaly (MCA) 900 – 1250C.E.; and (iv) the Little Ice Age (LIA) 1400 – 1850C.E.

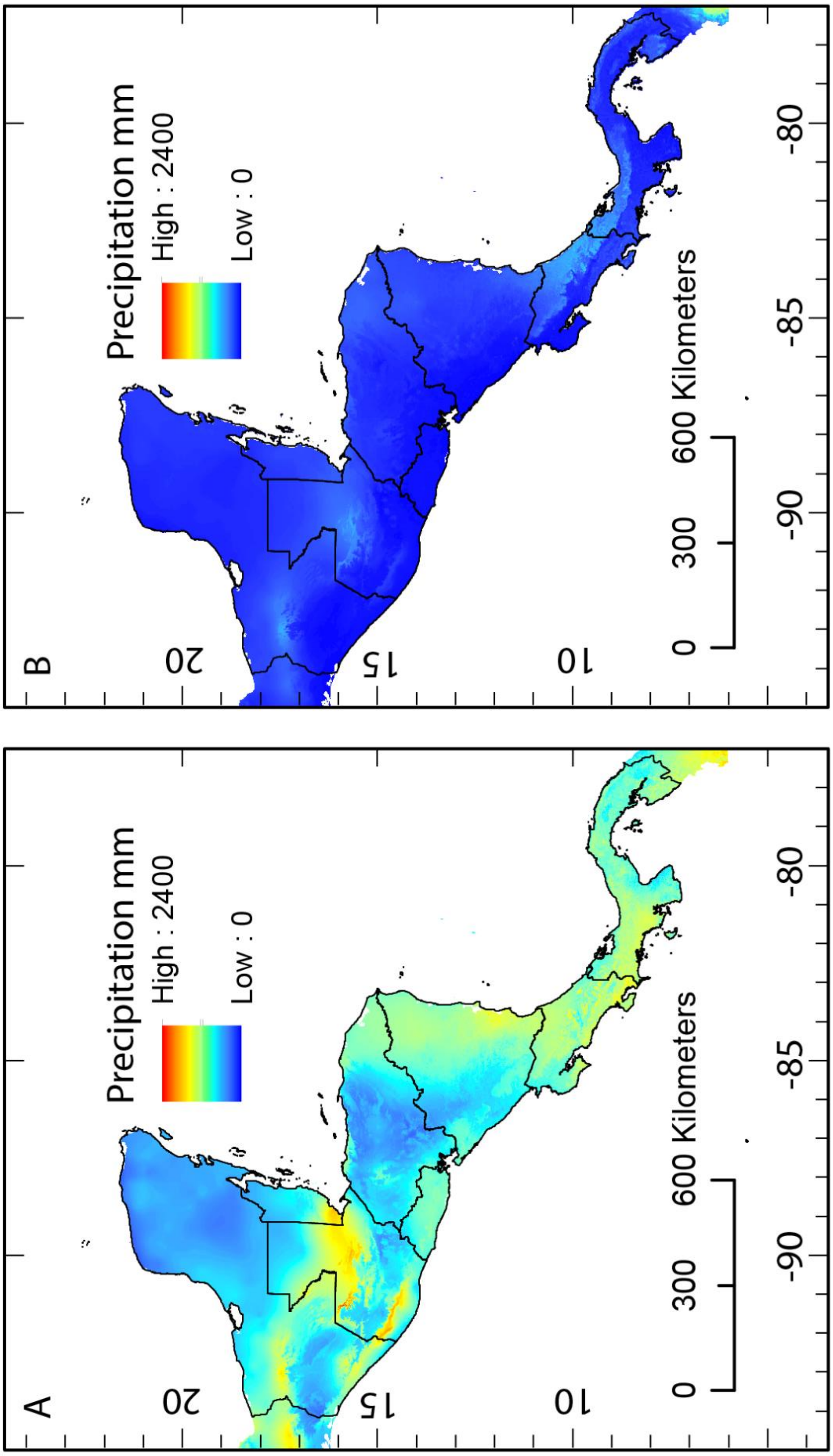


Figure 1.2 Precipitation across the Central American Isthmus during the wettest quarter (A) and the driest quarter (B). Data from Global Surface Summary of the Day (interpolating between weather stations: Sparks et al. 2017).

It has been suggested that patterns of climatic forcing during the Late Holocene 2000B.C.E. to present, are spatially and temporally heterogeneous, with signals increasingly masked by anthropogenic development after around 2000B.C.E. (Metcalfe et al. 2015). Other reviews focus on periods of drought relating to the collapse of the Maya civilization between 800-1100C.E. (e.g. Beach et al. 2015; Douglas et al. 2016). These review papers draw upon proxy evidence from both marine (e.g. the Cariaco Basin: Haug, 2001) and terrestrial (e.g. Neff et al. 2006) archives in and around the Central American region.

Driver: Burning

Modern burning across the Central American Isthmus is driven by the complex interaction between climate, people and vegetation (Bowman et al. 2011). Climate driven fire across the Central American Isthmus can be initiated by lightning strikes and/or prolonged periods of drought (e.g. Anderson & Wahl, 2016). The moist tropical forests of Central America rarely naturally burn, owing to the low frequency of lightning and high levels of moisture (Bowman et al. 2011). However, drier areas, such as the dry tropical forests and savannahs, experience more frequent natural fires due to the increased availability of seasonally desiccated biomass (Murphy & Lugo, 1986). Coastal regions may also experience increased magnitudes of burning after a hurricane because of increased fuel loads and lightning strikes (e.g. Urquhart, 2009).

Unilinear burning within i) previously unburned; (ii) once-burned; (iii) twice-burned; and (iv) more than twice-burned tropical forests can lead to complex relationships and feedbacks associated with climate, fuel loads, and taxa persistence on temporal and spatial scales (Cochrane, 1999a, Scott et al. 2013). Fire in previously unburnt tropical forests usually moves slowly along the ground with the intensity of a prescribed burn *c*.50kW m^{-2} (Pyne, 1984). These fires primarily consume dry leaf litter; however, cause mortality of around 95% to trees with thin tree bark (Uhl & Kauffman, 1990; Cochrane, 1999). As trees shed their fire damaged biomass the canopy of the forest opens (50 – 70%) allowing for greater solar heating and air movement in the understory, drying the underlying forest fuels (Scott et al. 2013). Fuel loads have been found to increase following an initial burn for up to 2 years after the initial event (Holdsworth & Uhl, 1997; Cochrane, 1999). Previously burnt forests are more susceptible to future burning events, particularly during dry seasons, as a result of these increased fuel loads (Cochrane, 1999a; 1999b).

A secondary fire event in a once burned forest are typically faster moving and more intense (Scott et al. 2013). Cochrane (1999a) estimates that heat release (Rothermel, 1983) in a once burned tropical forest can reach 7500kW m^{-2} and >7500kW m^{-2} in subsequent burns. Larger trees with thicker bark have little additional survival advantage during these more intensive burns with mortality of up to 98% (Peterson & Ryan, 1986). Fires in frequently impacted forests are substantially more severe in respect to intensity, flame height, penetration, residence time, and spread of burn. Recurring fires have the potential to remove trees from forested landscapes leaving either scrub or grasslands for 20 – 80 years (Kappelle, 2006).

Humans can influence fire regimes in several different ways such as changing fuel availability and structure, e.g. removing biomass through extraction of timber and deadwood, and controlling ignitions igniting more or fewer fires irrespective of season or weather (Bowman et al. 2011). Even today, humans cannot completely control the fires they set, nor completely control fires caused by natural ignitions. Nicaragua's dry season lasts from November to April each year, exacerbating the risk of forest fires (GARDAWORLD, 2018). In April 2018 for example, the anthropogenically initiated Indio Maiz forest fire destroyed 5484 hectares of primary tropical moist broadleaf forests on the Moskito coast of Nicaragua (Joaquin-Chamorro, 2018; The Guardian, 2018). The fire was thought to have been started by illegal anthropogenic settlement and poor agricultural practices. The damage caused to the flora and fauna of this vulnerable ecosystem is yet to be accounted for (The Guardian, 2018).

To my knowledge, no attempts to synthesise Holocene fire across the Central American Isthmus have been attempted. However, regional comparisons are discussed in detail (e.g. the Central Maya lowlands or highlands of Costa Rica), focusing upon the impacts of Early-Mid-Holocene climate (e.g. League & Horn, 2000; Lane et al. 2011; Correa-Metrio et al. 2012) and Late-Holocene anthropogenic agrarian and architectural practices (Correa-Metrio et al. 2012; Schüpbach et al. 2015; Anderson & Wahl, 2016).

Driver: Herbivory

Large herbivores are being increasingly recognised as significant drivers of vegetation change across most all of Earth's biomes (Chase et al. 2000; Hopcraft et al. 2009; Griffiths et al. 2011; Baker et al. 2013). The disturbance that they can cause to vegetation structures and composition through browsing and grazing is being increasingly investigated (Sinclair & Norton-Griffiths, 1979; Putman, 1986; Tubbs, 1986; 2001; Sinclair & Arcese, 1995; Gelorini et al. 2012 Baker et al. 2013; 2016). Grazing represents one of the main drivers of disturbance along with fire regimes, human activity and climatic variability (Jeffers et al. 2012). Landscapes altered by domesticated and wild herbivores across Central America are currently poorly understood with limited research examining their impacts through time.

Palynomorph analysis of dung fungal spores (*Sporormiella*) can be used to infer the presence and abundance of large herbivores in the past (Davis, 1987; van Geel et al. 2003; Davis & Shafer, 2006); however, *Sporormiella* representation is spatially sensitive to the distance from the dung source (Raper & Bush, 2009). There are currently no known palaeoenvironmental records for *Sporormiella* for the Central American region.

Driver: Population Growth and Land-Use Change

Population growth and land-use change across Central America has accelerated over the past 50 years and is projected to continue expanding in the future (Figure 1.3). Increasing human populations are closely linked to the expansion of urban settlements, forest conversion for subsistence maize farming and pasture creation (Carr, 2005; FAOSTAT, 2011).

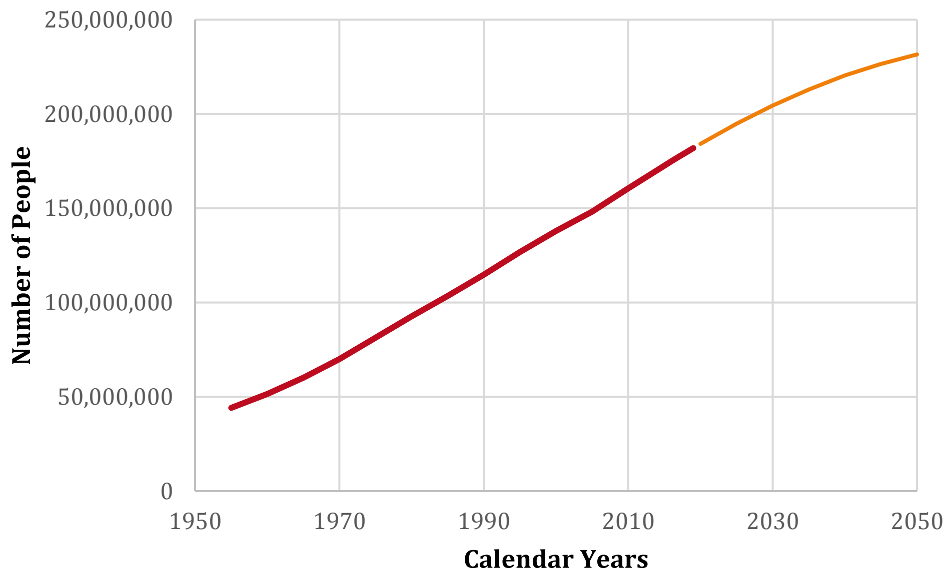


Figure 1.3 Population of Central America from 1950-2019C.E. and predicted population increase through to 2050 (Worldometers, 2019).

Guatemala, Nicaragua and Belize have been particularly impacted by increasing human populations with 6,866 km^2 of forest being converted into agricultural agricultural/herbaceous land between 2001-2010C.E. (Redo et al. 2012). From 1966-1994C.E. Guatemala lost 22% of its forest cover to agricultural settlement, around 7%

per decade (Bilsborrow, 2001), and a further 7% annually between 2001-2010C.E. (Redo et al. 2012). Similar patterns are also noted across areas of the Yucatan Peninsula (Rueda, 2010; Redo et al. 2012). Across northern Guatemala this deforestation is strongly associated with distance to human settlements and rapid population growth (Bray et al. 2008). Nicaragua experienced the highest deforestation rate of any country in Central America, losing 7,961 km^2 of forest from 2001-2010C.E., with most of this land being converted into extensive pastures (Redo et al. 2012); while in Honduras and El Salvador agricultural land cover declined by around 2,335 km^2 between 2001-2010C.E., coinciding with forest recovery. However, whilst there is a considerable body of knowledge relating to the present-day situation in the Central American Isthmus, far less appears to be known about the trends over longer periods of time.

Palaeoecological records can be used to infer anthropogenic impacts on forests through the analysis of proxy data such as pollen, charcoal, and dung fungal spores (*Sporormiella*); however, there are a variety of challenges associated with interpreting these data sets enabling human impacts to be disentabgled from natural drivers. Anthropogenic impacts are typically inferred from the palynological record through: (i) the identification of known cultigens, such as *Capsicum* (peppers), Cucurbitaceae (gourds), *Maranta arundinacea* (arrowroot), *Phaseolus* (beans), and *Zea mays* (Maize) (White, 1999); (ii) the presence of “weedy taxa”, such as, Amarathaceae, Compositae, and *Polygonum* (Dull, 2004a; Franco-Gaviria et al. 2018); (iii) abrupt reductions in all or select arboreal taxa, such as *Quercus* (Dull, 2004a; 2004b; 2007; Velez et al. 2011); and (iv) increases in local and regional burning (e.g. Dull, 2004a; 2004b; 2007; Anderson & Wahl, 2016). It is often only through the combination of multiple lines of evidence that human impacts can be inferred (e.g. reduced forest taxa combined with an increase in known cultigens and an increase in fire). Across Central America, many of the domesticated taxa are native and occur in the wild as well as being cultivated by humans

(White, 1999). Determining if a given taxa is in situ or anthropogenically introduced and cultivated is often a topic of debate within papers and is discussed within the context of the most likely scenario (e.g. Dull, 2004a; 2004b; 2007).

The high biodiversity within the tropics presents significant challenges when attempting to identify anthropogenic cultigens due to the morphological similarities of some cultivated taxa to their native counterparts e.g. Leguminosae *spp*.; however, some cultivated taxa such as *Zea mays* pollen are easily identifiable from other wild grasses and *Tripsacum* species due to its unique morphological properties including size (>65um), a 2:3 annulus aperture and greater wall thickness (see Dull, 2016). When *Zea mays* pollen is found in a palynological record, even in very low abundances, it is used to suggest anthropogenic presence (e.g. Anchukaitis & Horn, 2005).

In order to distinguish between anthropogenic and climate driven burning it is important to take a multi-proxy approach by using independent proxies to reconstruct climate, vegetation, and fire and where possible use multiple proxies to reconstruct fire (Schüpbach et al. 2015). It is not possible to differentiate between anthropogenic and naturally occurring fires from charcoal records alone (Anderson & Wahl, 2016).

From this brief introduction and overview of current knowledge on the vegetation dynamics of this region, it becomes apparent that there are some significant knowledge gaps in terms of spatial variations and temporal patterns in drivers of vegetation and land use change. This thesis aimed to fill these knowledge gaps by addressing the following 4 questions:

1. What is the current, published, science evidence-based knowledge for vegetation dynamics and drivers of change across Central America?
2. What have been the dominant drivers of change for the vegetation dynamics of the mixed-coniferous forests of Central America during the Pre-Columbian Era?
3. How has Colonial and Post-Colonial land-use change influenced the current landscape, and what implications does this have for the future?
4. How resilient are the dry tropical forests of the Central America’s Isthmus to climatic and anthropogenic perturbations?

To answer the above research questions, I employed a multi-disciplinary and multiproxy approach that included a range of field, laboratory and statistical techniques. Multiple proxies (e.g. fossil pollen, macroscopic and microscopic charcoal, diatoms and dung fungal spores – *Sporormiella*) were extracted from sediment cores collected from Guatemala and Nicaragua and were used to reconstruct the long-term dynamics of precipitation, fire, herbivorous animal abundance, and vegetation dynamics. I specifically focused my research on two biomes that are currently though to be most at risk from climate change and human impact namely: (i) coniferous forests; and, (ii) dry broadleaf forests.

1.1 Overview of Chapters

This thesis is organised into four papers (Chapters 2, 3, 4, and 5) and are integrated into a final concluding chapter (Chapter 6). The first paper (Chapter2) provides a systematic-evidence based review to address the first research question, determining the state of knowledge for drivers of vegetation change through the Holocene. This synthesis illustrates some of the key knowledge gaps which are addressed in the following three chapters.

The subsequent chapters (3, 4, and 5) present primary data collection to address these knowledge gaps. The second paper (Chapter 3) aims to examine the role of anthropogenically driven fire and how it has influenced vegetation change in the coniferous forest biome of Central America over the past 6000 years, thus addressing research question number two. The third paper (Chapter 4) explores land-use change and the impacts of colonial and post-colonial activities, 1524C.E. to present, in mixed coniferous (pine-oak) forests. In here I have integrated palaeoecological data with historical records and earth observation satellite data in order to attempt to provide a continuous baseline record of change to present day, addressing research question number three. The fourth paper (Chapter 5) addresses the resilience of vegetation within the Central American Dry Corridor (dry tropical forests) to climatic and anthropogenic forcing exploring whether some vegetation biomes are more resilient than others, addressing research question number four.

Chapter 2: Environmental proxy evidence for climate, burning and biota across the Central American isthmus spanning the Holocene.

In this chapter I present the results of a systematic review of published long-term ecological proxy data (e.g. pollen, $\delta^{18}O$, charcoal and *Sporomiella*) from terrestrial depositional archives, across the Central American Isthmus. I Identified 521 published data records covering all or part of the Holocene 12000 cal B.P. (10000B.C.E.) to present. These were mapped to show the spatial and temporal extent of palaeoecological research across the Central American Isthmus. Data sets presenting reconstructions for precipitation (δ18O), burning (macroscopic fossil charcoal and microscopic fossil charcoal), flora (fossil pollen), and herbivorous animal abundance (fossil dung fungal spores - *Sporomiella*) were identified to address: (i) the extent of terrestrial palaeoenvironmental records for the region; (ii) areas best and least represented across the Central American Isthmus; (iii) the periods of time that are best and least represented. By analysing these records, it was demonstrated how precipitation has spatially and temporally varied through time across this region. Also, to emerge from this synthesis was evidence of the most active periods of burning during the Holocene and their spatial extent. Finally, this synthesis highlighted how the biota have been impacted by climatic changes and anthropogenic changes (specifically agrarian practices) during the Holocene. This paper represents the first systematic approach to mapping all terrestrial palaeoenvironmental records for the Central American Isthmus, and synthesis for $\delta^{18}O$, charcoal and pollen records.

Chapter 3: The legacy of Pre-Columbian fire on the pine-oak forests of upland Guatemala.

In this chapter I investigated a 6000-year lacustrine record from the uplands of the Southern Maya Area to understand the dominant drivers of change of the mixed coniferous (pine-oak) forests during the Pre-Columbian period. The pine-oak forest of this region is particularly important because of its species diversity and complex successional composition. Past vegetation, anthropogenic use of fire, and herbivory presence were reconstructed using proxy analysis of fossil pollen, macroscopic charcoal, microscopic charcoal, and dung fungal spores (*Sporormiella*) from a lake sedimentary sequence dated between 6000 – 426 cal yrs B.C.E. (4000B.C.E. – 1524C.E.) The aims were to identify (i) the natural baseline vegetation of the region: (ii) when human impact and agrarian practices began in the Maya uplands; and (iii) what impacts the Maya had on forest structure, composition, and successional regeneration. I found that the natural baseline for vegetation was predominantly forested and comprised of a mix of oak and pine forest taxa. The broadleaf component of these pine oak forests was found to have been substantially impacted by anthropogenic activities, particularly burning for agriculture and for the creation of lime. I also found the earliest evidence for agriculture in the Southern Maya Area, 3950B.C.E., predating the surrounding lowlands by *c.*350 years.

Chapter 4: A palynological perspective on the impacts of European contact: historic deforestation, ranching and agriculture in the Cuchumatanes highlands, Guatemala.

This chapter investigates the impact of land use change upon the vegetation of the Cuchumatanes Highlands and surrounding areas, during the Colonial 1524-1821C.E. and Post-Colonial 1821-2015C.E. periods. I aimed to identify (i) how and when anthropogenic practices, involving different types of land use change, impacted vegetation composition during the past 500 years; and (ii) if the palaeo-palynological and charcoal proxy data could be independently validated using satellite data. This is the first study that has attempted to quantitatively validate a charcoal proxy record with satellite data from within the Central American Isthmus. The construction of new settlements following the Spanish Conquest resulted in the decline of mountain hard wood forest (MHWF) taxa, such as oak and sweet gum, in favour of more open herbaceous and shrubby taxa such as grasses and wax myrtle. The decline in MHWFs was compounded by pastoral expansions in the 18th century for the rearing of livestock and the expansion of urban settlements in the 19th and 20th centuries. Bovid seed predation is suggested as the dominant factor in preventing the MHWF's from re-establishing over the past 500 years. Validation of the source distance for charcoal influx using satellite data revealed a 16km radius for macroscopic charcoal and 180km radius for microscopic charcoal.

Chapter 5: The apparent resilience of the Central American dry Corridor to extreme variations in climate over the past c.1200 years.

This chapter examines the impacts of two contrasting periods of climate, the Medieval Climate Anomaly 900-1250C.E. and the Little Ice Age, 1400-1850C.E. and anthropogenic activities upon the dry tropical forests within the Central American Dry Corridor (CADC) of Central Pacific Nicaragua. Here I present a *c.*1200-year record reconstructing vegetation, hydrological dynamics, fire activity and herbivorous animal abundance. The aims of this chapter were to (i) identify the past hydroclimatic changes within the Nicaraguan region of CADC; (ii) assess how the Dry Tropical Forests (DTF) responded to identified climatic shifts; and (iii) assess how anthropogenic activities have impacted the DTF of Central Pacific Nicaragua. This is the first palynological and dung fungal spore record to be reconstructed for the Central Pacific Nicaraguan region exploring multiple biological proxies for evidence of climatic and anthropogenic impacts. Evidence for wetter conditions during the Medieval Climate Anomaly and drier conditions during the Little Ice Age were found. The DTF were found to be highly resilient to these shifts in precipitation, responding through species reorganisation within the DTF assemblage; however, turnover between species was found to be at its highest after the identified periods of heightened seasonality. Patterns of fire were found to be intrinsically linked to precipitation. There is no evidence of substantial anthropogenic activity during the late Pre-Columbian era 840-1522C.E.; however, after the arrival of the Spanish 1522C.E. some human impact is evident.

Chapter 6: General discussion and concluding remarks

This chapter summarises the main findings from Chapters 2, 3, 4, and 5 and offers concluding remarks with discussions for future research.

1.2 References

Adomat, F. and Gischler, E., 2017. Assessing the suitability of Holocene environments along the central Belize coast, Central America, for the reconstruction of hurricane records. *International Journal of Earth Sciences*, 106(1), pp.283-309.

Alfaro, E.J., 2000. Some characteristics of the precipitation annual cycle in Central America and their relationships with its surrounding tropical oceans. *Top. Meteor. Oceanog*, *7*(2), pp.99-115.

Anchukaitis, K.J. and Horn, S.P., 2005. A 2000-year reconstruction of forest disturbance from southern Pacific Costa Rica. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *221*(1-2), pp.35-54.

Anderson, L. and Wahl, D., 2016. Two Holocene paleofire records from Peten, Guatemala: Implications for natural fire regime and prehispanic Maya land use. *Global and Planetary Change*, 138, pp.82-92.

Baker, A.G., Bhagwat, S.A. and Willis, K.J., 2013. Do dung fungal spores make a good proxy for past distribution of large herbivores?. *Quaternary Science Reviews, 62*, pp.21-31.

Baker, A.G., Cornelissen, P., Bhagwat, S.A., Vera, F.W. and Willis, K.J., 2016. Quantification of population sizes of large herbivores and their long- term functional role in ecosystems using dung fungal spores. *Methods in Ecology and Evolution*, *7*(11), pp.1273-1281.

Beach, T., Luzzadder-Beach, S., Cook, D., Dunning, N., Kennett, D.J., Krause, S., Terry, R., Trein, D. and Valdez, F., 2015. Ancient Maya impacts on the Earth's surface: An Early Anthropocene analog?. *Quaternary Science Reviews*, 124, pp.1-30.

Bilsborrow R.E., Carr D.L., 2001. Tradeoffs or Synergies? Agricultural Intensification, Economic Development and the Environment, eds Lee DR, Barrett CB (CABI Publishing, Wallingford, UK), pp. 35–55.

Bowman, D.M., Balch, J., Artaxo, P., Bond, W.J., Cochrane, M.A., D’antonio, C.M., DeFries, R., Johnston, F.H., Keeley, J.E., Krawchuk, M.A. and Kull, C.A., 2011. The human dimension of fire regimes on Earth. *Journal of biogeography*, 38(12), pp.2223-2236.

Bray, D.B., Duran, E., Ramos, V.H., Mas, J.F., Velazquez, A., McNab, R.B., Barry, D. and Radachowsky, J., 2008. Tropical deforestation, community forests, and protected areas in the Maya Forest. *Ecology and Society*, 13(2).

Carr, D., 2009. Population and deforestation: why rural migration matters. Progress in Human Geography, 33(3), pp.355-378.

Chase, J., Leibold, M., Downing, A., 2000. The effects of productivity, herbivory, and plant species turnover in grassland food webs. Ecology 81, 2485-2497.

Chiabai, A., 2015. Climate change impacts on tropical forests in Central America: an ecosystem service perspective. Routledge.

Cochrane, M.A., Alencar, A., Schulze, M.D., Souza, C.M., Nepstad, D.C., Lefebvre, P. and Davidson, E.A., 1999a. Positive feedbacks in the fire dynamic of closed canopy tropical forests. *Science*, *284*(5421), pp.1832-1835.

Cochrane, M.A. and Schulze, M.D., 1999b. Fire as a Recurrent Event in Tropical Forests of the Eastern Amazon: Effects on Forest Structure, Biomass, and Species Composition 1. *Biotropica*, *31*(1), pp.2-16.

CI (Conservation International). 2007. Biodiversity hotspots: the most remarkable places on Earth are also the most threatened. CI, Arlington, Virginia. Available from http://www.biodiversityhotspots.org (Accessed 26 April 2018).

Corrales, L., Bouroncle, C. and Zamora, J.C., 2015. An overview of forest biomes and ecoregions of Central America. In *Climate Change Impacts on Tropical Forests in Central America* (pp. 17-38). Routledge.

Correa-Metrio, A., Bush, M.B., Cabrera, K.R., Sully, S., Brenner, M., Hodell, D.A., Escobar, J. and Guilderson, T., 2012. Rapid climate change and no-analog vegetation in lowland Central America during the last 86,000 years. *Quaternary Science Reviews*, 38, pp.63-75.

Davis, O.K., 1987. Spores of the dung fungus Sporormiella e increased abundance in historic sediments and before Pleistocene megafaunal extinction. Quaternary Research 28, 290-294.

Davis, O.K., Shafer, D.S., 2006. Sporormiella fungal spores, a palynological means of detecting herbivore density. Palaeogeography, Palaeoclimatology, Palaeoecology 237, 40-50.

Griffiths, C.J., Hansen, D.M., Jones, C.G., Zuël, N., Harris, S., 2011. Resurrecting extinct interactions with extant substitutes. Current Biology 21, 762-765.

DiNezio, P. N., Clement, A. C., & Vecchi, G. A. (2010). Reconciling differing views on tropical Pacific climate change. *EOS, Transactions, American Geophysical Unio, 91*, 141–152.

Dinerstein, E., Olson, D., Joshi, A., Vynne, C., Burgess, N.D., Wikramanayake, E., Hahn, N., Palminteri, S., Hedao, P., Noss, R. and Hansen, M., 2017. An ecoregion-based approach to protecting half the terrestrial realm. *BioScience*, 67(6), pp.534-545.

Douglas, P.M., Demarest, A.A., Brenner, M. and Canuto, M.A., 2016. Impacts of climate change on the collapse of lowland Maya civilization. *Annual Review of Earth and Planetary Sciences*, 44, pp.613-645.

Dull, R.A., 2004a. An 8000-year record of vegetation, climate, and human disturbance from the Sierra de Apaneca, El Salvador. *Quaternary Research,* 61(2), pp.159-167.

Dull, R.A., 2004b. A Holocene record of Neotropical savanna dynamics from El Salvador. *Journal of Paleolimnology*, 32(3), pp.219-231.

Dull, R.A., 2007. Evidence for Forest Clearance, Agriculture, and Human- Induced Erosion in Precolumbian El Salvador. *Annals of the Association of American Geographers*, 97(1), pp.127-141.

Dull, R.A., 2016. The Maize Revolution A View from El Salvador. *Histories of Maize in Mesoamerica: Multidisciplinary Approaches*.

Enfield, D.B. and Alfaro, E.J., 1999. The dependence of Caribbean rainfall on the interaction of the tropical Atlantic and Pacific Oceans. *Journal of Climate,* 12(7), pp.2093-2103.

FAOSTAT (Food and Agriculture Organisation of the United Nations), 2011. Food and Agriculture Data. Available at http://faostat.fao.org/default.aspx. [Accessed May 12, 2018].

Ford, A. and Nigh, R., 2009. Origins of the Maya forest garden: Maya resource management. *Journal of Ethnobiology*, *29*(2), pp.213-236.

Franco-Gaviria, F., Correa-Metrio, A., Cordero-Oviedo, C., López-Pérez, M., Cárdenes-Sandí, G.M. and Romero, F.M., 2018. Effects of late Holocene climate variability and anthropogenic stressors on the vegetation of the Maya highlands. Quaternary Science Reviews, 189, pp.76-90.

GardaWorld, 2018. Nicaragua: Major wildfire in Indio Maíz biological reserve. Available at: https://www.garda.com/crisis24/news-alerts/108451/nicaragua-major-wildfire-in-indio-maiz-biological-reserve-update-1. [Accessed 22 Apr. 2018].

Geist, H.J. and Lambin, E.F., 2001. What Drives Tropical Deforestation. A meta-analyis of proximate and underlying causes of deforestation based on subnational case study evidence. *LUCC Report Series*, *4*.

Gillespie, T.W., Grijalva, A. and Farris, C.N., 2000. Diversity, composition, and structure of tropical dry forests in Central America. *Plant ecology*, *147*(1), pp.37-47.

Giannini, A., Chiang, J. C., Cane, M. A., Kushnir, Y., & Seager, R. (2001). The ENSO teleconnection to the Tropical Atlantic Ocean: Contributions of the remote and local SSTs to rainfall variability in the tropical Americas. *Journal of Climate, 14*, 4530– 4544.

Haug, G.H., Hughen, K.A., Sigman, D.M., Peterson, L.C. and Röhl, U., 2001. Southward migration of the intertropical convergence zone through the Holocene. *Science*, 293(5533), pp.1304-1308.

Harvey, C.A., Komar, O., Chazdon, R., Ferguson, B.G., Finegan, B., Griffith, D.M., Martinez- Ramos, M., Morales, H., Nigh, R., Soto-Pinto L. and Van Breugel, M., 2008. Integrating agricultural landscapes with biodiversity conservation in the Mesoamerican hotspot. *Conservation biology*, 22(1), pp.8-15.

Holdsworth, A.R. and Uhl, C., 1997. Fire in Amazonian selectively logged rain forest and the potential for fire reduction. Ecological applications, 7(2), pp.713-725.

Hopcraft, J.G.C., Olff, H., Sinclair, A.R.E., 2009. Herbivores, resources and risks: alternating regulation along primary environmental gradients in savannas. Trends in Ecology & Evolution 25, 119-128.

IPCC (Intergovernmental Panel on Climate Change), 2014. IPCC (2014) Climate Change 2014 Mitigation of Climate Change. Working Group 3 Contribution to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change (IPCC). Technical Summary and Chapter 6 (Assessing Transformation Pathways). Available at: https://www.eea.europa.eu/data-and-maps/indicators/atmospheric-greenhouse-gas-concentrations-10/ipcc-2014 [Accessed 26 April 2018].

Islebe, G.A., Torrescano-Valle, N., Aragón-Moreno, A.A., Vela-Peláez, A.A. and Valdez-Hernández, M., 2018. The Paleoanthropocene of the Yucatán Peninsula: palynological evidence of environmental change. *Boletín de la Sociedad Geológica Mexicana*, *70*(1).

Joaquin-Chamorro. 2018. Lessons learned from Indio Maíz. La Prensa. Available at: https://www.theguardian.com/world/2018/apr/11/nicaragua-rainforest-fire-costa-rica .[Accessed 25/04/2018].

Kappelle, M., 2006. Neotropical montane oak forests: overview and outlook. In *Ecology and conservation of neotropical montane oak forests*. Springer, Berlin, Heidelberg.

Lane, C.S., Horn, S.P., Mora, C.I., Orvis, K.H. and Finkelstein, D.B., 2011. Sedimentary stable carbon isotope evidence of late Quaternary vegetation and climate change in highland Costa Rica. *Journal of Paleolimnology*, 45(3), pp.323-338.

League, B.L. and Horn, S.P., 2000. A 10 000 year record of Paramo fires in Costa Rica. *Journal of Tropical Ecology*, pp.747-752.

Metcalfe, S. E., O'Hara, S. L., Caballero, M., & Davies, S. J. (2000). Records of Late Pleistocene–Holocene climatic change in Mexico - a review. *Quaternary Science Reviews*, *19* (7), 699–721.

Metcalfe, S. E., Barron, J. A., Davies, S. J. (2015). The Holocene history of the North American Monsoon: ‘known knowns’ and ‘known unknowns’ in understanding its spatial and temporal complexity. *Quaternary Science Reviews*, 120, 1-27.

Murphy, P.G. and Lugo, A.E., 1986. Ecology of tropical dry forest. *Annual review of ecology and systematics*, *17*(1), pp.67-88.

Nájera Acevedo, A. 2006. The conservation of the thorn scrub and dry forest of the Motagua Valley, Guatemala: promoting the protection of a unique ecoregion. Lyonia 9(2), pp.7-19.

Neff, H., Pearsall, D.M., Jones, J.G., Arroyo, B., Collins, S.K. and Freidel, D.E., 2006. Early Maya adaptive patterns: Mid-late Holocene paleoenvironmental evidence from Pacific Guatemala. *Latin American Antiquity*, 17(3), pp.287-315.

Parsons, J.J., 1955. The Miskito pine savanna of Nicaragua and Honduras. *Annals of the Association of American Geographers*, *45*(1), pp.36-63.

Peterson, D.L. and Ryan, K.C., 1986. Modeling postfire conifer mortality for long-range planning. Environmental Management, 10(6), pp.797-808.

Piperno, D.R., Bush, M.B. and Colinvaux, P.A., 1990. Paleoenvironments and human occupation in late-glacial Panama. *Quaternary Research*, 33(1), pp.108-116.

Piperno, D.R., Bush, M.B. and Colinvuax, P.A., 1991. Paleoecological perspectives on human adaptation in Central Panama. II The Holocene. *Geoarchaeology*, 6(3), pp.227-250.

Piperno, D.R., 2006. Quaternary environmental history and agricultural impact on vegetation in Central America. *Annals of the Missouri Botanical Garden*, 93(2), pp.274-296.

Piperno, D.R., 2011. The origins of plant cultivation and domestication in the New World tropics: patterns, process, and new developments. *Current anthropology*, 52(S4), pp.S453-S470.

Pither, R. and Kellman, M., 2002. Tree species diversity in small, tropical riparian forest fragments in Belize, Central America. *Biodiversity & Conservation*, 11(9), pp.1623-1636.

Putman, R.J., 1986. Grazing in Temperate Ecosystems: Large Herbivores and the Ecology of the New Forest. Croom Helm, London.

Pyne, S.J., 1984. *Introduction to wildland fire. Fire management in the United States*. John Wiley & Sons.

Raper, D. and Bush, M., 2009. A test of Sporormiella representation as a predictor of megaherbivore presence and abundance. Quaternary Research, 71(3), pp.490-496.

Redo, D.J., Grau, H.R., Aide, T.M. and Clark, M.L., 2012. Asymmetric forest transition driven by the interaction of socioeconomic development and environmental heterogeneity in Central America. *Proceedings of the National Academy of Sciences*, 109(23), pp.8839-8844.

Rothermel, R.C., 1983. How to predict the spread and intensity of forest and range fires. United States. Intermountain Forest and Range Experiment Station. USDA Forest Service general technical report INT (USA).

Rueda X., 2010. Understanding deforestation in the southern Yucatan: Insights from a sub-regional, multi-temporal analysis. Reg Environ Change 10, pp.175–190.

Rzedowski, J., 2006. Vegetación de México. 1ra. Edición digital, Comisión Nacional para el Conocimiento y Uso de la Biodiversidad, México, 504.

Schüpbach, S., Kirchgeorg, T., Colombaroli, D., Beffa, G., Radaelli, M., Kehrwald, N.M. and Barbante, C., 2015. Combining charcoal sediment and molecular markers to infer a Holocene fire history in the Maya Lowlands of Petén, Guatemala. *Quaternary Science Reviews*, 115, pp.123-131.

Scott, A.C., Bowman, D.M., Bond, W.J., Pyne, S.J. and Alexander, M.E., 2013. Fire on earth: an introduction. John Wiley & Sons

Sinclair, A.R.E., Arcese, P., 1995. Serengeti II, Dynamics, Management and Conservation of an Ecosystem. Chicago University Press, Chicago.

Sinclair, A.R.E., Norton-Griffiths, M., 1979. Serengeti: Dynamics of an Ecosystem. Chicago University Press, Chicago.

Sparks, A., Hengl, T., Nelson, A., 2017. Global Surface Summary of the Day – GSOD. Available at: https://data.noaa.gov/dataset/dataset/global-surface-summary-of-the-day-gsod. [Accessed 13/03/2017].

Stansell, N.D., 2013. Radiocarbon ages for the timing of debris avalanches at Mombacho Volcano, Nicaragua. *Bulletin of volcanology*, *75*(1), p.686.

The Guardian, 2018. Nicaragua fires: aid from Costa Rica rejected as blaze destroys rainforest. Available at: https://www.theguardian.com/world/2018/apr/11/nicaragua-rainforest-fire-costa-rica .[Accessed 25/04/2018].

Tubbs, C.R., 1986. The New Forest. Collins, London.

Tubbs, C.R., 2001. The New Forest: History, Ecology and Conservation, second ed. New Forest Ninth Centenary Trust, Lyndhurst.

Uhl, C. and Kauffman, J.B., 1990. Deforestation, fire susceptibility, and potential tree responses to fire in the eastern Amazon. *Ecology*, *71*(2), pp.437-449

Urquhart, G.R., 2009. Paleoecological record of hurricane disturbance and forest regeneration in Nicaragua. *Quaternary International*, 195(1-2), pp.88-97.

Veblen, T.T., 1978. Forest preservation in the western highlands of Guatemala. *Geographical Review*, pp.417-434.

Velez, M.I., Curtis, J.H., Brenner, M., Escobar, J., Leyden, B.W. and Popenoe de Hatch, M., 2011. Environmental and cultural changes in highland Guatemala inferred from Lake Amatitlán sediments. *Geoarchaeology*, 26(3), pp.346-364.

White, C.D., 1999. Reconstructing Ancient Maya Diet. University of Utah Press.

World Food Programme, 2016. El Nino in Latin America and the Caribbean. Available at: https://reliefweb.int/sites/reliefweb.int/files/resources/WFP%20El%20Nino%20in%20Latin%20America%20and%20the%20Caribbean%20External%20Situation%20Report%20%231%2030%20May%202016_0.pdf. [Accessed: 22 Apr. 2018].

Worldometers, 2018. Central America Population. Available at: http://www.worldometers.info/world-population/central-america-population/ [Accessed: 25 Jan 2019].

Young, C.A., 2008. Belize's ecosystems: Threats and challenges to conservation in Belize. *Tropical Conservation Science*, *1*(1), pp.18-33.

2. A TALE OF ISOTOPES AND FIRE: ENVIRONMENTAL PROXY EVIDENCE FOR CLIMATE, BURNING AND BIOTA ACROSS THE CENTRAL AMERICAN ISTHMUS SPANNING THE HOLOCENE

William J. Harvey[1], Gillian Petrokofsky[1], Sandra Nogué[2], Nathan Stansell[3], Katherine J. Willis[1]

[1]Long-Term Ecology Laboratory, Department of Zoology, University of Oxford, Oxford, UK

[2]School of Geography and Environmental Sciences, University of Southampton, Highfield, Southampton, UK

[3]Department of Geology and Environmental Geosciences, Northern Illinois University, De Kalb, IL, USA

To be submitted to Quaternary Science Reviews

2.1 Abstract

This paper presents the results of a systematic review of previously published proxy data ($\delta^{18}O$, charcoal, pollen, and *Sporormiella*) from terrestrial depositional archives from the Central American Isthmus spanning the Holocene *c.*12000-0 cal yrs B.P. (10000B.C.E. – 1950C.E.). One hundred and seventy-nine data sets presenting reconstructions for precipitation ($\delta^{18}O$), burning (macroscopic charcoal and microscopic charcoal), vegetation (pollen), and herbivorous animal abundance (*Sporormiella*) were reviewed to determine regional patterns of change and their possible drivers. From this review it is apparent that the majority of published palaeoenvironmental data sets from within the Central American Isthmus have come from lowland Mexico, Guatemala and Belize and Costa Rica. They also mainly focus on the last 4000 years.

From these records it is apparent that there is spatial and temporal heterogeneity in precipitation events across the Central American Isthmus durin the Holocene. Sites that span the Early Holocene report increasingly wetter conditions from *c.*12000-8000 cal yrs B.P. (10000 – 6000B.C.E.). There is a particular focus on the spatial patterns and mechanisms forcing changes in precipitation over the last 2000 years with emphasis on the nature and timing of hydrological extremes including the Medieval Climate Anomaly (1050 – 650 cal yrs B.P./950 – 1250C.E.), and Little Ice Age (550 – 100 cal yrs B.P./1400 – 1850C.E.). Patterns of mechanistic forcing remain unresolved.

Fire is indicated to have been an important driver of ecosystem dynamics since the onset of the Holocene *c.*12000 cal yrs B.P. (10000B.C.E.). Periods of widespread burning have been identified at sixteen intervals during this time. Fire events were driven by a combination of climatic events, and anthropogenic activities including agricultural practices and burning for lime production.

Mesic forest taxa are reported to increase from the Early Holocene 12000 – 8000 cal yrs B.P. (10000 – 6000B.C.E.) driven by warmer wetter conditions, and agrarian practices

are reported to be the largest anthropogenic driver of vegetation change from the Middle-Late Holocene *c.*6000 - 0 cal yrs B.P. (4000B.C.E. – 1950C.E.).

Knowledge gaps identified include: (i) Our understanding of the heterogenous patterns of precipitation across the Central American Isthmus throughout the Holocene are still poorly understood due to spatially and temporally limited records; (ii) the timing of widespread climatically driven fire and spatially heterogenous anthropogenic burning are currently not well understood or quantified; (iii) unravelling the origins and spread of agriculture across Central America requires further spatial and temporal coverage; (iv) there are limited published papers that focus their discussions upon the Historical period (Post-European conquest c.1500); (v) understanding the resilience of different vegetation types to drivers of change should be a dominant focus of future research enabling measures to be taken for conservation and climate change management applying adaptation strategies to vulnerable biomes; and (vi) there are currently zero *Sporormiella* records for the Central American Isthmus.

2.2 Objective of the systematic evidence map

This paper presents the results of a systematic review highlighting the scientific evidence published to date to demonstrate how vegetation dynamics in the Central American Isthmus, have been impacted by climatic changes, fire and anthropogenic activities (specifically agrarian practices) throughout the Holocene. It also represents the first systematic approach to mapping all terrestrial palaeoenvironmental records from across the Central American Isthmus, and synthesis for proxy data ($\delta^{18}O$, charcoal and pollen) representing precipitation, fire and vegetation for the last 12000 years.

We aimed to identify: (i) what terrestrial palaeoenvironmental records exist, (ii) which areas are best and least represented (to highlight evidence gaps); (iii) what periods of time are best and least represented; (iv) how precipitation has varied spatially and temporally through time and the driving mechanisms; (v) when and where the most active periods of burning were and the dominant drivers; and (vii) how biota have been impacted by both climatic changes and anthropogenic changes.

Proxy data (e.g. pollen, $\delta^{18}O$, charcoal and *Sporormiella*) from terrestrial depositional archives were identified and mapped following best practice for systematic evidence reviews (CEE, 2018). Results from the evidence base were summarised to show the spatial and temporal extent of contemporary research. Data sets presenting reconstructions for precipitation ($\delta^{18}O$), burning (charcoal), vegetation (pollen), and herbivorous animal abundance (*Sporomiella*) were selected for review.

Overall, I aimed to address the question "What is the terrestrial palaeoenvironmental evidence base for $\delta^{18}O$, charcoal, pollen, and *Sporormiella* (drivers/indicators of vegetation change) across the Central American Isthmus spanning the Holocene?" by answering the subsiderary questions: (i) how have patterns of precipitation varied during the Holocene across the Central America Isthmus?; (ii) when and where are the most active periods of burning and what are the dominant drivers?; and (iii) how has the vegetation been impacted by climatic and people?

2.3 Methods

Scientific evidence review and synthesis methodology is now widely used across many sectors of society and has become a recognised standard for accessing, appraising and synthesising scientific information (CEE, 2018). The need for rigour, objectivity and transparency in reaching conclusions from a body of scientific information is evident in many areas of policy and practice, including questions relating to the environment. While systematic reviews and systematic maps have mostly been adopted for policy-relevant questions, the methods that dictate their conduct are of interest to academic literature reviews generally, given that transparency and repeatability are the cornerstones of science.

Search Strategy

The search strategy followed guidance outlined in Livoreil et al. (2017). Four search strings were refined with iterative testing using three online databases: Web of Science core collection, Scopus and CAB Abstracts. These search strings comprised geographic location, type of archive, time period, and proxies and were combined using Boolean operators (see Supplementary Information). The geographic location was limited to terrestrial studies between the Isthmus of Tehuantepec and the Isthmus of Panama. Database searching took place in July 2017 in both English and Spanish. Although the databases allow for a language limit, I did not apply any, in order to retrieve papers published in other languages which had an English or Spanish title, abstract or key words.

Bibliographic Databases: Sources of publications

1. Web of Science Core Collection (published by Clarivate Analytics), https://clarivate.com/products/web-of-science/
2. SCOPUS, published by Elsevier B.V. http://www.elsevier.com/online-tools/scopus/
3. CAB Abstracts published by CAB International, Wallingford, UK http://www.cabi.org/

Comprehensiveness of search

The search strings were iteratively tested using a test library of papers known to be of central relevance to the current review (SI) to ensure that the search was comprehensive but not too broad (Livoreil et al 2017). Search strings were refined several times to remove terms containing generic nomenclature while still maintaining all relevant papers. Additional search terms were added to ensure inclusion of papers which did not specify a period of time (e.g. Horn et al. 1998), or were too specific in their period of time (e.g. Urquhart, 2009).

While covering a very wide range of academic journals in the sciences, social sciences, and humanities, these three databases do not index all journals. Prominent archaeological journals on Central America of relevance to the current paper which are absent from these databases include: 'World Archaeology', 'Annual Review of Anthropology' and 'Ancient Mesoamerica'. Other limitations to this approach included the exclusive use of only 3 online databases. These databases only present literature back until 1910C.E. (CAB Abstracts), 1945C.E. (Web of Science), and 1990 (Scopus). With the exception of CAB Abstracts, which includes non-journal articles (e.g. books, book chapters, reports), these databases index little “grey literature” -or “dark data” which is abundant but difficult to access (Heidorn, 2008; Mahood et al. 2014). However, even using just these three databases a large number of publications were retrieved.

Study eligibility criteria

Each study had to satisfy each of the following criteria in order to be included:

(i) present novel primary data;

(ii) be situated within the Central American Isthmus; and

(iii) be a temporal study.

Studies that failed to meet the criteria were excluded from the review. Records that presented only syntheses, reviews, remote sensing data or models were also excluded.

Screening process

Following good practice guidance (Frampton et al. 2017), screening was conducted in two stages. Firstly, simultaneous title and abstract screening of the 6914 papers was carried out using Abstrackr software (Wallace, 2018). Abstrackr is a free online tool into which a formatted citation list is uploaded. The list can be assessed for abstract screening by several reviewers. Each paper was screened by two reviewers to reduce bias. Reviewers individually appraised studies. Whenever there was doubt of the inclusion, reviewers discussed with each other in order to reach a common understanding of the application of the inclusion criteria. I applied a widely used statistic for assessing screener agreement, Cohen’s kappa, which considers the level of agreement between screeners that would occur by chance (Altman, 1991). A kappa of 0.6277 was established between reviewers on a test sample of 100 studies. The final unweighted kappa was 0.5704, which showed good agreement, as well as consistency between reviewers and confidence that the inclusion criteria were clear enough to identify all the relevant papers in the searched databases. The second stage was full text screening. Full texts that met the eligibility criteria for inclusion were then reviewed for coding and data extraction.

Systematic map database

Data extracted included: reference, title, author(s), journal, year of publication, language, country, number of sites, name of sites, longitude, latitude, elevation, type of archive, outcomes, proxies, dating methods, and time span.

2.4 Results

Literature search & paleoenvironmental proxy data

The literature search returned 10,082 publications of which 3,168 were removed as duplicates. There were 6,914 papers screened from which 332 were reviewed at full text level (Figure 2.1). Individual study sites and proxies were recorded, separating papers with multiple study sites and/or proxies from each publication (Figures 2.1 & 2.2). Proxy data was extracted for 123 publications which presented 101 study sites and 521 proxy records (Figure 2.1 & 2.2a). While there are many different proxy data sets which can be used to provide information for precipitation, burning, vegetation, and herbivorous animal abundance $\delta^{18}O$, charcoal, pollen, and *Sporormiella* were chosen as the most consistently used proxies in the returned results from the literature search. There were 86 publications that reported proxy data for $\delta^{18}O$, charcoal and pollen which encompassed 76 sites and 179 records (Figure 2.2b). There were 0 publications returned for *Sporormiella* data sets.

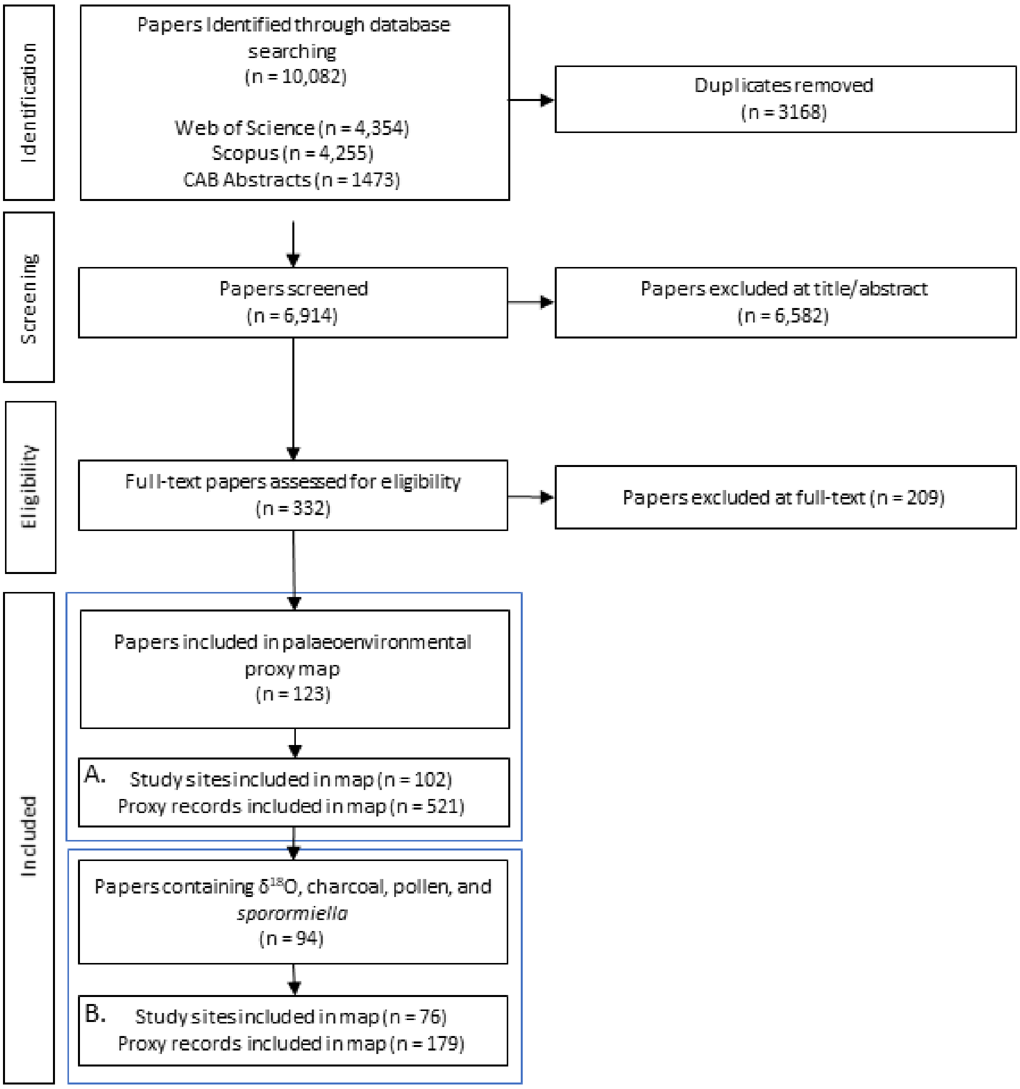


Figure 2.1 Overview of article inclusion and screening. All palaeoenvironmental records (A). Palaeoenvironmental records presenting $\delta^{18}O$, charcoal, pollen and *Sporormiella* proxies (B).

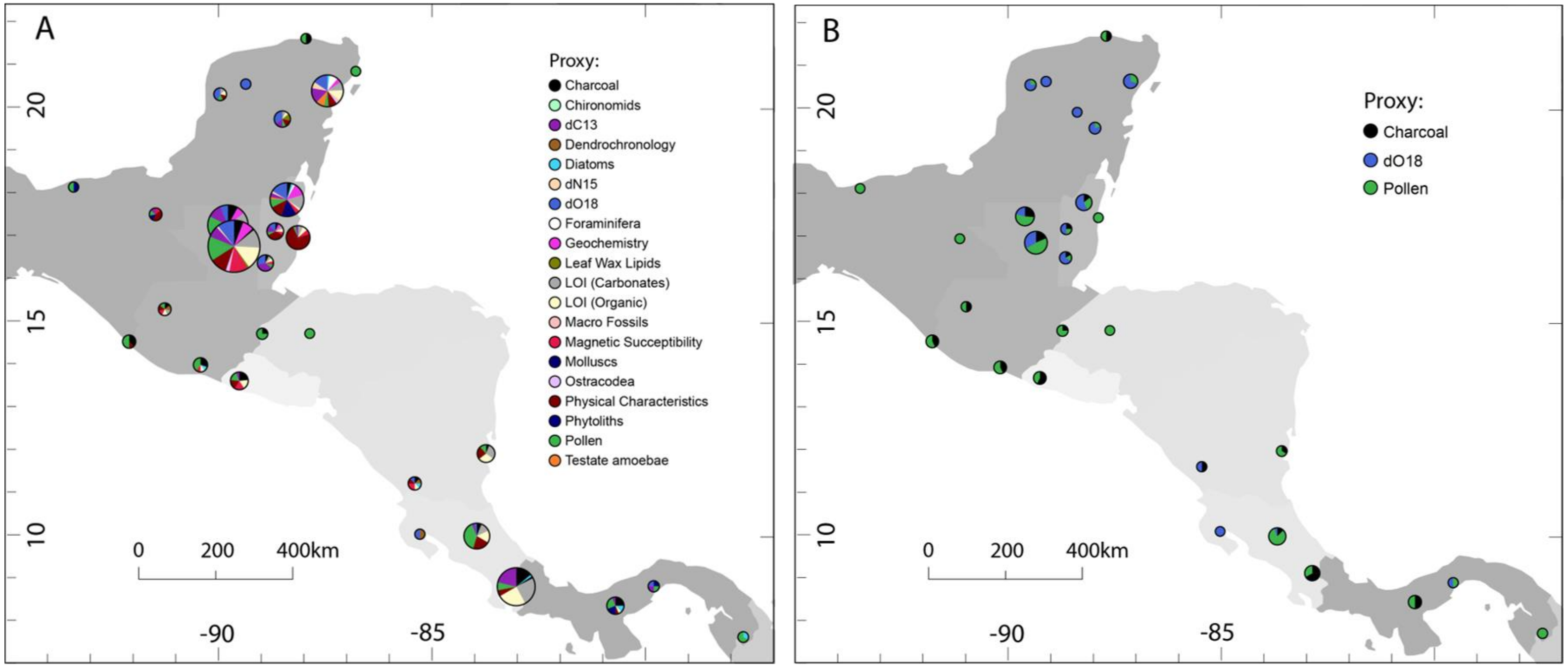


Figure 2.2 Systematic map of all palaeoenvironmental proxy data published from depositional archives in Central America (A). Systematic map of palaeoenvironmental proxy data δ18O, charcoal, pollen, or *Sporormiella* (B). https://oxlel.github.io/evidencemaps/centrala

Characteristics of proxies used in palaeoenvironmental studies

Results revealed 123 publications reporting 102 terrestrial sites containing 521 palaeoenvironmental data sets spanning the Holocene (Figure 2.2a). These studies have a geographic focus on lowland Guatemala (30%), Belize (19%), Mexico (18%) and Costa Rica (18%) comprising a total of 85% of records. Topographically 84% of records were collected from lowland sites and 16% from upland sites. Depositional archives included: beach sediments (0.8%); cave sediments (3%); tree-rings (1%); lake sediments (70%); palaeosols (1%); peat sediments (2%); river sediments (4%); salt playa sediments (2%); soil sediments (6%); speleothems (4%); swamp sediments (7%).

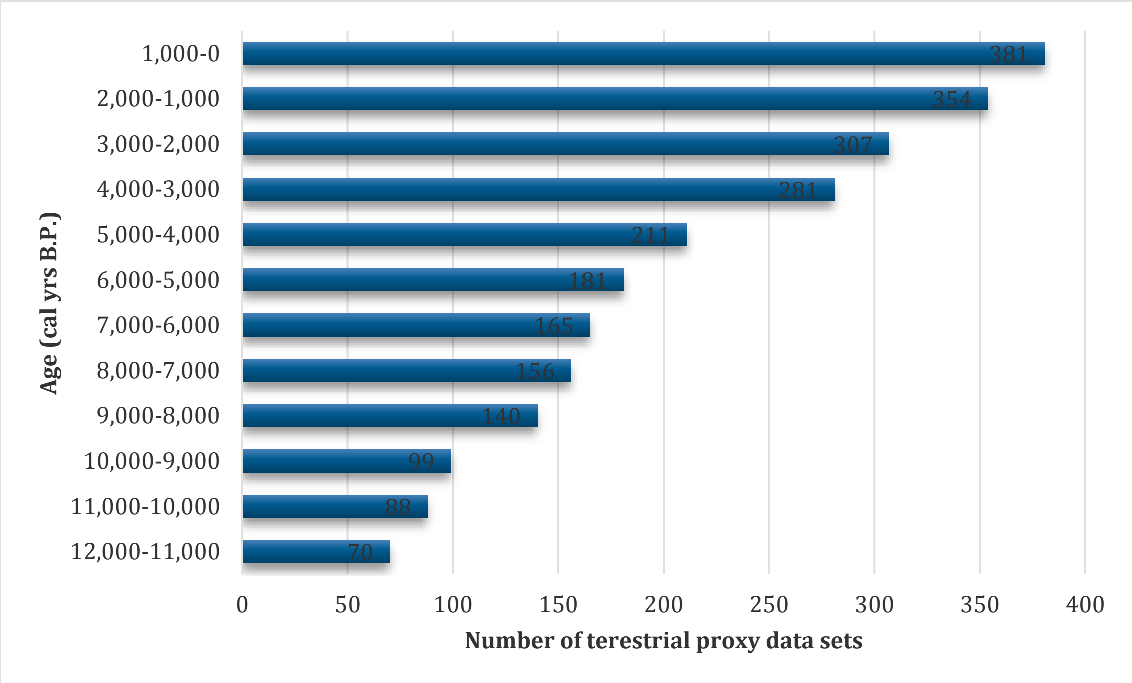


Figure 2.3 Number of terrestrial paleoenvironmental data sets across the Central American Isthmus spanning the Holocene.

Spatially, the largest data gaps are records from Chiapas (Mexico), southern and central El Salvador, Honduras and Nicaragua (only 8.8% of palaeoenvironmental records have been generated from these regions). This is suggested to be a result of limited depositional archives preserved in these regions but also because of geopolitical access. Temporal coverage of the Central American Isthmus denotes the lowest temporal coverage between 12000-11000 cal yrs B.P. and the highest cover from 1000-0 cal yrs B.P. The number of palaeoenvironmental records available increases throughout the Holocene (Figure 2.3).

Characteristics of $\delta^{18}O$ data sets used to reconstruct past precipitation

A number of studies have been published detailing changes apparent in the proxy $\delta^{18}O$ and used to infer precipitation as driven by synoptic interoceanic hydroclimatic systems. These include 22 terrestrial sites that present 48 temporal data sets for $\delta^{18}O$ across the Central American Isthmus during the Holocene (Figure 2.2b & 2.4). The types of records preserving a signal for $\delta^{18}O$ in these records include: speleothems (25%); lake sediments (58%); and river sediments (17%). Within the lake and river sediments 36 records $\delta^{18}O$ were extracted from a combination of: inorganic/bulk carbonates (6%); organic carbonates: Ostracoda (44%), Gastrapoda *spp*. (44%); Cephalopoda (3%); and Charophyta (3%). Spatially, all records published are from lowland areas and are predominantly clustered on: the Yucatan peninsula and Quintana Roo, Mexico (31.8%); the Petén district, Guatemala (13.6%); and across Belize (31.8%). Spatial and temporal coverage improves from c.4000-0 cal yrs B.P. (Figure 2.4). The most complete coverage for the Holocene can be found from Lake Petén Itza and Hillbank (Figure 2.5).

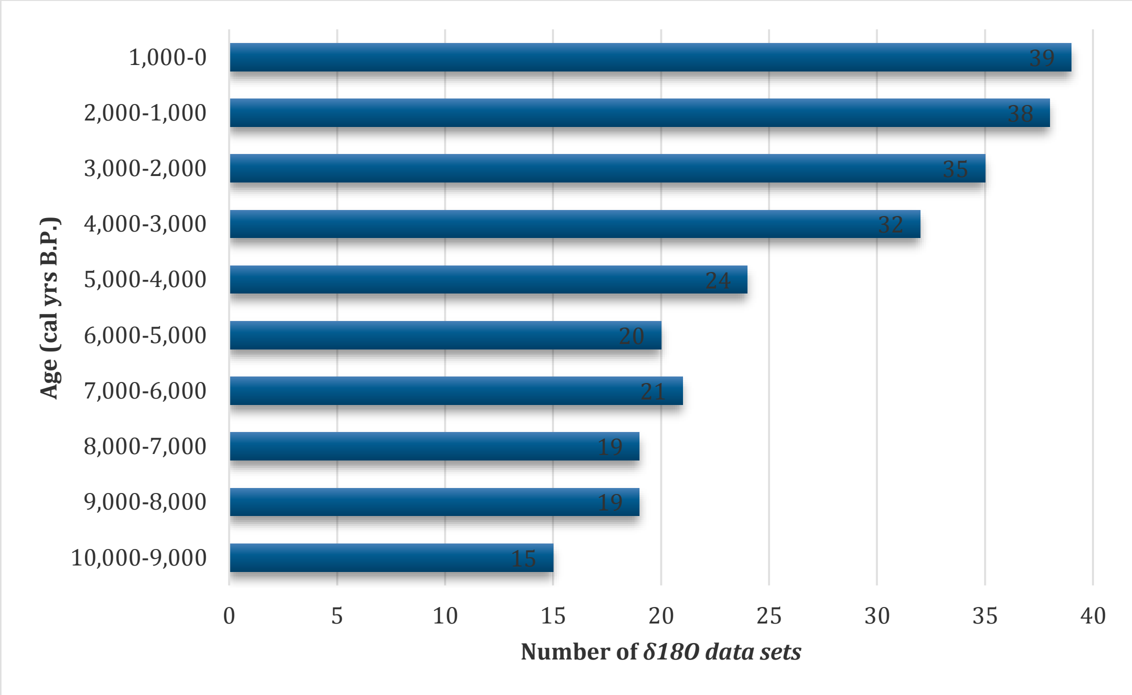


Figure 2.4 Number of terrestrial $\delta^{18}O$ data sets across the Central American Isthmus spanning the Holocene.

Overall results from these papers indicate that patterns of precipitation have been largely spatial and temporally heterogenous throughout the whole of the Holocene 12000 – 0 cal yrs B.P. (10000B.C.E. – 1950C.E.); however, during the Early Holocene 12000 – 8000 cal yrs B.P. (10000 – 6000B.C.E.) all records indicate increasingly wetter conditions up to around 8000 cal yrs B.P. (6000B.C.E.). There is a particular focus on the spatial patterns and mechanisms forcing changes in precipitation from 2000 – 0 cal yrs B.P. (0 – 1950C.E.) with emphasis on the nature and timing of hydrological extremes including the Medieval Climate Anomaly (MCA) 1050 – 650 cal yrs B.P. (900 – 1250C.E.), and Little Ice Age (LIA) 550 – 100 cal yrs B.P. (1400 – 1850C.E.). Widespread intensive drought, referred to as the Maya Terminal Classic drought, is also reported across many locations *c.*1050 cal yrs B.P. (Table 2.1; & Figure 2.5). Wetter and drier are relative to each record as reported by the authors.

Table 2.1 Homogenous precipitation changes reported across the Central American Isthmus.

Time	**Precipitation**	**References**
12,000 – 8,000 cal yrs B.P. (10,000 – 6000B.C.E.)	Wetter	Curtis et al. 1998; Rosenmeier et al. 2002a; 2002b; Lachniet et al. 2004; Hillesheim et al. 2005; Metcalfe et al. 2009; Pérez et al. 2010; Escobar et al. 2012; Wahl et al. 2014; Anderson & Walh, 2016
1050-650 cal yrs B.P. (900 – 1250C.E.) Medieval Climate Anomaly	Wet/Dry	Hodell et al. 1995; 2001; 2007; Curtis et al. 1996; Metcalfe et al. 2009; Medina-Elizalde et al. 2010; Kennett et al. 2012; Wahl et al. 2014; Anderson & Wahl 2016; Akers et al. 2016
	Wetter	Hodel et al. 2005; Stansell et al. 2013
550-100 cal yrs B.P. (1400 – 1850C.E.) Little Ice Age	Drier	Hodel et al. 2005; Stansell et al. 2013
	Wet/Dry	Hodell et al. 1995; 2001; 2007; Curtis et al. 1996; Metcalfe et al. 2009; Medina-Elizalde et al. 2010; Kennett et al. 2012; Wahl et al. 2014; Anderson & Wahl 2016; Akers et al. 2016
1050 cal yrs B.P. (900C.E.) Terminal Classic Drought	Dry	Hodel et al. 1995; 2001; 2005; 2007; Curtis et al. 1996; Lachniet et al. 2004; Webster et al. 2007; Medina-Elizalde et al. 2010; Kennett et al. 2012; Wahl et al. 2014; Anderson & Wahl, 2016; Akers et al. 2016; Smyth et al. 2017

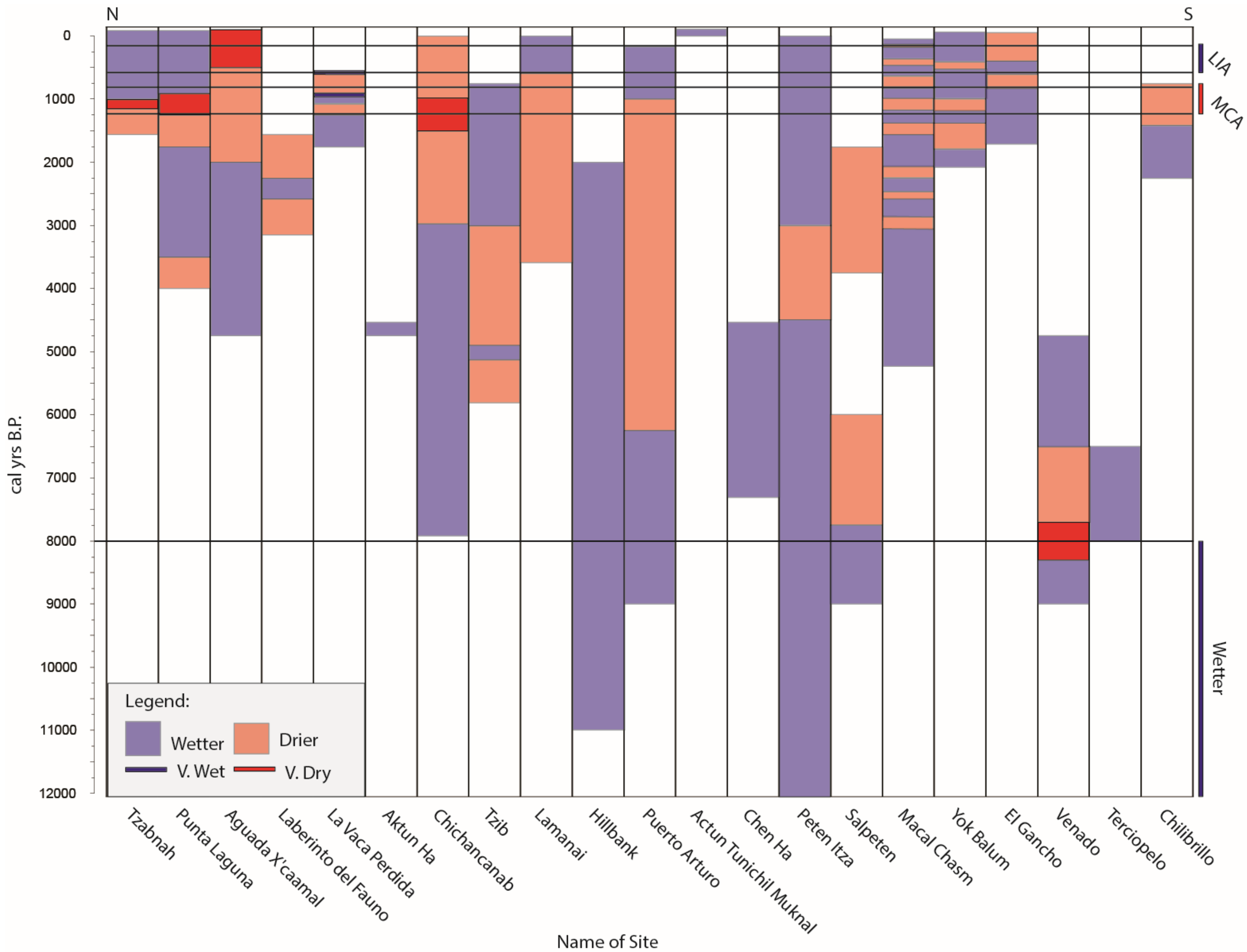


Figure 2.5 Visual composite of $\delta^{18}O$ records across the Central American Isthmus spanning the Holocene, displaying the reported hydroclimatic conditions. Sites are arranged by degree of latitude, north to south.

Characteristics of charcoal data sets used to reconstruct past patterns in burning

There are 30 terrestrial sites reported in 28 publications that present 43 temporal data sets of burning across Central America during the Holocene (Figure 2.2b & 2.6). There are 11 macro-charcoal, 21 micro-charcoal, and 11 undefined, combined or total-charcoal data sets (Figure 2.7). All data sets have been extracted from sedimentary archives.

Charcoal data sets are clustered from lowland regions of Central America (76.7%) of which Guatemala is the most represented (30%) (Figure 2.6). Reported periods of increased burning are highlighted for each record (Figure 2.7). Complete temporal coverage for the Holocene is only available from Lake Petén Itza (Schüpbach et al. 2015), Miquil Meadow (Caffrey et al. 2011) and La Yeguada (Piperno et al. 1990; 1991). There are 12 sites which cover the Early to Middle Holocene (12000-4000 cal yrs B.P.), of which 7 are in Guatemala. The last 2000 years present the most records for comparison (36 data sets) which cover a greater geographical area, and present records at much higher resolutions (Figure 2.7).

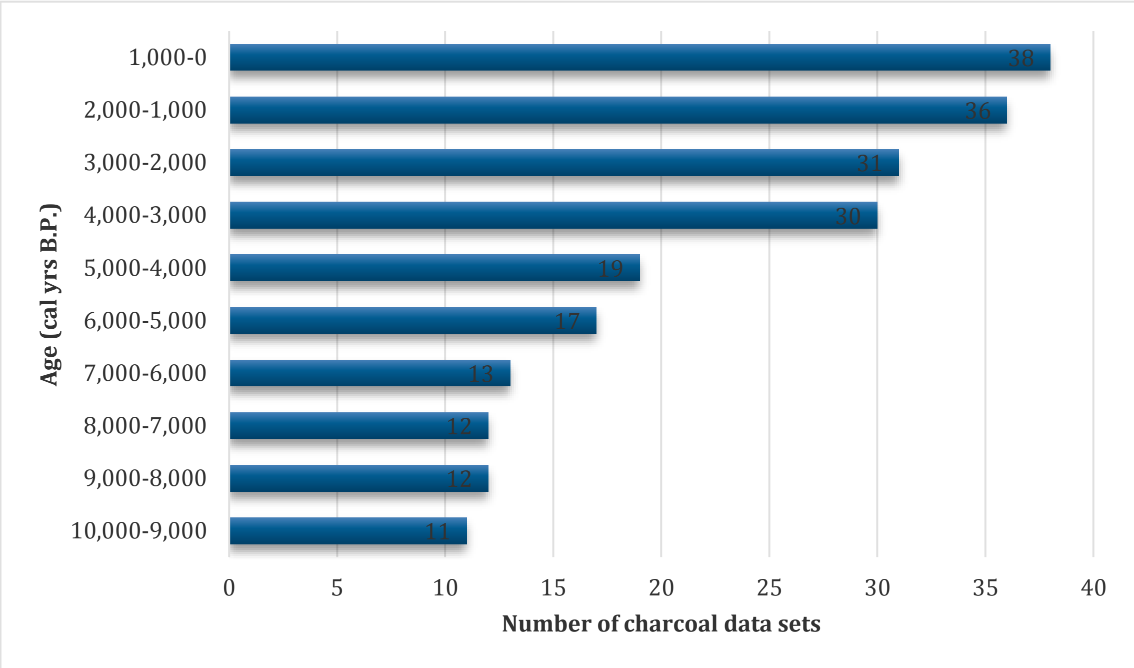


Figure 2.6 Number of charcoal data sets spanning the Holocene.

There are 16 widespread burning periods identified through the Holocene. One of these periods was attributed to purely climatic forcing, six periods to anthropogenic only; and nine to both climate and anthropogenic (Table 2.2; & Figure 2.7).

Table 2.2 Contiguous burning periods identified from charcoal data sets across the Central American Isthmus.

Time	No. Sites	Dominant Driver(s)	References
*c.*8000 cal yrs B.P. (6000B.C.E.)	3	Climate: wetter warmer conditions, increased fuel loads and storm-initiated ignitions.	Caffrey et al. 2011; Correa-Metrio et al. 2012; Schüpbach et al. 2015; Anderson & Wahl, 2016
*c.*5200 cal yrs B.P. (3200B.C.E.)	4	Anthropogenic: Onset of widespread agriculture.	Neff et al. 2006; Correa-Metrio et al. 2012; Schüpbach et al. 2015; Anderson & Wahl, 2016
*c.*4200 cal yrs B.P. (2050B.C.E.)	6		Horn, 1993; League & Horn, 2000; Neff et al. 2006; Caffrey et al. 2011; Lane et al. 2011; Correa-Metrio et al. 2012; Schüpbach et al. 2015; Anderson & Wahl, 2016
*c.*3600 cal yrs B.P. (1650B.C.E.)	5	Anthropogenic: Expansion of agrarian practices and populations.	Horn, 1993; League & Horn, 2000; Neff et al. 2006; Caffrey et al. 2011; Lane et al. 2011; Aragón-Moreno et al. 2012; Correa-Metrio et al. 2012; Schüpbach et al. 2015
*c.*3400 cal yrs B.P. (1450B.C.E.)	6	Climatic and anthropogenic: Hurricane Elisenda and continued expansion of agrarian practices and human populations.	Horn, 1993; Pohl et al. 1996; League & Horn, 2000; Neff et al. 2006; Caffrey et al. 2011; Lane et al. 2011; Aragón-Moreno et al. 2000; Correa-Metrio et al. 2012; Schüpbach et al. 2015
*c.*3250 cal yrs B.P. (1300B.C.E.)	6		Pohl et al. 1996; Neff et al. 2006; Caffrey et al. 2011; Aragón-Moreno et al. 2012; Correa-Metrio et al. 2012; Schüpbach et al. 2015
*c.*2750 cal yrs B.P. (800B.C.E.)	4	Anthropogenic and Climatic: Continued expansion of agrarian practices and human populations. Influenced by heterogenous climatic events.	Horn, 1993; League & Horn, 2000; Clement & Horn, 2001; Rue et al. 2002; Dull, 2004a; 2004b; Caffrey et al. 2011; Lane et al. 2011; Correa-Metrio et al. 2012; Schüpbach et al. 2015
*c.*2500 cal yrs B.P. (550B.C.E.)	6		Horn, 1993; League & Horn, 2000; Clement & Horn, 2001; Rue et al. 2002; Caffrey et al. 2011; Lane et al. 2011; Correa-Metrio et al. 2012; Walsh et al. 2014; Schüpbach et al. 2015
*c.*2000 cal yrs B.P. (50B.C.E.)	9		Piperno et al. 1991; Horn, 1993; League & Horn, 2000; Clement & Horn, 2001; Neff et al. 2006; Dull, 2007; Kennedy & Horn, 2008; Caffrey et al. 2012; Lane et al. 2011; Rushton et al. 2013; Walsh et al. 2014; Luzzadder-Beach et al. 2017
*c.*1350 cal yrs B.P. (650C.E.)	8	Climatic and anthropogenic: Combination of climatic and anthropogenic expansions. Highly debated and spatially dependant.	Piperno et al. 1991; Horn, 1993; League & Horn, 2000; Rue et al. 2002; Anchukaitis & Horn, 2005; Wahl et al. 2007; 2013; Kennedy & Horn, 2008; Lane et al. 2011; Walsh et al. 2014
*c.*1150 cal yrs B.P.	5		Piperno et al. 1991; Northrop & Horn, 1996; Dull, 2004a; 2004b; Avnery et al. 2011; Correa- Metrio et al. 2016

(850C.E.)		Turmoil linked to large collapses in Central American Civilizations.	
c.1050 cal yrs B.P. (950C.E.)	5		Piperno et al. 1990; 1991; Northrop & Horn, 1996; Kennedy & Horn, 2008; Aragón-Moreno et al. 2012; Correa-Metrio et al. 2016
c.750 cal yrs B.P. (1200C.E.)	8	Climate and anthropogenic: Hurricane and agrarian practices.	Piperno et al. 1990; 1991; Horn, 1993; League & Horn, 2000; Rue et al. 2002; Kennedy & Horn, 2008; Aragón-Moreno et al. 2012; Avnery et al. 2011; Lane et al. 2011
c.450 cal yrs B.P. (1500C.E.)	8	Anthropogenic: agrarian practices.	Piperno et al. 1991; Horn, 1993; League & Horn, 2000; Dull, 2004a; 2004b; Wahl et al. 2007; Lane et al. 2011; Walsh et al. 2014; Anderson & Wahl, 2016
c.150 cal yrs B.P. (1800C.E.)	4		Piperno et al. 1991; Horn, 1993; League & Horn, 2000; Lane et al. 2011; Aragón-Moreno et al. 2012; Walsh et al. 2014
c.50 cal yrs B.P. (1900C.E.)	6		Piperno et al. 1991; Horn, 1993; League & Horn, 2000; Lane et al. 2011; Aragón-Moreno et al. 2012; Walsh et al. 2014; Anderson & Wahl, 2016

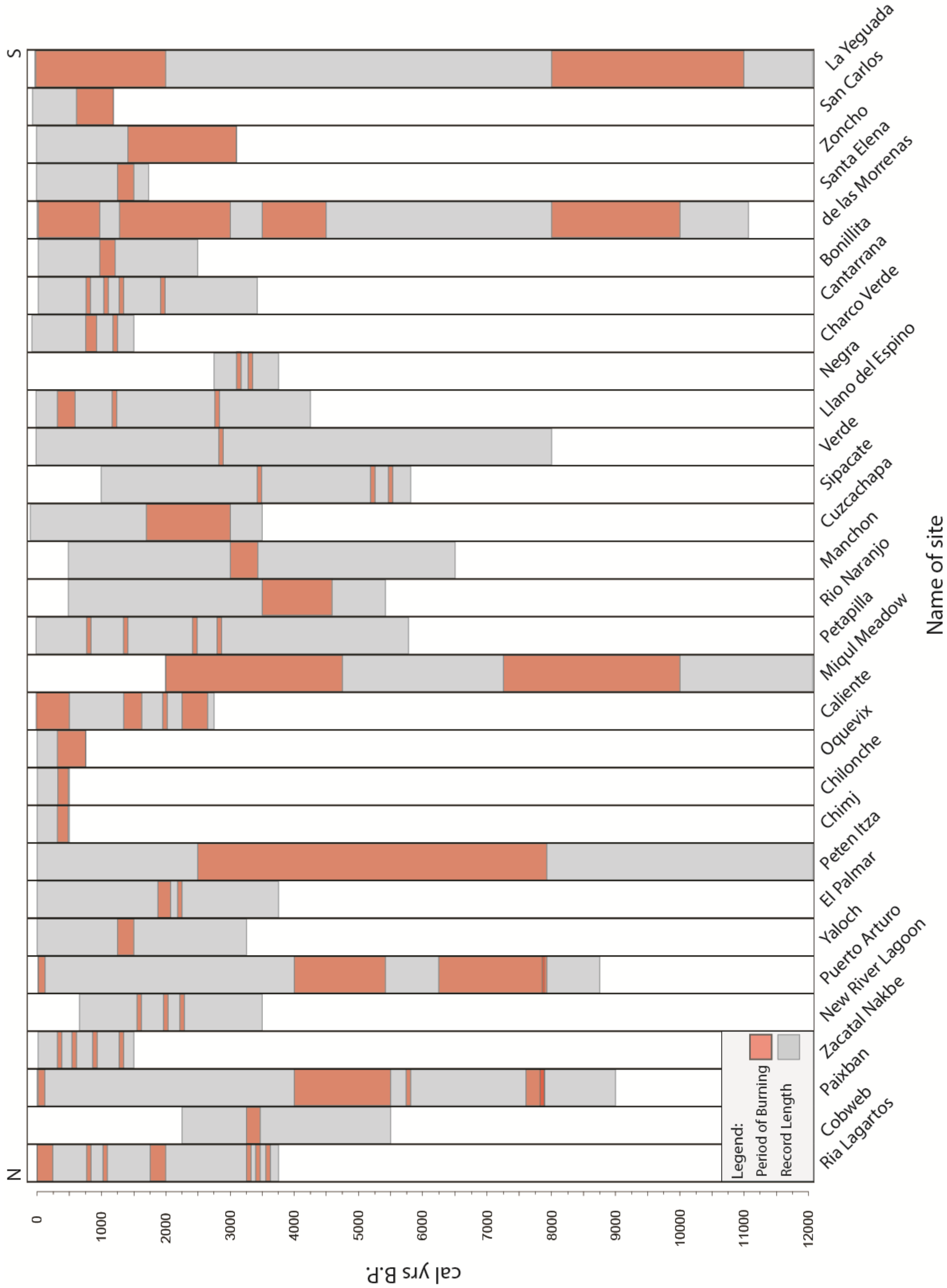


Figure 2.7 Visual composite of charcoal records across the Central American Isthmus spanning the Holocene, displaying reported burning. Sites are arranged by degree of latitude, north to south.

Characteristics of palynological data sets used to examine vegetation dynamics

There are 56 terrestrial sites reported in 64 publications presenting 80 palaeo-palynological data sets (Figure 2.2a & 2.8). These are concentrated in the lowlands of Mexico (16.3%), Guatemala (36%), and Costa Rica (20%). Few records exist for upland sites (16.3%) or from El Salvador (4%), Honduras (5%) or Nicaragua (3%). Most records have been extracted from modern day (as defined by Dinerstein et al. 2017) moist tropical forests (76%) and mangroves (15%), while few records have been produced from coniferous forests (6%) and dry tropical forests (3%), and none from grasslands, savannahs and shrublands (0%) or xeric shrublands (0%).

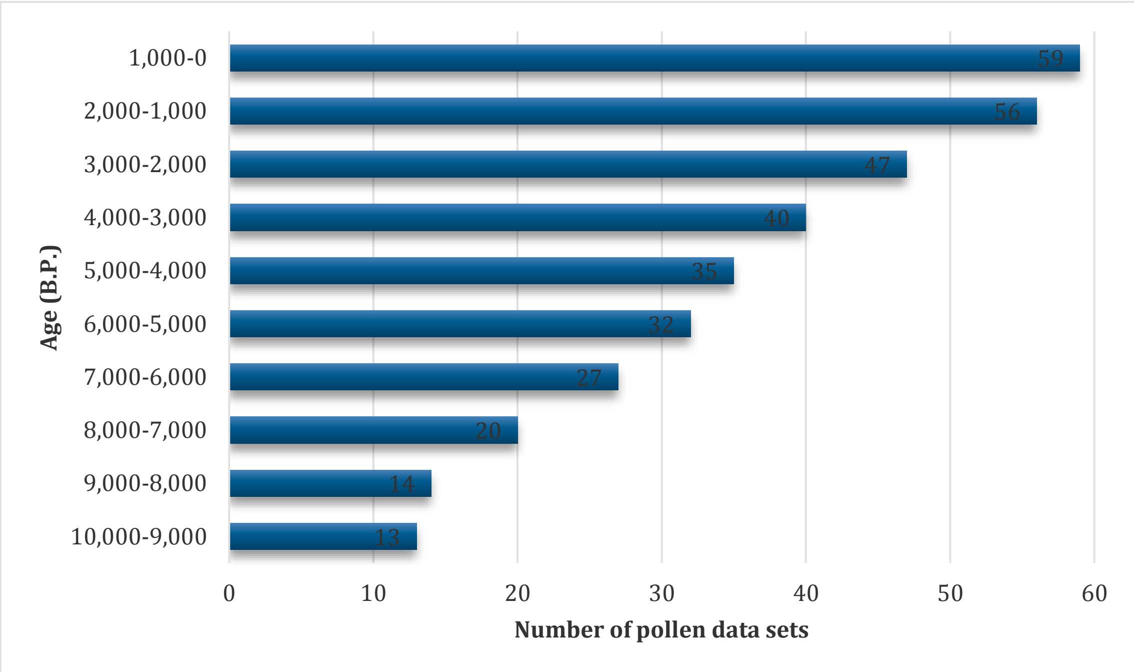


Figure 2.8 Number of pollen data sets spanning the Holocene.

When the impacts of climate and anthropogenic alteration to vegetation composition are compared, it is apparent that many papers have had a dominant focus on agrarian practices and land clearance (Figure 2.9 & 2.10). In comparision, studies that examine vegetation responses to climate driven process (e.g. precipitation, natural burning and storm events) are often presented in conjunction with anthropogenic disturbance. Palynological evidence for anthropogenic activity is reported from across 40 locations in 67 data sets. Of these data sets palynological evidence for agriculture is presented at 78% of sites. Taxa reported include: Cucurbitaceae, *Manihot, Maranta arundinacea*, *Phaseolus*, *Piper*, and *Zea mays* (Tables 2.3 & 2.4).

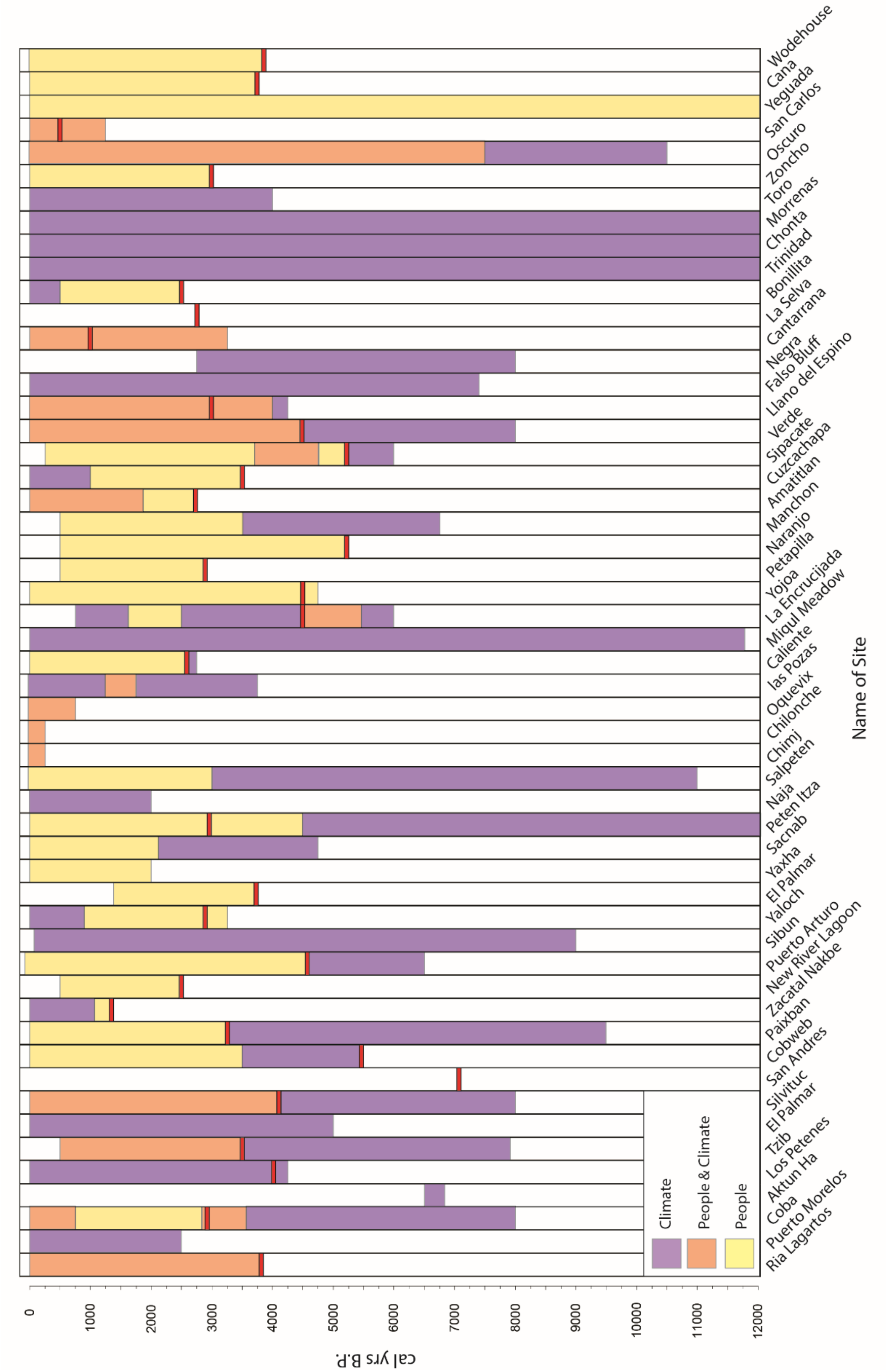


Figure 2.9 Visual composite of palynological records across the Central American Isthmus spanning the Holocene, displaying reported drivers of vegetation change and first appearances of agriculture. Sites are arranged by degree of latitude, north to south.

Table 2.3 Earliest palynological evidence of agriculture from across the Central American Isthmus.

Site Name	**Evidence**	**Time**	**Reference**
San Andres	Zea mays	7050 cal yrs B.P. (5100B.C.E.)	Pope et al. 2001
San Andres	Manihot	6550 cal yrs B.P. (4600B.C.E.)	Pope et al. 2001
Sipacate	Zea mays	5450 cal yrs B.P. (3500B.C.E.)	Neff et al. 2006
Cobweb Swamp	Zea mays	5350 cal yrs B.P. (3400B.C.E.)	Pohl et al. 1996
La Encrucijada Biosphere Reserve	Cucurbitaceae	4900 cal yrs B.P. (2950B.C.E.)	Joo-Chang et al. 2015
Lago Purerto Arturo	Zea mays	4600 cal yrs B.P. (2650B.C.E.)	Wahl et al. 2006; 2007; 2014; Anderson & Wahl, 2016
Lake Yojoa	Zea mays	4600 cal yrs B.P. (2650B.C.E.)	Rue, 1987
Lower Rio Naranjo	Zea mays	4550 cal yrs B.P. (2600B.C.E.)	Neff et al. 2006
Laguna Verde	Zea mays	4440 cal yrs B.P. (2490B.C.E.)	Dull,2004b
Aguada Petapilla	Zea mays	4250 cal yrs B.P. (2300B.C.E.)	Rue et al. 2002
Biosphere Reserve of Los Petenes	Zea mays	4100 cal yrs B.P. (2150B.C.E.)	Gutiérrez-Ayala et al. 2012
Lake Silvituc	Zea mays	4100 cal yrs B.P. (2150B.C.E.)	Torrescano-Valle & Islebe, 2015
Lake Silvituc	Cucurbitaceae	4100 cal yrs B.P. (2150B.C.E.)	Torrescano-Valle & Islebe, 2015
Lake Wodehouse	Zea mays	3910 cal yrs B.P. (1960B.C.E.)	Bush & Colinvaux, 1994
Cana Swamp	Zea mays	3740 cal yrs B.P. (1790B.C.E.)	Bush & Colinvaux, 1994
Laguna Cuzcachapa	Zea mays	3710 cal yrs B.P. (1760B.C.E.)	Dull, 2007
New River Lagoon	Zea mays	3580 cal yrs B.P. (1630B.C.E.)	Rushton et al. 2015

Lago Paixban	Zea mays	3500 cal yrs B.P. (1550B.C.E.)	Wahl et al. 2016
Lake Tzib	Zea mays	3500 cal yrs B.P. (1550B.C.E.)	Carrillo-Bastos et al. 2010
R¡a Lagartos Biosphere Reserve	Zea mays	3460 cal yrs B.P. (1510B.C.E.)	Aragón-Moreno et al. 2012
R¡a Lagartos Biosphere Reserve	Cucurbitaceae	3400 cal yrs B.P. (1450B.C.E.)	Aragón-Moreno et al. 2012
Laguna Yaloch	Zea mays	3330 cal yrs B.P. (1350B.C.E.)	Wahl et al. 2013
El Palmar	Zea mays	3150 cal yrs B.P. (1200B.C.E.)	Luzzadder-Beach et al. 2017
Lake Peten Itza	Zea mays	3000 cal yrs B.P. (1050B.C.E.)	Islebe et al. 1996; Mueller et al. 2009
Laguna Zoncho	Zea mays	2940 cal yrs B.P. (960B.C.E.)	Clement & Horn, 2001
Laguna del Espino	Zea mays	2910 cal yrs B.P. (930B.C.E.)	Dull, 2004a
La Selva Biological Station	Zea mays	2700 cal yrs B.P. (750B.C.E.)	Horn & Kennedy, 2001
Petapilla	Zea mays	2670 cal yrs B.P. (720B.C.E.)	McNeil et al. 2010
Lake Amatitlán	Zea mays	2600 cal yrs B.P. (650B.C.E.)	Velez et al. 2011
Bonillita	Zea mays	2560 cal yrs B.P. (610B.C.E.)	Northrop & Horn, 1996
Bonillita	Sechium sp.	2470 cal yrs B.P. (520B.C.E.)	Northrop & Horn, 1996
Lake Amatitlán	Phaseolus sp.	2350 cal yrs B.P. (400B.C.E.)	Velez et al. 2011
Agua Caliente	Zea mays	2300 cal yrs B.P. (350B.C.E.)	Walsh et al. 2014
La Encrucijada Biosphere Reserve	Zea mays	2300 cal yrs B.P. (350B.C.E.)	Joo-Chang et al. 2015
El Palmar	Maranta arundinacea	2260 cal yrs B.P. (-310B.C.E.)	Luzzadder-Beach et al. 2017
Lake Tzib	Citrullus sp.	2250 cal yrs B.P. (300B.C.E.)	Carrillo-Bastos et al. 2010
Lake Tzib	Piper sp.	2250 cal yrs B.P.	Carrillo-Bastos et al. 2010

		(300B.C.E.)	
El Palmar	Cucurbitaceae	1720 cal yrs B.P. (230C.E.)	Luzzadder-Beach et al. 2017
Aguada Zacatal Nakbe	Zea mays	1260 cal yrs B.P. (690C.E.)	Wahl et al. 2007
Cantarrana	Zea mays	1070 cal yrs B.P. (880C.E.)	Kennedy & Horn, 2008
Petapilla	Zea mays	780 cal yrs B.P. (1170C.E.)	Rue, 1987
Coba	Zea mays	770 cal yrs B.P. (1160C.E.)	Leyden et al. 1998
Lake San Carlos	Zea mays	400 cal yrs B.P. (1500C.E.)	Correa-Metrio et al. 2016

Plotting the first palynological appearances of agrarian taxa across the Central American Isthmus and interpolating between sites enables us to visualise the spread of agriculture as (Figure 2.10). Originating in San Andres, Mexico, agrarian practices appear to have spread along coastal regions e.g. La Encrucijada Biosphere Reserve, Sipacate and the Lower Rio Naranjo on the Pacific coast, as well as Cobweb Swamp on the Caribbean coast. There is currently no palynological evidence of agrarian practises in Nicaragua and limited evidence in Honduras.

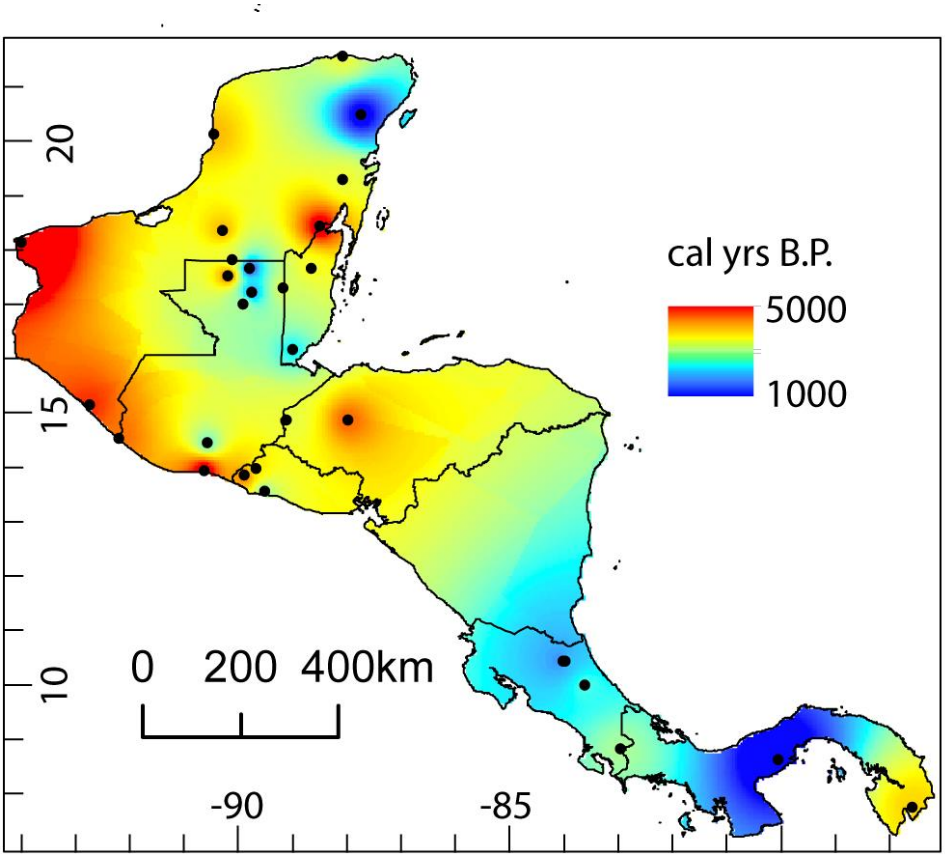


Figure 2.10 First evidence of cultigens as reported from in palaeo-palynological records across the Central American Isthmus.

Table 2.4 Cultigens reported from the palynological records across the Central American Isthmus.

Cultigen	Common Name	Reference
Cucurbitaceae: **e.g. Sechium & Citrullus**	Gourds Chayote Watermelon	Northrop & Horn, 1996; Carrillo-Bastos et al. 2010; Aragón-Moreno et al. 2012; Joo-Chang et al. 2015; Torrescano-Valle & Islebe, 2015; Luzzadder-Beach et al. 2017
Manihot	Cassava	Pope et al. 2001
Maranta arundinacea	Arrowroot	Luzzadder-Beach et al. 2017
Phaseolus	Beans	Velez et al. 2011
Piper	Pepper	Carrillo-Bastos et al. 2010
Zea mays	Corn	Rue, 1987; Bush & Colinvaux, 1994; Islebe et al. 1996; Northrop & Horn, 1996; Pohl et al. 1996; Leyden et al. 1998; Clement & Horn, 2001; Horn & Kennedy, 2001; Pope et al. 2001; Rue et al. 2002; Dull, 2004a; 2004b; 2007; Neff et al. 2006; Wahl et al. 2006; 2007; 2013; 2014; 2016; Kennedy & Horn, 2008; Mueller et al. 2009; Carrillo-Bastos et al. 2010; McNeil et al. 2010; Velez et al. 2011; Aragón-Moreno et al. 2012; Gutiérrez-Ayala et al. 2012; Walsh et al. 2014; Joo-Chang et al. 2015; Rushton et al. 2015; Torrescano-Valle & Islebe, 2015; Anderson & Wahl, 2016; Correa-Metrio et al. 2016 Luzzadder-Beach et al. 2017

Limitations of the Systematic Map

My systematic search and summary of the literature is limited to the studies I was able to find using the established protocol. Despite our efforts to be inclusive with search terms and languages, some important studies were undoubtedly missed. This is particularly true of the archaeological literature and "grey literature" which was not well covered in our search.

We attempted to conduct a quantitative numerical analysis upon the collected data sets; however, this proved unsuccessful due to the ability to homogenise data sets to a standard criterium. Problems arose when attempting to compare (i) multiple methodologies; (ii) dating and chronology and control methods, (iii) resolution of data sets, (iv) access to the full reported data sets.

Methodological approaches vary between studies, for example the use of different species of ostracodea for $\delta^{18}O$ measurements, the use of point sampling for charcoal verses continuous sampling, and the number of samples collected representing different periods of time. There are numerous problems associated with accurately dating and presenting depositional records inclusive of the events represented within them causing significant uncertenty when attempting to compare several records. This is due to a number of factors including: (i) the need to re-evaluate dates, specifically radiocarbon, to ensure suitable material was originally selected for dating; (ii) the presentation of dates in the literature includes un-calibrated and uncorrected dates (e.g Horn, 1993; Whitmore et al. 1996; Islebe et al. 1996; Horn & Kennedy, 2001); (iii) the inclusion of dates known to have been impacted by the 'hard-water error' (e.g. Whitmore et al. 1996; Leyden et al. 1998; Gabriel et al. 2009); (iv) the presentation of data against depth instead of time (e.g. Slade et al. 2013; Torrescano-Valle & Islebe, 2015; Luzzadder-Beach et al. 2017); and (v) variance in the methods used for interpolation or modelling of ages when creating an age-depth model (e.g. Rosenmeier et al. 2002; Avnery et al. 2011; Stansell et al. 2012; Anderson & Wahl, 2016). These uncertenties need to be carefully considered when interpreting and comparing both individual and multiple records.

2.5 Discussion

The finding of this systematic review are discussed in relation to the three sub-questions originally posed: (i) How have patterns of precipitation varied during the Holocene across the Central America Isthmus?; (ii) When and where are the most active periods of burning and what are the dominant drivers?; and (iii) How has the vegetation been impacted by climatic and anthropogenic changes?

i. How have patterns of precipitation varied during the Holocene across the Central America Isthmus?

The Early Holocene is defined by increasingly wetter conditions from *c.*12000 – 8000 cal yrs B.P. (10000 – 6000B.C.E.); however, evidence for the spatial extent represented by the terrestrial $\delta^{18}O$ records is limited to the lowlands of Central Guatemala (Hodell et al. 1995; Curtis et al. 1998; Rosenmeier et al. 2002a; Hillesheim et al. 2005; Pérez et al. 2010; Escobar et al. 2012; Wahl et al. 2014; Anderson & Wahl 2016) and Panama (Lachniet et al. 2004). While it is widely reported that warmer and wetter conditions prevailed across the rest of the Central American Isthmus, more $\delta^{18}O$ terrestrial records would be required to assess this claim. The northerly movement of the Inter Tropical Convergence Zone is the primary mechanism attributed to driving precipitation change in the Early-Middle Holocene *c.*12000 – 6000 cal yrs B.P. (10000 – 4000B.C.E.) (Hodell et al. 1995; Curtis et al. 1998; Hillesheim et al. 2005; Pérez et al. 2010; Metcalfe et al. 2009; Escobar et al. 2012; Wahl et al. 2014; Anderson & Wahl 2016). For records that span the Early-Middle Holocene authors have suggested that lakes have formed or expanded in the lowlands of Guatemala: Lago Puerto Arturo (Anderson & Wahl 2016), Lake Salpeten (Rosenmeier et al. 2002a), and Lake Peten Itza (Curtis et al. 1998). Evidence for the formation of these lakes is presented through the presence of aquatic fauna (*Ostracoda spp.*) in Lake Peten Itza (Curtis et al. 1998), and the lacustrine stratigraphy in Lago Puerto Arturo (Anderson & Wahl 2016), and Lake Salpeten (Rosenmeier et al. 2002a).

Lachniet et al. (2004a) present evidence for a drying event at 8200 cal yrs B.P. (6150B.C.E.) from Venado Cave, Panama; however, this is not reflected in the records from lowland Guatemala (Hodell et al. 1995; Curtis et al. 1998; Rosenmeier et al. 2002a; Hillesheim et al. 2005; Pérez et al. 2010; Escobar et al. 2012; Wahl et al. 2014; Anderson & Wahl 2016). While this event may have impacted other regions, further records from Panama and the rest of the Central American Isthmus would be required to assess whether this drying event impacted other parts of Central America or was localised to Panama.

Precipitation during the Middle Holocene 8000 – 4000 cal yrs B.P. (6000 – 4000B.C.E.) is spatially and temporally variable with limited regional patterns (Figure 2.5). The highest levels of precipitation for lowland Guatemala and Costa Rica are reported to have occurred between *c.*8000 – 6000 cal yrs B.P. (6000 – 4000B.C.E.), a period referred to as the Holocene Thermal Maximum (Hodel et al. 2005; Lachniet et al. 2009; Anderson & Wahl 2016; Pollock et al. 2016). These authors suggest that wetter conditions persisted until *c.*6000 cal yrs B.P. (4000B.C.E.) at which point many records diverge, presenting heterogeneity across space and through time (Figure 2.5). Anderson & Wahl, (2016) suggest that this increasing heterogeneity is related to the establishment of the seasonal monsoon *c.*7600B.P. (5450B.C.E.) whereby the North Atlantic Oscillation (NAO) and El Nino Southern Oscillation (ENSO) became increasingly influential factors driving changes in precipitation. Haug et al. (2001), Moy et al. (2002), Lachniet et al. (2004), and

Wahl et al. 2014 suggest that ENSO has been particularly prominent from *c*.3500 cal yrs B.P. (1500B.C.E.) to the present day.

Records from the Late Holocene 4000-0 cal yrs B.P. (2000B.C.E. – 1950C.E.) show the greatest spatial coverage for the Central American Isthmus; they report increasing heterogeneity (Figure 2.5). Precipitation reconstructions for the latter half of the Late Holocene 2000 – 0 cal yrs B.P. (0 – 1950C.E.) have primarily focused on the impacts and timings of hydrological extremes, including the Medieval Climate Anomaly (MCA) 900-1250C.E. and Little Ice Age (LIA) 1400-1850C.E. (Hodell et al. 1995; 2005; 2007 Curtis et al. 1996; 1998; Rosenmeier et al. 2002; Lachniet et al. 2004; Webster et al. 2007; Metcalfe et al. 2009; Carrillo-Bastos et al. 2010; Medina-Elizalde et al. 2010; Velez et al. 2011; Stansell et al. 2013; Kennett et al. 2012; Akers et al. 2016; Correa- Metrio et al. 2016; Smyth et al. 2017). These records show broad patterns of temporally heterogenous droughts during the MCA (Hodell et al. 1995; 2001; 2007; Curtis et al. 1996; Metcalfe et al. 2009; Medina-Elizalde et al. 2010; Kennett et al. 2012; Wahl et al. 2014; Anderson & Wahl 2016; Akers et al. 2016) including the widely reported Terminal Classic drought c.1050 cal yrs B.P. (900C.E.) (Hodell et al. 1995; 2001; 2005; 2007; Curtis et al. 1996; Lachniet et al. 2004; Webster et al. 2007; Medina-Elizalde et al. 2010; Kennett et al. 2012; Wahl & Anderson, 2014; Anderson & Wahl, 2016; Akers et al. 2016; Smyth et al. 2017). This drought coincided with the Terminal Maya Collapse c.1000 cal yrs B.P. (950C.E.) (Smyth et al. 2017).

Several mechanisms for the drivers of precipitation changes discussed above have been proposed. Stansell et al. (2013) suggests that changes in the North Atlantic, Gulf of Mexico and Caribbean Sea surface temperature (SST) (collectively known as the Intra-American Sea, IAS) are closely related to pressure anomalies associated with the NAO. These anomalies are thought to influence the pressure gradient of the ITCZ and cyclonic/anti-cyclonic Hadley cells either side of the Central American Isthmus (Giannini *et al.* 2001; Poveda et al. 2006). Lachniet et al. (2004) and Stansell et al. (2013) further suggests that positive pressure anomalies are associated with the NAO, and that these usually coincide with lower SST, stronger trade winds, and overall dryer conditions inclusive of the 8200 cal yrs B.P. (6200B.C.E.) drought event. Similarly, these authors report that negative anomalies associated with the NAO are inversely associated with higher SST, weaker trade winds, and wetter conditions, such as the onset of the Holocene.

The role and importance of the influence of ENSO on the climate of the Central American Isthmus has been increasingly debated in recent years (DiNezio et al. 2010; Hlinka et al. 2014); however, Wahl et al. (2014) suggest that an overall increase in ENSO activity after 3500 cal yrs B.P. (1500B.C.E.) is associated with a more southerly ITCZ. In particular, the position of the ITCZ is reported by Stansell et al. (2013) and Wahl et al. (2014) to be tied to phases of the NAO and ENSO. Thus, a positive phase of ENSO combined with a positive anomaly in the NAO can result in decreased precipitation in the IAS; however, Wahl et al. (2014) also proposes that anomalously strong positive ENSO events could override this pattern. Correa-Metrio et al. (2012) and Stansell et al. (2013) suggest that high ENSO activity in the transition between the MCA and LIA led to a large hydrological shift from relatively wetter conditions to drier conditions in Central Pacific Nicaragua and from relatively drier conditions to wetter conditions in Panama. In some lowland sites in Mexico, outside the geographic remite of this systematic review, the LIA has been associated with a trend of cooling, higher winter precipitation and forest expansion (Lozano-Garcia, 2007). Such records further highlight the heterogenous responses of the Mesoamerican region to shifts in hydroclimate.

It should also be noted that most evidence for the prevalence and impacts of ENSO through the Holocene have been recorded in marine records and not terrestrial records, which can be found summarised in Metcalfe et al. (2015). Correa-Metrio et al. (2012) suggest that the role ENSO plays on controlling the timings and intensity of the wet and dry seasons are the most significant in terms of impact to water availability and vegetation, particularly in concurrent years of El Niño or La Nina.

While the synthesis presented for Holocene precipitation across the Central American Isthmus largely reiterates that of Metcalfe et al. (2015), the current systematic review identified four additional terrestrial publications which were previously missed (Curtis et al. 1998; Hodell et al. 2007; Frappier et al. 2007; 2013; Lachniet et al. 2009). These records provide further evidence for wetter conditions at the onset of the Holocene linked to the ITCZ (Curtis et al. 1998; Lachniet et al. 2009), the terminal classic drought, c.1050B.P. and a high-resolution record of recent (1978-2001C.E.) tropical cyclones in Belize (Frappier et al. 2007). There is still substantial research that is required to understand the spatial heterogeneity of climate over space and time, while altitude is undoubtably a contributing factor, further records are required from higher altitude regions to draw together tangible conclusions.

ii. When and where are the most active periods of burning and what are the dominant drivers?

Piperno et al. (1990; 1991) report that fire has been an important component of ecosystem forest dynamics across the Central American Isthmus since the early Holocene *c.*12000 cal yrs B.P. (10000B.C.E.). Increasing regional burning between *c.*12000 – 4000 cal yrs B.P. (10000 – 2000B.C.E.) is documented across all records; however, peaks in local burning show spatial variation. It is suggested that high fire activity between *c.*10500 – 5000 cal yrs B.P. (8500 – 3000B.C.E.) is linked to rising temperatures at the onset to the Holocene bringing about more pronounced seasonality which facilitated more convective storms, frequent ignitions and increased fuel loads (Piperno et al. 1990; 1991; Horn, 1993; Caffrey et al. 2011; Lane et al. 2011; Correa-Metrio et al. 2012; Anderson & Wahl, 2016).

The co-occurrence of increased moisture and fire from 9000 – 6000 cal yrs B.P. (7000-4000B.C.E.) is further suggested by Caffrey et al. (2011), Correa-Metrio et al. (2012), Schüpbach et al. (2015), Anderson & Wahl, (2016), to be a response to more frequent storm activity associated with increases in both precipitation and lightning. The apparent concurrent burning across sites at 8000 cal yrs B.P. (6000B.C.E.) and 6000 cal yrs B.P. (4000B.C.E.) are attributed to this regional climatic forcing (Table 2.2).

The relationship between climate and fire is reported by Anderson & Wahl (2016) to decouple between c.5000 – 4500 cal yrs B.P. (3000 – 2500B.C.E.) across lowland Guatemala. Neff et al. (2006), Correa-Metrio et al. (2012), Schüpbach et al. (2015) and Anderson & Wahl (2016) report that burning events before *c.*5000 cal yrs B.P. (3000B.C.E.) are linked to climate, while events after 4500 cal yrs B.P., (2500B.C.E.) are linked to a mix of climatic and anthropogenic signals.

After the establishment of sedentary agriculturalists in Petén, 4600 cal yrs B.P. (2600B.C.E.), Wahl et al. (2006; 2007; 2014) suggest that anthropogenic influences impact fire regimes through manipulation of fuel loads and the introduction human-caused ignitions. Many authors argue that the signal of natural and anthropogenic ignitions of fire are difficult to independently separate after this time (Correa-Metrio et al. 2012; Schüpbach et al. 2015; Anderson & Wahl 2016; Anderson & Wahl 2016).

Dull (2004a) reports that reduced burning in the lowlands *c.*3500 cal yrs B.P. (1500B.C.E.) of El Salvador resulted from a positive feedback between deforestation and precipitation. Lawton et al. (2001) argues that lowland deforestation impacted the mean cloud base height, causing reductions in available moisture and precipitation in lowland areas. The resulting effect was less burning from reduced vegetation growth and thus lower fuel loads.

Severe storms, such as "Hurricane Elisenda", 3200 cal yrs B.P. (1250B.C.E.) along the Pacific coast of Nicaragua are reported by Urquhart, (2009), who suggests that they enabled large-scale burning events to manifest after impact. Damage to forest vegetation led to increased fuel loads which then ignited into high magnitude fires.

The resilience review by Cole et al. (2014) suggests that successive regeneration of fuel loads after high-magnitude fire periods are typically much slower after low-magnitude high-frequency fire peridos. Urquhart (2009) reports that during fuel load recovery and regeneration, frequent but low-magnitude burning is common until forest taxa (Urticaceae, Moraceae, Combretaceae, Melastomataceae, and Ulmaceae) are able to re-establish, this is further reported to result in several secondary peaks of burning over a re-establishment period.

Many authors report that early agricultural practices involved the use of fire through *Swidden*, and *Milpa* cycling (Walsh et al. 2014; Joo-Chang et al. 2015; Rushton et al. 2015; Torrescano-Valle & Islebe, 2015; Anderson & Wahl, 2016; Correa-Metrio et al. 2016; Luzzadder-Beach et al. 2017). The term "*Swidden*" is derived from "*svithinn*", in Old Norse which translates to "clearing in the forest to be burned" and the term *Milpa* is derived from Nahuatl meaning "maize field" (Nigh & Diemont, 2013). The use of *Swidden* for practicing *Milpa* is often identified through the combined interpretation of charcoal-palaeo-palynological data sets (Table 2.3).

As populations expanded during the Pre-Classic, 4000 – 3000 cal yrs B.P. (2000 – 1000B.C.E), and Classic, 3000 – 1350 cal yrs B.P. (2000 – 600B.C.E.) periods, state-level societies emerged in the Northern Isthmus, which led to sedentary habitation and the demand for sustenance (Coe, 1966). Schüpbach et al. (2015) and Anderson & Wahl, (2016) report that as a result of this sedentary habitation, agriculture expanded and resources were increasingly managed. Initial peaks of burning are reported by Dull et al. (2004a), Correa-Metrio et al. (2012), Schüpbach et al. (2015) and Anderson & Wahl,

(2016) preceeding agriculture, indicating an initial clearance phase, which is often followed by reduced burning as the surrounding vegetation is managed. However, as populations continued to expand in Mexico, Guatemala, Belize and El Salvador, greater areas were required for agriculture, resulting in larger areas being subject to *Swidden* and *Milpa*. Dull et al. (2004b) report the formation of savanna type vegetation from previously more forest-dominated landscapes in El Salvador as a direct result of anthropogenic management of vegetation through use of fire. Schüpbach et al. (2015) state that repeatedly anthropogenically-disturbed areas in lowland Guatemala recover vegetative biomass more slowly due to frequent but low-magnitude fires.

Anderson & Wahl, (2016) suggest that burning vegetation for lime (plaster) production is a further potential driver of vegetation change. Lime plaster was created by the Maya through the burning of powdered limestone ($CaCO_3$). This releases the carbon component of the limestone leaving behind calcium oxide (CaO) which was mixed with water to create quicklime (Abrams & Rue, 1988). This type of lime plaster was used to cover temples, monuments and houses across the Maya area (Villaseñor, 2010).

Anderson & Wahl (2016) calculate that 196km^2 of mature forest would have been extracted and burnt repeatedly on 10 year regrowth cycles to create the amount of lime plaster required to cover the monuments and structures within the El Mirador arcahological complex in Peten, Guatemala.

Horn, (1993), League & Horn, (2000), Dull, (2004a; 2004b), Wahl et al. (2007), Lane et al. (2011), Walsh et al. (2014) and Anderson & Wahl, (2016) report that the impacts of fire and burning during the historic period c.450 cal yrs B.P. (1500C.E.) are primarily attributed to anthropogenic drivers, primarily associated with agrarian practices.

iii. How has the vegetation been impacted by climatic and anthropogenic changes?

Mueller et al. (2009) report that that the transition into the Holocene is marked by the expansion of mesic forest taxa (Moraceae, *Brosimim alicastrum*, Euphorbiaceae, and *Bursera*). Many authors suggest that this change was driven by climate forcing at the end of the Younger Dryas, c.11700 cal yrs B.P. (9750B.C.E.) (Hodell et al. 1995; Curtis et al. 1998; Hillesheim et al. 2005; Metcalfe et al. 2009; Perez et al. 2010; Escobar et al. 2012; Wahl et al. 2014; Schüpbach et al. 2015; Anderson & Wahl 2016).

It is suggested that wetter and warmer conditions facilitated this initial shift in vegetation, with modern distributions of tropical moist forests beginning to establish in Panama from *c.*14000 cal yrs B.P. (12000B.C.E.) (Piperno et al. 1990; 1991; Bush et al. 1992), in Costa Rica from *c.*13000 cal yrs B.P. (11000B.C.E.) (Islebe & Hooghiemstra, 1997; Hooghiemstra et al. 1992), and in lowland Guatemala by *c.*11250 cal yrs B.P. (9300B.C.E.) (Hillesheim et al 2005; Correa-Metrio et al. 2012). Curtis et al. (1998), Hillesheim et al. (2005), Mueller et al. (2009) and Correa-Metrio et al. (2012) suggest that these mesic forests fully established by *c.*8500-8000 cal yrs B.P. (6500 – 6000B.C.E.).

After this initial homogenous climatically-driven shift, vegetation is reported to have responded hetrogenously to a combination of climatic and anthropogenic forcing (Figure 2.9). Land clearance for agriculture is suggested to be the driving factor for most of the major vegetation changes in Central America after *c.*4000 cal yrs B.P. (2000B.C.E.) (Figure 2.10).

Evidence of agriculture is typically interpreted as evidence for anthropogenic manipulation of the surrounding vegetation and environment. The first palynological evidence for agriculture is reported by Pohl et al. (1996) from San Andres, Tobasco, Mexico, *c.*7050 cal yrs B.P. (5000B.C.E.). Rue (1987), Pohl et al. (1996), Dull, (2004a;

2004b), Neff et al. (2006), Wahl et al. (2006; 2007; 2014), Joo-Chang et al. (2015) and Anderson & Wahl, (2016) then report the spread of agriculture across Guatemala and its adjacent territories between *c.*5500-4500 cal yrs B.P. (3500 – 2500B.C.E.) (Figure 10).

Dull (2004a; 2004b) reports a decline in mesic and high forest taxa *Pinus*, *Quercus* and *Liquidambar*, and increases in open-habitat taxa, Poaceae and Compositae, and disturbance taxa Ameranthaceae, *Ambrosia* and *Polygonum.* Vegetation changes are suggested to be heterogenous at each site and provide evidence for local variation, such as that caused by anthropogenic activities, and not necessarily regionally climatically-driven change.

There are eight cultigens identified in the palaeo-palynological record used to indicate anthropogenic presence (Tables 2.3 & 2.4), including *Zea mays*, which is believed to have been used as one of fifteen staple crops eaten by early humans in Central America (White, 1999).

The initial appearance of cultigens in the palynological record from the Tabasco region, Mexico (Pope et al. 2001); the Pacific coast of Mexico and Guatemala (Neff et al. 2006; Gutiérrez-Ayala et al. 2012; Joo-Chang et al. 2015); and around Cob Web Swamp, northern Belize (Pohl et al. 1996) suggests that widespread agriculture developed north of Honduras, moving from North to South, around 1300 years before the rest of Central America (Figure 2.9 & 2.10). This coincides with the onset and development of sedentary state-level societies in this region, beginning c.4000 cal yrs B.P. (2000B.C.E.). Agricultural practices are also reported to move from the base of Panama, North *c.*2700 cal yrs B.P. (700B.C.E.).

The rise of civilizations in this formative period include the Pre-Classic Maya and Olmec societies. Trade is noted to be one of the key components of Pre-Columbian societal rise and success, with commodities including obsidian, jade, hematite, mica, turquoise, serpentine, salt, copal, ceramics, cacao, tobacco, textiles, feathers and marine shells (Hirth, 1978; 2013; Hammond, 1972; Smith, 2003a; 2003b; Blanton & Fargher, 2012; Golitko & Feinman, 2015). Of these traded materials, obsidian has been widely used to trace early routes of commerce (Hammond, 1972; McKillop, 1996; Golitko & Feinman, 2015).

Patterns of agricultural expansion corroborate routes for obsidian commerce across Mexico, Guatemala, Belize and Honduras (Golitko & Feinman, 2015). Sites of early agriculture are therefore suggested to have been used to facilitate early routes of trade, which then proceeded to expand and develop across the Isthmus.

An absence of palynological evidence for agriculture from Southern Honduras through to Greater Nicoya (Figure 2.10) has led to our suggestion that there was limited or no agrarian practices for this region; however, given the limited number of palynological records currently available, this has to remain somewhat speculative. Only five of the sixteen palynological records from Costa Rica and Panama report evidence for the presence of cultigens (Figure 2.10). Early agriculture in the Southern Isthmus appears to have spread from the South of Panama *c.*3700 cal yrs B.P. (1750B.C.E.) through to Costa Rica *c.*3000 cal yrs B.P. (1050B.C.E.) (Figure 2.10).

After European contact *c.*450 cal yrs B.P. (1500C.E.) Deevey et al. (1979), Curtis et al. (1998), Neff et al. (2006), Mueller et al. (2009), Caffrey et al. (2011) report limited changes to the vegetation. This is possibly because the reported palynological records are low in temporal resolution - greater than 200 years between samples (Deevey et al. 1979; Curtis et al. 1998; Mueller et al. 2009) or are missing sediment from the last *c.*500 years (Neff et al. 2006; Caffrey et al. 2011). There are, however, a number of records which report changes in forest cover after the initial arrival of the Spanish *c.*450 – 350 cal yrs B.P. (1500-1600C.E.) in lowland Guatemala (Brenner et al. 1990; Wahl, 2016; Anderson & Wahl, 2016), Mexico (Leyden, 1987) and El Salvador (Dull, 2004a; 2007), suggesting that reductions in local human populations enabled the forests to recover and expand over the following century. Only Dull, (2004a; 2007) and Velez et al. (2011) reports further vegetation changes after this initial recovery phase.

2.6 Summary

Through systematically mapping palaeoenvironmental proxy records $\delta^{18}O$, charcoal and pollen I have identified patterns of spatial and temporal change for precipitation, fire and vegetation across the Central American Isthmus spanning the Holocene. The majority of terrestrial palaeoenvironmental data sets have been produced from lake sediment records from Mexico, Guatemala and Belize within the area covering the extent of the Mayan empire. These records best represent the Late-Holocene. Relatively few records have been produced from El Salvador, Honduras, Nicaragua and Panama, indicating that these areas have been comparatively understudied and require further research. There are currently no *Sporormiella* records for the region.

There is little agreement in the literature on mechanisms driving changes in precipitation, nor their regional impacts across the Central American Isthmus spanning the Holocene. Fluctuations in climate are noted to impact vegetation dynamics through (i) changes in water availability including drought events such as the Terminal Maya Collapse; and (ii) increases in the frequency and magnitude of burning events, impacting ignitions in the Early Holocene, and fuel loads through the impact of hurricanes. Burning associated with anthropogenic activities is heterogenous but prominent from *c.*5000 cal yrs B.P. (3000B.C.E.). The role of fire across different vegetation types is not well explored and warrants further research to determine the relative importance of fire in shaping and maintaining different vegetation types including mixed coniferous forests and savannah.

Identification of palynological grains for known domesticated agricultural taxa suggests that agrarian practices spread with the trade routes developed by the Olmec and Maya civilizations in the North of the Central American Isthmus, before it later spread to the South.

The limited focus upon the colonial/post-colonial period warrants further research to enable integration of long-term ecological records with historical documentation and modern measurements. This will enable more quantitative approaches to be applied to the palaeoecological records generating values that can then be applied to modern day model or to establish baselines.

Understanding the resilience of different vegetation types to drivers of change, i.e. precipitation, fire, and anthropogenic activities, should be a dominant focus of future research enabling measures to be taken for conservation and climate change management applying adaptation strategies to vulnerable biomes.

Knowledge gaps identified

The systematic methodological approach to identifying and mapping palaeoenvironmental records has allowed us to identify six knowledge gaps:

1. The heterogenous patterns of precipitation across the Central American Isthmus throughout the Holocene are poorly understood due to spatially and temporally limited records. In order to address this knowledge gap high resolution $\delta^{18}O$ proxy data sets from upland regions in Pacific Guatemala, El Salvador, Honduras and Nicaragua are required. The identified spatial heterogeneity of precipitation reported across latitudes and elevations through time makes the generation of these records particularly important. Independent hydro-climatic records are required from each site to be able to interpret precipitation for a given location.

Using marine records (e.g. Metcalfe et al. 2015) or nearby terrestrial records, which reconstruct hydro-cliamte, is an inadequate method for infering precipitation for a location due to the identified heterogeneity across space and time.

2. The timing of widespread climatically-driven fire and spatially-heterogenous anthropogenic burning are not well understood or quantified. Most records have been collected from lowland tropical moist broadleaf forests in lowland Mexico and Guatemala. Fire is likely to have played an important role in driving vegetation diversity and structure, particularly where human populations were dense.
3. Unravelling the origins and spread of agriculture across Central America requires further spatial and temporal coverage. Additional palynological records, particularly from the uplands of Chiapas and Guatemala, and from Honduras to Southern Nicaragua will be required to further understand the origin and spread of agriculture across space and through time. Consolidation of the palaeo-palynological data with archaeological records could help to clarify this understanding.
4. Records of the Colonial and Post-Colonial periods (Post-European conquest c.1500) are limited, largely owing to the often-unsuccessful extraction of the top sediments of a record. Comparing high-resolution palaeo-records with historical documentation and modern-day measurements could help to bridge the gap between modern ecology and long-term ecology.
5. Identifying the recovery and resilience of vegetation after a disturbance event such as natural hazards (hurricanes and volcanic eruptions) fire, and agricultural activities is integral to our understanding of different types of ecosystem resilience and the factors that help contribute towards increasing the resilience of a given

ecosystem. Using the palynological records identified in this study, disturbance events and rates of recovery could be quantitatively identified and analysed from high resolution data sets using locally defined thresholds. This would enable measures to be taken for conservation and climate change management adaptation strategies in vulnerable biomes.

6. There are currently no *Sporormiella* records for the Central American Isthmus spanning the Holocene. Collecting this data will help inform knowledge of the impacts of herbivory across the region through time.

2.7 Acknowledgemnets

This research was funded by the Natural Environment Research Council of the United Kingdom NE/L002612/1, US National Science Foundation EAR-1502989 and St Edmund Hall, University of Oxford.

2.8 References

Abrams, E.M. and Rue, D.J., 1988. The causes and consequences of deforestation among the prehistoric Maya. *Human Ecology*, 16(4), pp.377-395.

Akers, P.D., Brook, G.A., Railsback, L.B., Liang, F., Iannone, G., Webster, J.W., Reeder, P.P., Cheng, H. and Edwards, R.L., 2016. An extended and higher-resolution record of climate and land use from stalagmite MC01 from Macal Chasm, Belize, revealing connections between major dry events, overall climate variability, and Maya sociopolitical changes. *Palaeogeography, palaeoclimatology, palaeoecology*, 459, pp.268-288.

Altman, D.G. 1991. Measuring agreement. In: Altman D.G. (Ed.), Practical statistics for medical research. London: Chapman and Hall.

Anchukaitis, K.J. and Horn, S.P., 2005. A 2000-year reconstruction of forest disturbance from southern Pacific Costa Rica. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 221(1-2), pp.35-54.

Anderson, L. and Wahl, D., 2016. Two Holocene paleofire records from Peten, Guatemala: Implications for natural fire regime and prehispanic Maya land use. *Global and Planetary Change*, 138, pp.82-92.

Aragón-Moreno, A.A., Islebe, G.A. and Torrescano-Valle, N., 2012. A~ 3800-yr, high-resolution record of vegetation and climate change on the north coast of the Yucatan Peninsula. *Review of palaeobotany and palynology*, 178, pp.35-42.

Avnery, S., Dull, R.A. and Keitt, T.H., 2011. Human versus climatic influences on late-Holocene fire regimes in southwestern Nicaragua. *The Holocene*, 21(4), pp.699-706.

Blanton, R. E., & Fargher, L. F. (2012). Market cooperation and the evolution of the pre-Hispanic Mesoamerican world-system. In S. J. Babones & C. Chase-Dunn (Eds.), Routledge handbook of world-systems analysis (pp. 11–20). London: Routledge.

Brenner, M., Leyden, B. and Binford, M.W., 1990. Recent sedimentary histories of shallow lakes in the Guatemalan savannas. *Journal of Paleolimnology*, 4(3), pp.239-252.

Bush, M.B., Piperno, D.R., Colinvaux, P.A., De Oliveira, P.E., Krissek, L.A., Miller, M.C. and Rowe, W.E., 1992. A 14 300- Yr Paleoecological Profile of a Lowland Tropical Lake in Panama. *Ecological Monographs*, 62(2), pp.251-275.

Bush, M.B. and Colinvaux, P.A., 1994. Tropical forest disturbance: paleoecological records from Darien, Panama. *Ecology*, 75(6), pp.1761-1768.

CAB International, 2018. Available at: http://www.cabdirect.org/ .[Accessed 22 Aug. 2017].

Caffrey, M.A., Taylor, M.J. and Sullivan, D.G., 2011. A 12,000-year Record of Vegetation and Climate Change from the Sierra de Los Cuchumatanes, Guatemala. *Journal of Latin American Geography*, 10(2), pp.129-151.

Carrillo-Bastos, A., Islebe, G.A., Torrescano-Valle, N. and González, N.E., 2010. Holocene vegetation and climate history of central Quintana Roo, Yucatán Península, Mexico. *Review of Palaeobotany and Palynology*, 160(3-4), pp.189-196.

Clement, R.M. and Horn, S.P., 2001. Pre-Columbian land-use history in Costa Rica: a 3000-year record of forest clearance, agriculture and fires from Laguna Zoncho. *The Holocene*, 11(4), pp.419-426.

Coe, M.D. and Houston, S.D., 1966. *The maya*. London: Thames and Hudson.

Cole, L.E., Bhagwat, S.A. and Willis, K.J., 2014. Recovery and resilience of tropical forests after disturbance. *Nature communications*, 5, p.3906.

CEE (Collaboration for Environmental Evidence). 2018. *Guidelines and Standards for Evidence synthesis in Environmental Management*. [Edited by Pullin, AS, Frampton GK, Livoreil B, Petrokofsky G]. Version 5.0. Available at: www.environmentalevidence.org/information-for-authors [Accessed 26 April 2018].

Correa-Metrio, A., Bush, M.B., Cabrera, K.R., Sully, S., Brenner, M., Hodell, D.A., Escobar, J. and Guilderson, T., 2012. Rapid climate change and no-analog vegetation in lowland Central America during the last 86,000 years. *Quaternary Science Reviews*, 38, pp.63-75.

Correa- Metrio, A., Vélez, M.I., Escobar, J., St- Jacques, J.M., López- Pérez, M., Curtis, J. and Cosford, J., 2016. Mid- elevation ecosystems of Panama: future uncertainties in light of past global climatic variability. *Journal of Quaternary Science*, 31(7), pp.731-740.

Curtis, J.H., Hodell, D.A. and Brenner, M., 1996. Climate variability on the Yucatan Peninsula (Mexico) during the past 3500 years, and implications for Maya cultural evolution. *Quaternary Research*, 46(1), pp.37-47.

Curtis, J.H., Brenner, M., Hodell, D.A., Balser, R.A., Islebe, G.A. and Hooghiemstra, H., 1998. A multi-proxy study of Holocene environmental change in the Maya lowlands of Peten, Guatemala. *Journal of paleolimnology*, 19(2), pp.139-159.

Dinerstein, E., Olson, D., Joshi, A., Vynne, C., Burgess, N.D., Wikramanayake, E., Hahn, N., Palminteri, S., Hedao, P., Noss, R. and Hansen, M., 2017. An ecoregion-based approach to protecting half the terrestrial realm. *BioScience*, 67(6), pp.534-545.

DiNezio, P., Clement, A. and Vecchi, G., 2010. Reconciling differing views of tropical Pacific climate change. *Transactions American Geophysical Union*, 91(16), pp.141-142.

Dull, R.A., 2004a. An 8000-year record of vegetation, climate, and human disturbance from the Sierra de Apaneca, El Salvador. *Quaternary Research*, 61(2), pp.159-167.

Dull, R.A., 2004b. A Holocene record of Neotropical savanna dynamics from El Salvador. *Journal of Paleolimnology*, 32(3), pp.219-231.

Dull, R.A., 2007. Evidence for Forest Clearance, Agriculture, and Human- Induced Erosion in Precolumbian El Salvador. *Annals of the Association of American Geographers*, 97(1), pp.127-141.

Elsevier, 2018. Scopus. Available at: http://www.elsevier.com/online-tools/scopus. [Accessed 22 Aug. 2017].

Escobar, J., Hodell, D.A., Brenner, M., Curtis, J.H., Gilli, A., Mueller, A.D., Anselmetti, F.S., Ariztegui, D., Grzesik, D.A., Pérez, L. and Schwalb, A., 2012. A∼ 43-ka record of paleoenvironmental change in the Central American lowlands inferred from stable isotopes of lacustrine ostracods. *Quaternary Science Reviews*, 37, pp.92-104.

Frampton, G. K., Livoreil, B. & Petrokofkey, G. 2017. Eligibility screening in evidence synthesis of environmental management topics. *Environmental Evidence*, 6, 27.

Frappier, A.B., Sahagian, D., Carpenter, S.J., González, L.A. and Frappier, B.R., 2007. Stalagmite stable isotope record of recent tropical cyclone events. *Geology*, 35(2), pp.111-114.

Frappier, A.B., 2013. Masking of interannual climate proxy signals by residual tropical cyclone rainwater: Evidence and challenges for low- latitude speleothem paleoclimatology. *Geochemistry, Geophysics, Geosystems*, 14(9), pp.3632-3647.

Giannini, A., Cane, M.A. and Kushnir, Y., 2001. Interdecadal changes in the ENSO teleconnection to the Caribbean region and the North Atlantic Oscillation. *Journal of Climate*, 14(13), pp.2867-2879.

Golitko, M. and Feinman, G.M., 2015. Procurement and distribution of pre-Hispanic Mesoamerican obsidian 900 BC–AD 1520: A social network analysis. *Journal of Archaeological Method and Theory*, 22(1), pp.206-247.

Graham, N.E., Hughes, M.K., Ammann, C.M., Cobb, K.M., Hoerling, M.P., Kennett, D.J., Kennett, J.P., Rein, B., Stott, L., Wigand, P.E. and Xu, T., 2007. Tropical Pacific–mid-latitude teleconnections in medieval times. *Climatic Change*, 83(1-2), pp.241-285.

Gutiérrez-Ayala, L.V., Torrescano-Valle, N. and Islebe, G.A., 2012. Reconstrucción paleoambiental del Holoceno tardío de la reserva Los Petenes, Península de Yucatán, México. *Revista mexicana de ciencias geológicas*, 29(3), pp.749-763.

Hammond, N. (1972). Obsidian trade routes in the Mayan area. *Science*, 178(4065), 1092–1093.

Haug, G.H., Hughen, K.A., Sigman, D.M., Peterson, L.C. and Röhl, U., 2001. Southward migration of the intertropical convergence zone through the Holocene. *Science*, 293(5533), pp.1304-1308.

Heidorn, P.B., 2008. Shedding light on the dark data in the long tail of science. *Library trends*, 57(2), pp.280-299.

Hillesheim, M.B., Hodell, D.A., Leyden, B.W., Brenner, M., Curtis, J.H., Anselmetti, F.S., Ariztegui, D., Buck, D.G., Guilderson, T.P., Rosenmeier, M.F. and Schnurrenberger, D.W., 2005. Climate change in lowland Central America during the late deglacial and early Holocene. *Journal of Quaternary Science*, 20(4), pp.363-376.

Hirth, K. G. (1978). Interregional trade and the formation of prehistoric gateway communities. *American Antiquity*, 43(1), 35–45.

Hirth, K. G. (2013). The merchant’s world: Commercial diversity and economics of interregional exchange in highland Mesoamerica. In K. G. Hirth & J. Pillsbury (Eds.), Merchants, markets, and exchange in the Pre-Columbian World (pp. 85–112). Washington, D.C.: Dumbarton Oaks Research Library & Collection.

Hlinka, J., Hartman, D., Jajcay, N., Vejmelka, M., Donner, R., Marwan, N., Kurths, J. and Palus, M., 2014. Regional and inter-regional effects in evolving climate networks. *Nonlinear Processes in Geophysics*, (21), pp.451–462, Hodell, D.A., Curtis, J.H. and Brenner, M., 1995. Possible role of climate in the collapse of Classic Maya civilization. *Nature*, 375(6530), pp.391.

Hodell, D.A., Brenner, M., Curtis, J.H. and Guilderson, T., 2001. Solar forcing of drought frequency in the Maya lowlands. *Science*, 292(5520), pp.1367-1370.

Hodell, D.A., Brenner, M. and Curtis, J.H., 2005. Terminal Classic drought in the northern Maya lowlands inferred from multiple sediment cores in Lake Chichancanab (Mexico). *Quaternary Science Reviews*, 24(12), pp.1413-1427.

Hodell, D.A., Brenner, M. and Curtis, J.H., 2007. Climate and cultural history of the northeastern Yucatan Peninsula, Quintana Roo, Mexico. *Climatic Change*, 83(1), pp.215-240.

Hooghiemstra, H., Cleef, A.M., Noldus, C.W. and Kappelle, M., 1992. Upper Quaternary vegetation dynamics and palaeoclimatology of the La Chonta bog area (Cordillera de Talamanca, Costa Rica). *Journal of Quaternary Science*, 7(3), pp.205-225.

Horn, S.P., 1993. Postglacial vegetation and fire history in the Chirripó Páramo of Costa Rica. *Quaternary Research*, 40(1), pp.107-116.

Horn, S.P. and Kennedy, L.M., 2001. Pollen evidence of maize cultivation 2700 BP at La Selva biological station, Costa Rica. *Biotropica*, 33(1), pp.191-196.

Horn, S.P., Rodgers III, J.C., Orvis, K.H. and Northrop, L.A., 1998. Recent land use and vegetation history from soil pollen analysis: testing the potential in the lowland humid tropics. *Palynology*, 22(1), pp.167-180.

Islebe, G.A., Hooghiemstra, H. and van't Veer, R., 1996. Holocene vegetation and water level history in two bogs of the Cordillera de Talamanca, Costa Rica. *Vegetation*, 124(2), pp.155-171.

Islebe, G.A. and Hooghiemstra, H., 1997. Vegetation and climate history of montane Costa Rica since the last glacial. *Quaternary Science Reviews*, 16(6), pp.589-604.

Joo-Chang, J.C., Islebe, G.A. and Torrescano-Valle, N., 2015. Mangrove history during middle-and late-Holocene in Pacific south-eastern Mexico. *The Holocene*, 25(4), pp.651-662.

Kennedy, L.M. and Horn, S.P., 2008. A late Holocene pollen and charcoal record from La Selva biological station, Costa Rica. *Biotropica*, 40(1), pp.11-19.

Kennett, D.J., Breitenbach, S.F., Aquino, V.V., Asmerom, Y., Awe, J., Baldini, J.U., Bartlein, P., Culleton, B.J., Ebert, C., Jazwa, C. and Macri, M.J., 2012. Development and disintegration of Maya political systems in response to climate change. *Science*, 338(6108), pp.788-791.

Lachniet, M.S., Asmerom, Y., Burns, S.J., Patterson, W.P., Polyak, V.J. and Seltzer, G.O., 2004. Tropical response to the 8200 yr BP cold event? Speleothem isotopes indicate a weakened early Holocene monsoon in Costa Rica. *Geology*, 32(11), pp.957-960.

Lachniet, M.S., Johnson, L., Asmerom, Y., Burns, S.J., Polyak, V., Patterson, W.P., Burt, L. and Azouz, A., 2009. Late Quaternary moisture export across Central America and to Greenland: evidence for tropical rainfall variability from Costa Rican stalagmites. *Quaternary Science Reviews*, 28(27-28), pp.3348-3360.

Lachniet, M.S., 2015. Are aragonite stalagmites reliable paleoclimate proxies? Tests for oxygen isotope time-series replication and equilibrium. *Geological Society of America Bulletin*, 127(11-12), pp.1521-1533.

Lane, C.S., Horn, S.P., Mora, C.I., Orvis, K.H. and Finkelstein, D.B., 2011. Sedimentary stable carbon isotope evidence of late Quaternary vegetation and climate change in highland Costa Rica. *Journal of Paleolimnology*, 45(3), pp.323-338.

Lawton, R.O., Nair, U.S., Pielke, R.A. and Welch, R.M., 2001. Climatic impact of tropical lowland deforestation on nearby montane cloud forests. *Science*, 294(5542), pp.584-587.

League, B.L. and Horn, S.P., 2000. A 10 000 year record of Paramo fires in Costa Rica. *Journal of Tropical Ecology*, pp.747-752.

Leyden, B.W., Brenner, M. and Dahlin, B.H., 1998. Cultural and Climatic History of Cobá, a Lowland Maya City in Quintana Roo, Mexico 1. *Quaternary Research*, 49(1), pp.111-122.

Livoreil, B., Glanville, J., Haddaway, N.R., Bayliss, H., Bethel, A., Lachapelle, F.F., Robalino, S., Savilaakso, S., Zhou, W., Petrokofsky, G. and Frampton, G., 2017. Systematic searching for environmental evidence using multiple tools and sources. *Environmental Evidence*, 6(1), p.23.

Lozano-García, S.M., Caballero, M., Ortega, B., Rodríguez, A. and Sosa, S., 2007. Tracing the effects of the Little Ice Age in the tropical lowlands of eastern Mesoamerica. Proceedings of the National Academy of Sciences of the United States of America, 104(41), pp.16200-16203.

Luzzadder- Beach, S., Beach, T., Garrison, T., Houston, S., Doyle, J., Román, E., Bozarth, S., Terry, R., Krause, S. and Flood, J., 2017. Paleoecology and Geoarchaeology at El Palmar and the El Zotz Region, Guatemala. *Geoarchaeology*, 32(1), pp.90-106.

Mahood, Q., Van Eerd, D. and Irvin, E., 2014. Searching for grey literature for systematic reviews: challenges and benefits. *Research synthesis methods*, *5*(3), pp.221-234.

Mann, M.E., Zhang, Z., Rutherford, S., Bradley, R.S., Hughes, M.K., Shindell, D., Ammann, C., Faluvegi, G. and Ni, F., 2009. Global signatures and dynamical origins of the Little Ice Age and Medieval Climate Anomaly. *Science*, 326(5957), pp.1256-1260.

McKillop, H., 1996. Ancient Maya trading ports and the integration of long-distance and regional economies: Wild Cane Cay in south-coastal Belize. *Ancient Mesoamerica*, *7*(1), pp.49-62.

McNeil, C.L., Burney, D.A. and Burney, L.P., 2010. Evidence disputing deforestation as the cause for the collapse of the ancient Maya polity of Copan, Honduras. *Proceedings of the National Academy of Sciences*, 107(3), pp.1017-1022.

Medina-Elizalde, M., Burns, S.J., Lea, D.W., Asmerom, Y., von Gunten, L., Polyak, V., Vuille, M. and Karmalkar, A., 2010. High resolution stalagmite climate record from the Yucatán Peninsula spanning the Maya terminal classic period. *Earth and Planetary Science Letters*, 298(1-2), pp.255-262.

Metcalfe, S., Breen, A., Murray, M., Furley, P., Fallick, A. and McKenzie, A., 2009. Environmental change in northern Belize since the latest Pleistocene. *Journal of Quaternary Science*, 24(6), pp.627-641.

Metcalfe, S.E., Barron, J.A. and Davies, S.J., 2015. The Holocene history of the North American Monsoon:'known knowns' and 'known unknowns' in understanding its spatial and temporal complexity. *Quaternary Science Reviews,* 120, pp.1-27.

Moy, C.M., Seltzer, G.O., Rodbell, D.T. and Anderson, D.M., 2002. Variability of El Niño/Southern Oscillation activity at millennial timescales during the Holocene epoch. *Nature*, 420(6912), p.162.

Mueller, A.D., Islebe, G.A., Hillesheim, M.B., Grzesik, D.A., Anselmetti, F.S., Ariztegui, D., Brenner, M., Curtis, J.H., Hodell, D.A. and Venz, K.A., 2009. Climate drying and associated forest decline in the lowlands of northern Guatemala during the late Holocene. *Quaternary Research*, 71(2), pp.133-141.

Neff, H., Pearsall, D.M., Jones, J.G., Arroyo, B., Collins, S.K. and Freidel, D.E., 2006. Early Maya adaptive patterns: Mid-late Holocene paleoenvironmental evidence from Pacific Guatemala. *Latin American Antiquity*, 17(3), pp.287-315.

Nigh, R. and Diemont, S.A., 2013. The Maya milpa: fire and the legacy of living soil. *Frontiers in Ecology and the Environment*, 11(s1), pp.45-54.

Northrop, L.A. and Horn, S.P., 1996. PreColumbian agriculture and forest disturbance in Costa Rica: palaeoecological evidence from two lowland rainforest lakes. *The Holocene*, 6(3), pp.289-299.

Pérez, L., Bugja, R., Massaferro, J., Steeb, P., Geldern, R.V., Frenzel, P., Brenner, M., Scharf, B. and Schwalb, A., 2010. Post-Columbian environmental history of Lago Petén Itzá, Guatemala. *Revista Mexicana de Ciencias Geológicas*, 27(3).

Piperno, D.R., Bush, M.B. and Colinvaux, P.A., 1990. Paleoenvironments and human occupation in late-glacial Panama. *Quaternary Research*, 33(1), pp.108-116.

Piperno, D.R., Bush, M.B. and Colinvuax, P.A., 1991. Paleoecological perspectives on human adaptation in Central Panama. II The Holocene. *Geoarchaeology*, 6(3), pp.227-250.

Pollock, A.L., van Beynen, P.E., DeLong, K.L., Polyak, V., Asmerom, Y. and Reeder, P.P., 2016. A mid-Holocene paleoprecipitation record from Belize. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 463, pp.103-111.

Pohl, M.D., Pope, K.O., Jones, J.G., Jacob, J.S., Piperno, D.R., Lentz, D.L., Gifford, J.A., Danforth, M.E. and Josserand, J.K., 1996. Early agriculture in the Maya lowlands. *Latin American Antiquity*, 7(4), pp.355-372.

Pope, K.O., Pohl, M.E., Jones, J.G., Lentz, D.L., Von Nagy, C., Vega, F.J. and Quitmyer, I.R., 2001. Origin and environmental setting of ancient agriculture in the lowlands of Mesoamerica. *Science*, 292(5520), pp.1370-1373.

Poveda, G., Waylen, P.R. and Pulwarty, R.S., 2006. Annual and inter-annual variability of the present climate in northern South America and southern Mesoamerica. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 234(1), pp.3-27.

Rosenmeier, M.F., Hodell, D.A., Brenner, M., Curtis, J.H. and Guilderson, T.P., 2002a. A 4000-year lacustrine record of environmental change in the southern Maya lowlands, Peten, Guatemala. *Quaternary Research*, 57(2), pp.183-190.

Rosenmeier, M.F., Hodell, D.A., Brenner, M., Curtis, J.H., Martin, J.B., Anselmetti, F.S., Ariztegui, D. and Guilderson, T.P., 2002b. Influence of vegetation change on watershed hydrology: implications for paleoclimatic interpretation of lacustrine δ18O records. *Journal of Paleolimnology*, 27(1), pp.117-131.

Rue, D.J., 1987. Early agriculture and early Postclassic Maya occupation in western Honduras. *Nature*, 326(6110), pp.285-286.

Rue, D., Webster, D. and Traverse, A., 2002. Late Holocene fire and agriculture in the Copan Valley, Honduras. *Ancient Mesoamerica*, 13(2), pp.267-272.

Rushton, E.A., Metcalfe, S.E. and Whitney, B.S., 2013. A late-Holocene vegetation history from the Maya lowlands, Lamanai, Northern Belize. *The Holocene*, 23(4), pp.485-493.

Schüpbach, S., Kirchgeorg, T., Colombaroli, D., Beffa, G., Radaelli, M., Kehrwald, N.M. and Barbante, C., 2015. Combining charcoal sediment and molecular markers to infer a Holocene fire history in the Maya Lowlands of Petén, Guatemala. *Quaternary Science Reviews*, 115, pp.123-131.

Smith, M. E. (2003a). Key commodities. In M. E. Smith & F. F. Berdan (Eds.), The Postclassic Mesoamerican world (pp. 117–125). Salt Lake City: The University of Utah Press.

Smith, M. E. (2003b). Information networks in Postclassic Mesoamerica. In M. E. Smith & F. F. Berdan (Eds.), The Postclassic Mesoamerican world (pp. 181–185). Salt Lake City: The University of Utah Press.

Stansell, N.D., Steinman, B.A., Abbott, M.B., Rubinov, M. and Roman-Lacayo, M., 2013. Lacustrine stable isotope record of precipitation changes in Nicaragua during the Little Ice Age and Medieval Climate Anomaly. *Geology*, 41(2), pp.151-154.

Stansell, N.D., 2013. Radiocarbon ages for the timing of debris avalanches at Mombacho Volcano, Nicaragua. *Bulletin of volcanology*, *75*(1), p.686.

Timmermann, A., Okumura, Y., An, S.I., Clement, A., Dong, B., Guilyardi, E., Hu, A., Jungclaus, J.H., Renold, M., Stocker, T.F. and Stouffer, R.J., 2007. The influence of a weakening of the Atlantic meridional overturning circulation on ENSO. *Journal of climate*, 20(19), pp.4899-4919.

Thomson Reuter, 2018. Web of Science. Available at: http://apps.webofknowledge.com/. [Accessed 22 Aug. 2017].

Torrescano-Valle, N. and Islebe, G.A., 2015. Holocene paleoecology, climate history and human influence in the southwestern Yucatan Peninsula. *Review of Palaeobotany and Palynology*, 217, pp.1-8.

Urquhart, G.R., 2009. Paleoecological record of hurricane disturbance and forest regeneration in Nicaragua. *Quaternary International*, 195(1-2), pp.88-97.

Velez, M.I., Curtis, J.H., Brenner, M., Escobar, J., Leyden, B.W. and Popenoe de Hatch, M., 2011. Environmental and cultural changes in highland Guatemala inferred from Lake Amatitlán sediments. *Geoarchaeology*, 26(3), pp.346-364.

Villaseñor, I., 2010. Building Materials of the Ancient Maya: A Study of Archaeological Plasters.

Wahl, D., Byrne, R., Schreiner, T. and Hansen, R., 2006. Holocene vegetation change in the northern Peten and its implications for Maya prehistory. *Quaternary Research*, 65(3), pp.380-389.

Wahl, D., Byrne, R., Schreiner, T. and Hansen, R., 2007. Palaeolimnological evidence of late-Holocene settlement and abandonment in the Mirador Basin, Peten, Guatemala. *The Holocene*, 17(6), pp.813-820.

Wahl, D., Estrada-Belli, F. and Anderson, L., 2013. A 3400 year paleolimnological record of prehispanic human–environment interactions in the Holmul region of the southern Maya lowlands. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 379, pp.17-31.

Wahl, D., Byrne, R. and Anderson, L., 2014. An 8700 year paleoclimate reconstruction from the southern Maya lowlands. *Quaternary Science Reviews*, 103, pp.19-25.

Wahl, D., Hansen, R.D., Byrne, R., Anderson, L. and Schreiner, T., 2016. Holocene climate variability and anthropogenic impacts from Lago Paixban, a perennial wetland in Peten, Guatemala. *Global and Planetary Change*, 138, pp.70-81.

Wallace, B., 2018. Abstrackr. Available at: http://abstrackr.cebm.brown.edu/. [Accessed 9 Sep. 2017].

Walsh, M.K., Prufer, K.M., Culleton, B.J. and Kennett, D.J., 2014. A late Holocene paleoenvironmental reconstruction from Agua Caliente, southern Belize, linked to regional climate variability and cultural change at the Maya polity of Uxbenká. *Quaternary Research*, 82(1), pp.38-50.

Webster, J.W., Brook, G.A., Railsback, L.B., Cheng, H., Edwards, R.L., Alexander, C. and Reeder, P.P., 2007. Stalagmite evidence from Belize indicating significant droughts at the time of Preclassic Abandonment, the Maya Hiatus, and the Classic Maya collapse. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 250(1-4), pp.1-17.

White, C.D., 1999. Reconstructing Ancient Maya Diet. University of Utah Press.

2.9 Supplementary Information

Web of Knowledge:

# 4	**<u>6,600,002</u>**	TS= (Pollen OR Polen OR "Fossil pollen" OR "Polen fósil" OR "Macro charcoal" OR "Macro carbon" OR "Micro charcoal" OR "Micro carbon" OR Isotope OR Isótopo OR dO18 OR δO18 OR "Tree ring" OR "Anillo de árbol" OR phytolith OR Fitolito OR Chironomid OR Diatom OR Diatomea OR Ostracod OR XRF OR "X-ray fluorescence" OR "Fluorescencia de rayos X" OR Geochemistry OR Geoquímica OR "Loss on ignition" OR "Pérdida por ignición" OR LOI OR Coleoptera OR Coleóptero OR "Magnetic Susceptibility" OR "Susceptibilidad magnética" OR "Sporormiella" OR "dung fungal spores" OR "Estiércol de hongos estiércol" OR Macrofossil OR Macrofósil OR Vegetation OR Vegetación OR Burning OR Fuego OR Plant OR Planta OR Tree OR Árbole OR Shrub OR Arbusto OR Herb OR Hierba OR Recovery OR Recuperación OR Resilience OR Resistencia OR Disturbance OR Disturbio OR Reconstruction OR Reconstrucción OR "Land use" OR "Uso del tierra" OR Human OR Humano OR Civilization OR Civilización) Indexes=SCI-EXPANDED, SSCI, A&HCI, CPCI-S, CPCI-SSH, BKCI-S, BKCI-SSH, ESCI, CCR-EXPANDED, IC Timespan=All years
# 3	**<u>1,920,853</u>**	TS= (Holocene OR Holoceno OR "Little Ice Age" OR "Pequeña Edad de Hielo" OR LIA OR "Medieval Climate Anomaly" OR "Anomalía del clima medieval" OR MCA OR "Medieval Warm Period" OR "Periodo cálido medieval" OR MWP OR "Palaeo Indian" OR Archaic OR Arcaico OR "Early Preclassic" OR "Preclásico Temprano" OR "Middle Preclassic" OR "Preclásico Medio" OR "Late Preclassic" OR "Preclásico Tardío" OR "Early Classic" OR "Clásico Temprano" OR "Late Classic" OR "Clásico Tardío" OR "Terminal Classic" OR "Clásico Terminal" OR "Early Post Classic" OR "Posclásico Temprano" OR "Late Post Classic" OR "Posclásico Tardío" OR "Colonial Period" OR "Spanish Conquest" OR "Conquista Española" OR "Periodo de contacto" OR "Independent Mexico" OR "México Independiente" OR "Time series" OR "Series de tiempo" OR Temporal OR Chronology OR Cronología OR Chron OR Cron OR Anthropocene OR Antropoceno OR History OR Historia OR Prehistory OR Prehistoria OR Quaternary OR Cuaternario) Indexes=SCI-EXPANDED, SSCI, A&HCI, CPCI-S, CPCI-SSH, BKCI-S, BKCI-SSH, ESCI, CCR-EXPANDED, IC Timespan=All years

# 2	**3,117,485**	TS= (Lake OR Lago OR Bog OR Pantano OR Swamp OR Pantano OR Cave OR Cueva OR Estuary OR Estuario OR Dendro OR Terrestrial OR Terrestre OR Marine OR Marina OR “Closed basin” OR “Cuenca Cerrada” OR “Open basin” OR “Cuenca abierta” OR Fluvial OR Aeolian OR Eólico OR Speleothem OR Core OR Núcleo OR Sediment OR Sedimento OR Midden OR Muladar OR Limnology OR Limnología OR Climatology OR Climatología OR Dendrochronology OR Dendrocronología OR Dendroclimatology OR Dendroclimatología OR Palaeo OR Paleo OR Climatology OR Climatología OR Ecological OR Ecológico OR Ecology OR Ecología OR Environment OR Ambiente OR Palynological OR Palynology OR Palaeoecology OR Paleoecology) Indexes=SCI-EXPANDED, SSCI, A&HCI, CPCI-S, CPCI-SSH, BKCI-S, BKCI-SSH, ESCI, CCR-EXPANDED, IC Timespan=All years
# 1	**421,267**	TS= (“Central America” OR Centroamérica OR Mesoamerica OR Mesoamérica OR Mexico OR Méjico OR Tabasco OR Chipas OR Campeche OR Yucatan OR Yucatán OR “Quintana Roo” OR Belize OR Belice OR Cayo OR Corozal OR “Orange Walk” OR “Stann Creek” OR Toledo OR Guatemala OR “Alta Verapaz” OR “Baja Verapaz” OR Chimaltenango OR Chiquimula OR “El Petén” OR “El Progreso” OR “El Quiché” OR Escuintla OR Huehuetenango OR Izabal OR Jalapa OR Jutiapa OR Quetzaltenango OR Retalhuleu OR Sacatepéquez OR “San Marcos” OR “Santa Rosa” OR Sololá OR Suchitepéquez OR Totonicapán OR Zacapa OR “El Salvador” OR “La Union” OR “San Miguel” OR “La Libertad” OR “Santa Ana” OR Usulután OR Ahuachapan OR Chalatenango OR Sonsonate OR Morazan OR “La Paz” OR “San Salvador” OR Cuscatlán OR Cabañas OR “San Vicente” OR Honduras OR Francisco OR Morazan OR Choluteca OR “El Paraiso” OR Lempira OR Olancho OR “Santa Bárbara” OR “La Paz” OR Copan OR Valle OR Comayagua OR Yoro OR Intibuca OR Cortes OR Colón OR Ocotepeque OR “Gracias a Dios” OR Atlántida OR “Islas de la Bahia” OR Nicaragua OR Nicoya OR Boaco OR Carazo OR Chinandega OR Chontales OR Estelí OR Granada OR Jinotega OR León OR Madriz OR Managua OR Masaya OR Matagalpa OR “Nueva Segovia” OR Rivas OR “Río San Juan” OR “Costa Caribe Norte” OR “North Caribbean Coast” OR “Costa Caribe Sur” OR “South Caribbean Coast” OR “Costa Rica” OR Alajuela OR Cartago OR Guanacaste OR Heredia OR Limón OR Puntarenas OR “San Jose” OR Panama OR Panamá OR Veraguas OR Chiriqui OR “Los Santos” OR Cocle OR Herrera OR “Bocas del Toro” OR Darien OR “Kuna Yala” OR “Panamá Oeste” OR “Panama West”)

Indexes=SCI-EXPANDED, SSCI, A&HCI, CPCI-S, CPCI-SSH, BKCI-S, BKCI-SSH, ESCI, CCR-EXPANDED, IC Timespan=All years

Scopus:

(TITLE-ABS-KEY ("Central America" OR centroamérica OR mesoamerica OR mesoamérica OR mexico OR méjico OR tabasco OR chipas OR campeche OR yucatan OR yucatán OR "Quintana Roo" OR belize OR belice OR cayo OR corozal OR "Orange Walk" OR "Stann Creek" OR toledo OR guatemala OR "Alta Verapaz" OR "Baja Verapaz" OR chimaltenango OR chiquimula OR "El Petén" OR "El Progreso" OR "El Quiché" OR escuintla OR huehuetenango OR izabal OR jalapa OR jutiapa OR quetzaltenango OR retalhuleu OR sacatepéquez OR "San Marcos" OR "Santa Rosa" OR sololá OR suchitepéquez OR totonicapán OR zacapa OR " El Salvador" OR "La Union" OR "San Miguel" OR "La Libertad" OR "Santa Ana" OR usulután OR ahuachapan OR chalatenango OR sonsonate OR morazan OR "La Paz" OR "San Salvador" OR cuscatlán OR cabañas OR "San Vicente" OR honduras OR francisco OR morazan OR choluteca OR "El Paraiso" OR lempira OR olancho OR "Santa Bárbara" OR "La Paz" OR copan OR valle OR comayagua OR yoro OR intibuca OR cortes OR colón OR ocotepeque OR "Gracias a Dios" OR atlántida OR "Islas de la Bahia" OR nicaragua OR nicoya OR boaco OR carazo OR chinandega OR chontales OR estelí OR granada OR jinotega OR león OR madriz OR managua OR masaya OR matagalpa OR "Nueva Segovia" OR rivas OR "Río San Juan" OR "Costa Caribe Norte" OR "North Caribbean Coast" OR "Costa Caribe Sur" OR "South Caribbean Coast" OR "Costa Rica" OR alajuela OR cartago OR guanacaste OR heredia OR limón OR puntarenas OR "San Jose" OR panama OR panamá OR veraguas OR chiriqui OR "Los Santos" OR cocle OR herrera OR "Bocas del Toro" OR darien OR "Kuna Yala" OR "Panamá Oeste" OR "Panama West")

TITLE-ABS-KEY (lake OR lago OR bog OR pantano OR swamp OR pantano OR cave OR cueva OR estuary OR estuario OR dendro OR terrestrial OR terrestre OR marine OR marina OR "Closed basin" OR "Cuenca Cerrada" OR "Open basin" OR "Cuenca abierta" OR fluvial OR aeolian OR eólico OR speleothem OR core OR núcleo OR sediment OR sedimento OR midden OR muladar OR limnology OR limnología OR climatology OR climatología OR dendrochronology OR dendrocronología OR dendroclimatology OR dendroclimatología OR palaeo OR paleo OR climatology OR climatología OR ecological OR ecológico OR ecology OR ecología OR environment OR ambiente OR palynological OR palynology OR palaeoecology OR paleoecology)

TITLE-ABS-KEY (holocene OR holoceno OR "Little Ice Age" OR "Pequeña Edad de Hielo" OR lia OR "Medieval Climate Anomaly" OR "Anomalía del clima medieval" OR mca OR "Medieval Warm Period" OR "Periodo cálido medieval" OR mwp OR "Palaeo Indian" OR archaic OR arcaico OR "Early Preclassic" OR "Preclásico Temprano" OR "Middle Preclassic" OR "Preclásico Medio" OR "Late Preclassic" OR "Preclásico Tardío" OR "Early Classic" OR "Clásico Temprano" OR "Late Classic" OR "Clásico Tardío" OR "Terminal Classic" OR "Clásico Terminal" OR "Early Post Classic" OR "Posclásico Temprano" OR "Late Post Classic" OR "Posclásico Tardío" OR "Colonial Period" OR "Spanish Conquest" OR "Conquista Española" OR "Periodo de contacto" OR "Independent Mexico" OR "México Independiente" OR "Time series" OR "Series de tiempo" OR temporal OR chronology OR cronología OR chron OR c ron OR anthropocene OR antropoceno OR history OR historia OR pr ehistory OR prehistoria OR quaternary OR cuaternario)) AND (

TITLE-ABS-KEY (pollen OR polen OR "Fossil pollen" OR "Polen fósil" OR "Macro charcoal" OR "Macro carbon" OR "Micro charcoal" OR "Micro carbon" OR isotope OR isótopo OR do18 OR δo18 OR "Tree ring" OR "Anillo de árbol" OR phytolith OR Fitolito OR

chironomid OR diatom OR diatomea OR ostracod OR xrf OR "X-ray fluorescence" OR "Fluorescencia de rayos X" OR geochemistry OR geoquímica OR "Loss on ignition" OR "Pérdida por ignición" OR loi OR coleoptera OR coleóptero OR "Magnetic Susceptibility" OR "Susceptibilidad magnética" OR "Sporormiella" OR "dung fungal spores" OR "Estiércol de hongos estiércol" OR macrofossil OR macrofósil OR vegetation OR vegetación OR burni ng OR fuego OR plant OR planta OR tree OR árbole OR shrub OR arbusto O R herb OR hierba OR recovery OR recuperación OR resilience OR resistencia O R disturbance OR disturbio OR reconstruction OR reconstrucción OR "Land use" OR "Uso del tierra" OR human OR humano OR civilization OR civilización))

CAB Abstracts:

"Central America" OR centroamerica OR mesoamerica OR mexico OR mejico OR tabasco OR chipas OR campeche OR yucatan OR "Quintana Roo" OR belize OR belice OR cayo OR corozal OR "Orange Walk" OR "Stann Creek" OR toledo OR guatemala OR "Alta Verapaz" OR "Baja Verapaz" OR chimaltenango OR chiquimula OR "El Peten" OR "El Progreso" OR "El Quiche" OR escuintla OR huehuetenango OR izabal OR jalapa OR jutiapa OR quetzaltenango OR retalhuleu OR sacatepequez OR "San Marcos" OR "Santa Rosa" OR solola OR suchitepequez OR totonicapan OR zacapa OR "El Salvador" OR "La Union" OR "San Miguel" OR "La Libertad" OR "Santa Ana" OR usulutan OR ahuachapan OR chalatenango OR sonsonate OR morazan OR "La Paz" OR "San Salvador" OR cuscatlan OR cabanas OR "San Vicente" OR honduras OR francisco OR morazan OR choluteca OR "El Paraiso" OR lempira OR olancho OR "Santa Barbara" OR "La Paz" OR copan OR valle OR comayagua OR yoro OR intibuca OR cortes OR colon OR ocotepeque OR "Gracias a Dios" OR atlantida OR "Islas de la Bahia" OR nicaragua OR nicoya OR boaco OR carazo OR chinandega OR chontales OR esteli OR granada OR jinotega OR leon OR madriz OR managua OR masaya OR matagalpa OR "Nueva Segovia" OR rivas OR "Rio San Juan" OR "Costa Caribe Norte" OR "North Caribbean Coast" OR "Costa Caribe Sur" OR "South Caribbean Coast" OR "Costa Rica" OR alajuela OR cartago OR guanacaste OR heredia OR limon OR puntarenas OR "San Jose" OR panama OR veraguas OR chiriqui OR "Los Santos" OR cocle OR herrera OR "Bocas del Toro" OR darien OR "Kuna Yala" OR "Panama Oeste" OR "Panama West"

lake OR lago OR bog OR pantano OR swamp OR pantano OR cave OR cueva OR estuary OR estuario OR dendro OR terrestrial OR terrestre OR marine OR marina OR "Closed basin" OR "Cuenca Cerrada" OR "Open basin" OR "Cuenca abierta" OR fluvial OR aeolian OR eolico OR speleothem OR core OR nucleo OR sediment OR sedimento OR midden OR muladar OR limnology OR limnologia OR climatology OR climatologia OR dendrochronology OR dendrocronologia OR dendroclimatology OR dendroclimatologia OR palaeo OR paleo OR climatology OR climatologia OR ecological OR ecologico OR ecology OR ecologia OR environment OR ambiente OR palynological OR palynology OR palaeoecology OR paleoecology

holocene OR holoceno OR "Little Ice Age" OR "Pequena Edad de Hielo" OR lia OR "Medieval Climate Anomaly" OR "Anomalia del clima medieval" OR mca OR "Medieval Warm Period" OR "Periodo calido medieval" OR mwp OR "Palaeo Indian" OR archaic OR arcaico OR "Early Preclassic" OR "Preclasico Temprano" OR "Middle Preclassic" OR "Preclasico Medio" OR "Late Preclassic" OR "Preclasico Tardio" OR "Early Classic" OR "Clasico Temprano" OR "Late Classic" OR "Clasico Tardio" OR "Terminal Classic" OR "Clasico Terminal" OR "Early Post Classic" OR "Posclasico Temprano" OR "Late Post Classic" OR "Posclasico

Tardio" OR "Colonial Period" OR "Spanish Conquest" OR "Conquista Espanola" OR "Periodo de contacto" OR "Independent Mexico" OR "Mexico Independiente" OR "Time series" OR "Series de tiempo" OR temporal OR chronology OR cronologia OR chron OR cron OR anthropocene OR antropoceno OR history OR historia OR prehistory OR prehistoria OR quaternary OR cuaternario

pollen OR polen OR "Fossil pollen" OR "Polen fosil" OR "Macro charcoal" OR "Macro carbon" OR "Micro charcoal" OR "Micro carbon" OR isotope OR isotopo OR do18 OR "Tree ring" OR "Anillo de arbol" OR chironomid OR diatom OR diatomea OR ostracod OR xrf OR "X-ray fluorescence" OR "Fluorescencia de rayos X" OR geochemistry OR geoquimica OR "Loss on ignition" OR "Perdida por ignicion" OR loi OR coleoptera OR coleoptero OR "Magnetic Susceptibility" OR "Susceptibilidad magnetica" OR "Sporormiella" OR "dung fungal spores" OR "Estiercol de hongos estiercol" OR macrofossil OR macrofosil OR vegetation OR vegetacion OR burning OR fuego OR plant OR planta OR tree OR arbole OR shrub OR arbusto OR herb OR hierba OR recovery OR recuperacion OR resilience OR resistencia OR disturbance OR disturbio OR reconstruction OR reconstruccion OR "Land use" OR "Uso del tierra" OR human OR humano OR civilization OR civilizacion

Test Library

Anderson, L. and Wahl, D., 2016. Two Holocene paleofire records from Peten, Guatemala: Implications for natural fire regime and prehispanic Maya land use. *Global and Planetary Change*, 138, pp.82-92.

Avnery, S., Dull, R.A. and Keitt, T.H., 2011. Human versus climatic influences on late-Holocene fire regimes in southwestern Nicaragua. *The Holocene*, 21(4), pp.699-706.

Bush, M.B. and Colinvaux, P.A., 1994. Tropical forest disturbance: paleoecological records from Darien, Panama. *Ecology*, 75(6), pp.1761-1768.

Clement, R.M. and Horn, S.P., 2001. Pre-Columbian land-use history in Costa Rica: a 3000-year record of forest clearance, agriculture and fires from Laguna Zoncho. *The Holocene*, 11(4), pp.419-426.

Correa- Metrio, A., Vélez, M.I., Escobar, J., St- Jacques, J.M., López- Pérez, M., Curtis, J. and Cosford, J., 2016. Mid- elevation ecosystems of Panama: future uncertainties in light of past global climatic variability. *Journal of Quaternary Science*, 31(7), pp.731-740.

Dull, R.A., 2004. A Holocene record of Neotropical savanna dynamics from El Salvador. *Journal of Paleolimnology*, 32(3), pp.219-231.

Dull, R.A., 2004. An 8000-year record of vegetation, climate, and human disturbance from the Sierra de Apaneca, El Salvador. *Quaternary Research*, 61(2), pp.159-167.

Hillesheim, M.B., Hodell, D.A., Leyden, B.W., Brenner, M., Curtis, J.H., Anselmetti, F.S., Ariztegui, D., Buck, D.G., Guilderson, T.P., Rosenmeier, M.F. and Schnurrenberger, D.W., 2005. Climate change in lowland Central America during the late deglacial and early Holocene. *Journal of Quaternary Science*, 20(4), pp.363-376.

Horn, S.P., Rodgers III, J.C., Orvis, K.H. and Northrop, L.A., 1998. Recent land use and vegetation history from soil pollen analysis: testing the potential in the lowland humid tropics. *Palynology*, 22(1), pp.167-180.

Islebe, G.A. and Hooghiemstra, H., 1997. Vegetation and climate history of montane Costa Rica since the last glacial. *Quaternary Science Reviews*, 16(6), pp.589-604.

Lachniet, M.S., Burns, S.J., Piperno, D.R., Asmerom, Y., Polyak, V.J., Moy, C.M. and Christenson, K., 2004. A 1500- year El Niño/Southern Oscillation and rainfall history for the isthmus of Panama from speleothem calcite. *Journal of Geophysical Research: Atmospheres*, 109(D20).

Metcalfe, S., Breen, A., Murray, M., Furley, P., Fallick, A. and McKenzie, A., 2009. Environmental change in northern Belize since the latest Pleistocene. *Journal of Quaternary Science*, 24(6), pp.627-641.

Neff, H., Pearsall, D.M., Jones, J.G., Arroyo, B., Collins, S.K. and Freidel, D.E., 2006. Early Maya adaptive patterns: Mid-late Holocene paleoenvironmental evidence from Pacific Guatemala. *Latin American Antiquity*, 17(3), pp.287-315.

Piperno, D.R., Bush, M.B. and Colinvaux, P.A., 1990. Paleoenvironments and human occupation in late-glacial Panama. *Quaternary Research*, 33(1), pp.108-116.

Piperno, D.R., Bush, M.B. and Colinvuax, P.A., 1991. Paleoecological perspectives on human adaptation in Central Panama. II The Holocene. *Geoarchaeology*, 6(3), pp.227-250.

Pohl, M.D., Pope, K.O., Jones, J.G., Jacob, J.S., Piperno, D.R., Lentz, D.L., Gifford, J.A., Danforth, M.E. and Josserand, J.K., 1996. Early agriculture in the Maya lowlands. *Latin American Antiquity*, 7(4), pp.355-372.

Slate, J.E., Johnson, T.C. and Moore, T.C., 2013. Impact of pre-Columbian agriculture, climate change, and tectonic activity inferred from a 5,700-year paleolimnological record from Lake Nicaragua. *Journal of paleolimnology*, 50(1), pp.139-149.

Taylor, Z.P., Horn, S.P. and Finkelstein, D.B., 2013. Maize pollen concentrations in Neotropical lake sediments as an indicator of the scale of prehistoric agriculture. *The Holocene*, 23(1), pp.78-84.

Urquhart, G.R., 2009. Paleoecological record of hurricane disturbance and forest regeneration in Nicaragua. *Quaternary International*, 195(1-2), pp.88-97.

Wahl, D., Hansen, R.D., Byrne, R., Anderson, L. and Schreiner, T., 2016. Holocene climate variability and anthropogenic impacts from Lago Paixban, a perennial wetland in Peten, Guatemala. *Global and Planetary Change*, 138, pp.70-81.

Whitmore, T.J., Brenner, M., Curtis, J.H., Dahlin, B.H. and Leyden, B.W., 1996. Holocene climatic and human influences on lakes of the Yucatan Peninsula, Mexico: an interdisciplinary, palaeolimnological approach. *The Holocene*, 6(3), pp.273-287.

Table 2.5 Sites represented in Figures 2.5, 2.7, 2.9, & 2.10

δ18O			
Name of Site	Longitude	Latitude	Reference
Tzabnah	20.75	-89.4667	Medina-Elizalde et al. 2010
Punta Laguna	20.64849	-87.6372	Curtis et al. 1996; Hodell et al. 2007
Aguada X'caamal	20.60167	-89.7025	Hodell et al. 2005
Laberinto del Fauno	20.5874	-87.134	Medina-Elizalde et al. 2016
La Vaca Perdida	20.37297	-89.5692	Smyth et al. 2017
Cenote Aktun Ha	20.27429	-87.4862	Gabriel et al. 2009
Lago Chichancanab	19.87	-88.77	Hodell et al. 1995; 2001
Lago Tzib	19.29693	-88.0701	Carrillo-Bastos et al. 2010
Lamanai	17.76333	-88.6519	Metcalfe et al. 2009
Hillbank	17.59937	-88.6992	Metcalfe et al. 2009
Lago Puerto Arturo	17.53333	-90.1833	Wahl, 2014; Anderson & Wahl, 2016
Actun Tunichil Muknal	17.11719	-88.8906	Frappier et al. 2007; Frappier, 2013
Chen Ha Cave	17	-89	Pollock et al. 2016
Lago Peten Itza	17	-89.779	Curtis et al. 1998; Hillesheim et al. 2005; Mueller et al. 2009; Perez et al. 2010; Escobar et al. 2012
Lago Salpeten	16.98567	-89.6744	Rosenmeier et al. 2002a; 2002b
Macal Chasm	16.883	-89.108	Webster et al. 2007; Akers et al. 2016
Yok Balum	16.20833	-89.0733	Kennett et al. 2012
El Gancho	11.906	-85.918	Stansell et al. 2013
Venado Cave	10.55475	-84.7684	Lachniet et al. 2004a
Terciopelo Cave	10.16667	-85.3333	Lachniet et al. 2009
Chilibrillo Cave	9.2	-79.7	Lachniet et al. 2004b
Charcoal			
Ria Lagartos Biosphere Reserve	21.57944	-88.0722	Aragón-Moreno et al. 2012
Cobweb Swamp	18.41948	-88.5161	Pohl et al. 1996
Lago Paixban	17.8	-90.1167	Anderson & Wahl, 2016
Aguada Zacatal Nakbe	17.66907	-89.7928	Wahl et al. 2007a
New River Lagoon	17.66667	-88.6667	Rushton et al. 2013
Lago Puerto Arturo	17.53333	-90.1833	Anderson & Wahl, 2016
Laguna Yaloch	17.30972	-89.1747	Wahl et al. 2013

El Palmar	17.22809	-89.7615	Luzzadder-Beach et al. 2017
Lago Peten Itza	17	-89.5	Correa-Metrio et al. 2012; Schüpbach et al. 2015
Aguada Chimj	16.85	-90.1333	Brenner et al. 1990
Aguada Chilonche	16.8	-90.0333	Brenner et al. 1990
Lago Oquevix	16.64869	-89.7502	Brenner et al. 1990
Agua Caliente	16.16667	-89	Walsh et al. 2014
Miqul Meadow	15.42344	-91.4387	Caffrey et al. 2011
Aguada Petapilla	14.867	-89.125	Rue et al. 2002
Lower Rio Naranjo	14.5405	-92.1889	Neff et al. 2006
Manchon	14.51711	-92.1188	Neff et al. 2006
Laguna Cuzcachapa	13.98323	-89.6713	Dull, 2007
Sipacate	13.94102	-90.6297	Neff et al. 2006
Laguna Verde	13.85417	-89.8856	Dull, 2004a
Laguna del Espino	13.57	-89.52	Dull, 2004b
Laguna Negra	12.04514	-83.9276	Urquhart, 2009
Charco Verde	11.47757	-85.6326	Avnery et al. 2011
Cantarrana	10.43972	-84.0067	Kennedy & Horn, 2008
Bonillita	9.994167	-83.6131	Northrop & Horn, 1996
Lago de las Morrenas	9.494794	-83.4867	Horn, 1993; League & Horn, 2000; Lane et al. 2011
Laguna Santa Elena	8.933333	-82.9333	Anchukaitis & Horn, 2005
Laguna Zoncho	8.813	-82.963	Clement & Horn, 2001
Lago San Carlos	8.625678	-80.0512	Correa- Metrio et al. 2016
Lago La Yeguada	8.45	-80.85	Piperno et al. 1990; 1991
Pollen			
Ria Lagartos Biosphere Reserve	21.57944	-88.0722	Aragón-Moreno et al. 2012
Puerto Morelos	20.84907	-86.8784	Islebe & Sanchez, 2002
Coba	20.49151	-87.7387	Leyden et al. 1998
Cenote Aktun Ha	20.27429	-87.4862	Gabriel et al. 2009
Biosphere Reserve of Los Petenes	20.13125	-90.4546	Gutiérrez-Ayala et al. 2012
Lago Tzib	19.29693	-88.0701	Carrillo-Bastos et al. 2010
El Palmar	18.44667	-88.5297	Torrescano & Islebe, 2006
Lago Silvituc	18.372	-90.2948	Torrescano & Islebe, 2015
San Andres	18.14063	-93.9886	Pope et al. 2001

Cobweb Swamp	17.93772	-88.3664	Jones, 1994; Pohl et al. 1996
Lago Paixban	17.8	-90.1167	Wahl et al. 2016; Anderson & Wahl, 2016
Aguada Zacatal Nakbe	17.66907	-89.7928	Wahl et al. 2007a
New River Lagoon	17.66667	-88.6667	Rushton et al. 2013
Lago Puerto Arturo	17.53333	-90.1833	Wahl et al. 2006; 2007b; 2014; Anderson & Wahl, 2016
Sibun River	17.47205	-88.2609	Monacci et al. 2011
Laguna Yaloch	17.30972	-89.1747	Wahl et al. 2013
El Palmar	17.22809	-89.7615	Luzzadder- Beach et al. 2017
Lago Yaxha	17.06255	-89.4053	Deevey et al. 1979
Lago Sacnab	17.06141	-89.3636	Deevey et al. 1979
Lago Peten Itza	17	-89.5	Islebe et al. 1996a; Curtus et al. 1998; Hillesheim et al. 2005; Mueller et al. 2009; 2010; Correa-Metrio et al. 2012
Lago Naja	16.991	-91.5916	Domínguez-Vázquez & Islebe, 2008
Lago Salpeten	16.98333	-89.6667	Leyden, 1987
Aguada Chimj	16.85	-90.1333	Brenner et al. 1990
Aguada Chilonche	16.8	-90.0333	Brenner et al. 1990
Lago Oquevix	16.64869	-89.7502	Brenner et al. 1990
Laguana las Pozas	16.2	-90.1	Johnston et al. 2001
Agua Caliente	16.16667	-89	Walsh et al. 2014
Miqul Meadow	15.42344	-91.4387	Caffrey et al. 2011
La Encrucijada Biosphere Reserve	15.14967	-92.751	Joo-Chang et al. 2015
Lago Yojoa	14.87372	-87.9838	Rue, 1987
Aguada Petapilla	14.867	-89.125	McNeil et al. 2010
Lower Rio Naranjo	14.5405	-92.1889	Rue et al. 2002
Lower Rio Naranjo	14.53871	-92.2023	Neff et al. 2006
Manchon	14.51711	-92.1188	Neff et al. 2006
Lago Amatitlan	14.45639	-90.5661	Velez et al. 2011
Laguna Cuzcachapa	13.98323	-89.6713	Dull, 2007
Sipacate	13.94102	-90.6297	Neff et al. 2006
Laguna Verde	13.85417	-89.8856	Dull, 2004a
Laguna del Espino	13.57	-89.52	Dull, 2004b
Falso Bluff Marsh	12.08769	-83.7001	McCloskey & Liu, 2012
Laguna Negra	12.04514	-83.9276	Urquhart, 2009
Cantarrana	10.43972	-84.0067	Kennedy & Horn, 2008

La Selva Biological Station	10.43333	-83.9833	Horn & Kennedy, 2001
Bonillita	9.994167	-83.6131	Northrop & Horn, 1996
Trinidad	9.833333	-84	Islebe et al. 1996b; Islebe & Hooghiemstra, 1997
La Chonta	9.683333	-83.95	Hooghiemstra et al. 1992; Islebe & Hooghiemstra, 1995; 1997
Lago de las Morrenas	9.483333	-83.4833	Horn, 1993; Lane et al. 2011
Bocas del Toro	9.333333	-82.3333	Phillips et al. 1997
Laguna Zoncho	8.813	-82.963	Clement & Horn, 2001
Monte Oscuro	8.705533	-79.7625	Piperno & Jones, 2003
Lago San Carlos	8.625678	-80.0512	Correa- Metrio et al. 2016
Lago La Yeguada	8.45	-80.85	Piperno et al. 1990; 1991; Bush et al. 1992
Cana Swamp	7.75	-77.5833	Bush & Colinvaux, 1994
Lago Wodehouse	7.75	-77.5833	Bush & Colinvaux, 1994

References

Akers, P.D., Brook, G.A., Railsback, L.B., Liang, F., Iannone, G., Webster, J.W., Reeder, P.P., Cheng, H. and Edwards, R.L., 2016. An extended and higher-resolution record of climate and land use from stalagmite MC01 from Macal Chasm, Belize, revealing connections between major dry events, overall climate variability, and Maya sociopolitical changes. *Palaeogeography, palaeoclimatology, palaeoecology*, 459, pp.268-288.

Anchukaitis, K.J. and Horn, S.P., 2005. A 2000-year reconstruction of forest disturbance from southern Pacific Costa Rica. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 221(1-2), pp.35-54.

Anderson, L. and Wahl, D., 2016. Two Holocene paleofire records from Peten, Guatemala: Implications for natural fire regime and prehispanic Maya land use. *Global and Planetary Change*, 138, pp.82-92.

Aragón-Moreno, A.A., Islebe, G.A. and Torrescano-Valle, N., 2012. A~ 3800-yr, high-resolution record of vegetation and climate change on the north coast of the Yucatan Peninsula. *Review of palaeobotany and palynology*, 178, pp.35-42.

Avnery, S., Dull, R.A. and Keitt, T.H., 2011. Human versus climatic influences on late-Holocene fire regimes in southwestern Nicaragua. *The Holocene*, 21(4), pp.699-706.

Brenner, M., Leyden, B. and Binford, M.W., 1990. Recent sedimentary histories of shallow lakes in the Guatemalan savannas. *Journal of Paleolimnology*, 4(3), pp.239-252.

Bush, M.B., Piperno, D.R., Colinvaux, P.A., De Oliveira, P.E., Krissek, L.A., Miller, M.C. and Rowe, W.E., 1992. A 14 300- Yr Paleoecological Profile of a Lowland Tropical Lake in Panama. *Ecological Monographs*, 62(2), pp.251-275.

Bush, M.B. and Colinvaux, P.A., 1994. Tropical forest disturbance: paleoecological records from Darien, Panama. *Ecology*, 75(6), pp.1761-1768.

Caffrey, M.A., Taylor, M.J. and Sullivan, D.G., 2011. A 12,000-year Record of Vegetation and Climate Change from the Sierra de Los Cuchumatanes, Guatemala. *Journal of Latin American Geography*, 10(2), pp.129-151.

Carrillo-Bastos, A., Islebe, G.A., Torrescano-Valle, N. and González, N.E., 2010. Holocene vegetation and climate history of central Quintana Roo, Yucatán Península, Mexico. *Review of Palaeobotany and Palynology*, 160(3-4), pp.189-196.

Clement, R.M. and Horn, S.P., 2001. Pre-Columbian land-use history in Costa Rica: a 3000-year record of forest clearance, agriculture and fires from Laguna Zoncho. *The Holocene*, 11(4), pp.419-426.

Correa-Metrio, A., Bush, M.B., Cabrera, K.R., Sully, S., Brenner, M., Hodell, D.A., Escobar, J. and Guilderson, T., 2012. Rapid climate change and no-analog vegetation in lowland Central America during the last 86,000 years. *Quaternary Science Reviews*, 38, pp.63-75.

Correa- Metrio, A., Vélez, M.I., Escobar, J., St- Jacques, J.M., López- Pérez, M., Curtis, J. and Cosford, J., 2016. Mid- elevation ecosystems of Panama: future uncertainties in light of past global climatic variability. *Journal of Quaternary Science*, 31(7), pp.731-740.

Curtis, J.H., Hodell, D.A. and Brenner, M., 1996. Climate variability on the Yucatan Peninsula (Mexico) during the past 3500 years, and implications for Maya cultural evolution. *Quaternary Research*, 46(1), pp.37-47.

Curtis, J.H., Brenner, M., Hodell, D.A., Balser, R.A., Islebe, G.A. and Hooghiemstra, H., 1998. A multi-proxy study of Holocene environmental change in the Maya lowlands of Peten, Guatemala. *Journal of paleolimnology*, 19(2), pp.139-159.

Deevey, E., Rice, D.S., Rice, P.M., Vaughan, H.H., Brenner, M. and Flannery, M.S., 1979. Mayan urbanism: impact on a tropical karst environment. *Science*, 206(4416), pp.298-306.

Domínguez-Vázquez, G. and Islebe, G.A., 2008. Protracted drought during the late Holocene in the Lacandon rain forest, Mexico. *Vegetation History and Archaeobotany*, 17(3), pp.327-333.

Dull, R.A., 2004a. An 8000-year record of vegetation, climate, and human disturbance from the Sierra de Apaneca, El Salvador. *Quaternary Research*, 61(2), pp.159-167.

Dull, R.A., 2004b. A Holocene record of Neotropical savanna dynamics from El Salvador. Journal of Paleolimnology, 32(3), pp.219-231.

Dull, R.A., 2007. Evidence for Forest Clearance, Agriculture, and Human- Induced Erosion in Precolumbian El Salvador. Annals of the Association of American Geographers, 97(1), pp.127-141.

Escobar, J., Hodell, D.A., Brenner, M., Curtis, J.H., Gilli, A., Mueller, A.D., Anselmetti, F.S., Ariztegui, D., Grzesik, D.A., Pérez, L. and Schwalb, A., 2012. A∼ 43-ka record of paleoenvironmental change in the Central American lowlands inferred from stable isotopes of lacustrine ostracods. Quaternary Science Reviews, 37, pp.92-104.

Frappier, A.B., Sahagian, D., Carpenter, S.J., González, L.A. and Frappier, B.R., 2007. Stalagmite stable isotope record of recent tropical cyclone events. Geology, 35(2), pp.111-114.

Frappier, A.B., 2013. Masking of interannual climate proxy signals by residual tropical cyclone rainwater: Evidence and challenges for low- latitude speleothem paleoclimatology. Geochemistry, Geophysics, Geosystems, 14(9), pp.3632-3647.

Gabriel, J.J., Reinhardt, E.G., Peros, M.C., Davidson, D.E., van Hengstum, P.J. and Beddows, P.A., 2009. Palaeoenvironmental evolution of Cenote Aktun Ha (Carwash) on the Yucatan Peninsula, Mexico and its response to Holocene sea-level rise. Journal of Paleolimnology, 42(2), pp.199-213.

Gutiérrez-Ayala, L.V., Torrescano-Valle, N. and Islebe, G.A., 2012. Reconstrucción paleoambiental del Holoceno tardío de la reserva Los Petenes, Península de Yucatán, México. Revista mexicana de ciencias geológicas, 29(3), pp.749-763.

Hillesheim, M.B., Hodell, D.A., Leyden, B.W., Brenner, M., Curtis, J.H., Anselmetti, F.S., Ariztegui, D., Buck, D.G., Guilderson, T.P., Rosenmeier, M.F. and Schnurrenberger, D.W., 2005. Climate change in lowland Central America during the late deglacial and early Holocene. Journal of Quaternary Science, 20(4), pp.363-376.

Hodell, D.A., Curtis, J.H. and Brenner, M., 1995. Possible role of climate in the collapse of Classic Maya civilization. Nature, 375(6530), p.391.

Hodell, D.A., Brenner, M., Curtis, J.H. and Guilderson, T., 2001. Solar forcing of drought frequency in the Maya lowlands. *Science*, 292(5520), pp.1367-1370.

Hodell, D.A., Brenner, M., Curtis, J.H., Medina-Gonzalez, R., Can, E.I.C., Albornaz-Pat, A. and Guilderson, T.P., 2005. Climate change on the Yucatan Peninsula during the little ice age. *Quaternary Research*, 63(2), pp.109-121.

Hodell, D.A., Brenner, M. and Curtis, J.H., 2007. Climate and cultural history of the northeastern Yucatan Peninsula, Quintana Roo, Mexico. *Climatic Change*, 83(1), pp.215-240.

Hooghiemstra, H., Cleef, A.M., Noldus, C.W. and Kappelle, M., 1992. Upper Quaternary vegetation dynamics and palaeoclimatology of the La Chonta bog area (Cordillera de Talamanca, Costa Rica). *Journal of Quaternary Science*, 7(3), pp.205-225.

Horn, S.P., 1993. Postglacial vegetation and fire history in the Chirripó Páramo of Costa Rica. *Quaternary Research*, 40(1), pp.107-116.

Horn, S.P. and Kennedy, L.M., 2001. Pollen evidence of maize cultivation 2700 BP at La Selva biological station, Costa Rica. *Biotropica*, 33(1), pp.191-196.

Islebe, G.A., Hooghiemstra, H. and Van der Borg, K., 1995. A cooling event during the Younger Dryas Chron in Costa Rica. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 117(1-2), pp.73-80.

Islebe, G.A., Hooghiemstra, H., Brenner, M., Curtis, J.H. and Hodell, D.A., 1996a. A Holocene vegetation history from lowland Guatemala. *The Holocene*, 6(3), pp.265-271.

Islebe, G.A., Hooghiemstra, H. and van't Veer, R., 1996b. Holocene vegetation and water level history in two bogs of the Cordillera de Talamanca, Costa Rica. *Vegetation*, 124(2), pp.155-171.

Islebe, G.A. and Hooghiemstra, H., 1997. Vegetation and climate history of montane Costa Rica since the last glacial. *Quaternary Science Reviews*, 16(6), pp.589-604.

Islebe, G. and Sánchez, O., 2002. History of late Holocene vegetation at Quintana Roo, Caribbean coast of Mexico. *Plant Ecology*, 160(2), pp.187-192.

Johnston, K.J., Breckenridge, A.J. and Hansen, B.C., 2001. Paleoecological evidence of an Early Postclassic occupation in the southwestern Maya lowlands: Laguna Las Pozas, Guatemala. *Latin American Antiquity*, 12(2), pp.149-166.

Jones, J.G., 1994. Pollen evidence for early settlement and agriculture in northern Belize. *Palynology*, 18(1), pp.205-211.

Joo-Chang, J.C., Islebe, G.A. and Torrescano-Valle, N., 2015. Mangrove history during middle-and late-Holocene in Pacific south-eastern Mexico. *The Holocene*, 25(4), pp.651-662.

Kennedy, L.M. and Horn, S.P., 2008. A late Holocene pollen and charcoal record from La Selva biological station, Costa Rica. *Biotropica*, 40(1), pp.11-19.

Kennett, D.J., Breitenbach, S.F., Aquino, V.V., Asmerom, Y., Awe, J., Baldini, J.U., Bartlein, P., Culleton, B.J., Ebert, C., Jazwa, C. and Macri, M.J., 2012. Development and disintegration of Maya political systems in response to climate change. *Science*, 338(6108), pp.788-791.

Lachniet, M.S., Asmerom, Y., Burns, S.J., Patterson, W.P., Polyak, V.J. and Seltzer, G.O., 2004a. Tropical response to the 8200 yr BP cold event? Speleothem isotopes indicate a weakened early Holocene monsoon in Costa Rica. *Geology*, 32(11), pp.957-960.

Lachniet, M.S., Burns, S.J., Piperno, D.R., Asmerom, Y., Polyak, V.J., Moy, C.M. and Christenson, K., 2004b. A 1500- year El Niño/Southern Oscillation and rainfall history for the isthmus of Panama from speleothem calcite. *Journal of Geophysical Research: Atmospheres*, 109(D20).

Lachniet, M.S., Johnson, L., Asmerom, Y., Burns, S.J., Polyak, V., Patterson, W.P., Burt, L. and Azouz, A., 2009. Late Quaternary moisture export across Central America and to Greenland: evidence for tropical rainfall variability from Costa Rican stalagmites. *Quaternary Science Reviews*, 28(27-28), pp.3348-3360.

Lane, C.S., Horn, S.P., Mora, C.I., Orvis, K.H. and Finkelstein, D.B., 2011. Sedimentary stable carbon isotope evidence of late Quaternary vegetation and climate change in highland Costa Rica. *Journal of Paleolimnology*, 45(3), pp.323-338.

League, B.L. and Horn, S.P., 2000. A 10 000 year record of Paramo fires in Costa Rica. *Journal of Tropical Ecology*, pp.747-752.

Leyden, B.W., 1987. Man and climate in the Maya lowlands. *Quaternary Research*, 28(3), pp.407-414.

Leyden, B.W., Brenner, M. and Dahlin, B.H., 1998. Cultural and Climatic History of Cobá, a Lowland Maya City in Quintana Roo, Mexico 1. *Quaternary Research*, 49(1), pp.111-122.

Luzzadder- Beach, S., Beach, T., Garrison, T., Houston, S., Doyle, J., Román, E., Bozarth, S., Terry, R., Krause, S. and Flood, J., 2017. Paleoecology and Geoarchaeology at El Palmar and the El Zotz Region, Guatemala. *Geoarchaeology*, 32(1), pp.90-106.

McCloskey, T.A. and Liu, K.B., 2012. A sedimentary-based history of hurricane strikes on the southern Caribbean coast of Nicaragua. *Quaternary Research*, 78(3), pp.454-464.

McNeil, C.L., Burney, D.A. and Burney, L.P., 2010. Evidence disputing deforestation as the cause for the collapse of the ancient Maya polity of Copan, Honduras. *Proceedings of the National Academy of Sciences*, 107(3), pp.1017-1022.

Medina-Elizalde, M., Burns, S.J., Lea, D.W., Asmerom, Y., von Gunten, L., Polyak, V., Vuille, M. and Karmalkar, A., 2010. High resolution stalagmite climate record from the

Yucatán Peninsula spanning the Maya terminal classic period. *Earth and Planetary Science Letters*, 298(1-2), pp.255-262.

Medina-Elizalde, M., Burns, S.J., Polanco-Martínez, J.M., Beach, T., Lases-Hernández, F., Shen, C.C. and Wang, H.C., 2016. High-resolution speleothem record of precipitation from the Yucatan Peninsula spanning the Maya Preclassic Period. *Global and Planetary Change*, 138, pp.93-102.

Metcalfe, S., Breen, A., Murray, M., Furley, P., Fallick, A. and McKenzie, A., 2009. Environmental change in northern Belize since the latest Pleistocene. *Journal of Quaternary Science*, 24(6), pp.627-641.

Monacci, N.M., Meier-Grünhagen, U., Finney, B.P., Behling, H. and Wooller, M.J., 2011. Paleoecology of mangroves along the Sibun River, Belize. *Quaternary Research*, 76(2), pp.220-228.

Mueller, A.D., Islebe, G.A., Hillesheim, M.B., Grzesik, D.A., Anselmetti, F.S., Ariztegui, D., Brenner, M., Curtis, J.H., Hodell, D.A. and Venz, K.A., 2009. Climate drying and associated forest decline in the lowlands of northern Guatemala during the late Holocene. *Quaternary Research*, 71(2), pp.133-141.

Mueller, A.D., Islebe, G.A., Anselmetti, F.S., Ariztegui, D., Brenner, M., Hodell, D.A., Hajdas, I., Hamann, Y., Haug, G.H. and Kennett, D.J., 2010. Recovery of the forest ecosystem in the tropical lowlands of northern Guatemala after disintegration of Classic Maya polities. *Geology*, 38(6), pp.523-526.

Neff, H., Pearsall, D.M., Jones, J.G., Arroyo, B., Collins, S.K. and Freidel, D.E., 2006. Early Maya adaptive patterns: Mid-late Holocene paleoenvironmental evidence from Pacific Guatemala. *Latin American Antiquity*, 17(3), pp.287-315.

Northrop, L.A. and Horn, S.P., 1996. PreColumbian agriculture and forest disturbance in Costa Rica: palaeoecological evidence from two lowland rainforest lakes. *The Holocene*, 6(3), pp.289-299.

Pérez, L., Bugja, R., Massaferro, J., Steeb, P., Geldern, R.V., Frenzel, P., Brenner, M., Scharf, B. and Schwalb, A., 2010. Post-Columbian environmental history of Lago Petén Itzá, Guatemala. *Revista Mexicana de Ciencias Geológicas*, 27(3).

Phillips, S., Rouse, G.E. and Bustin, R.M., 1997. Vegetation zones and diagnostic pollen profiles of a coastal peat swamp, Bocas del Toro, Panama. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 128(1-4), pp.301-338.

Piperno, D.R., Bush, M.B. and Colinvaux, P.A., 1990. Paleoenvironments and human occupation in late-glacial Panama. *Quaternary Research*, 33(1), pp.108-116.

Piperno, D.R., Bush, M.B. and Colinvuax, P.A., 1991. Paleoecological perspectives on human adaptation in Central Panama. II The Holocene. *Geoarchaeology*, 6(3), pp.227-250.

Piperno, D.R. and Jones, J.G., 2003. Paleoecological and archaeological implications of a Late Pleistocene/Early Holocene record of vegetation and climate from the Pacific coastal plain of Panama. *Quaternary Research*, 59(1), pp.79-87.

Pohl, M.D., Pope, K.O., Jones, J.G., Jacob, J.S., Piperno, D.R., Lentz, D.L., Gifford, J.A., Danforth, M.E. and Josserand, J.K., 1996. Early agriculture in the Maya lowlands. *Latin American Antiquity*, 7(4), pp.355-372.

Pollock, A.L., van Beynen, P.E., DeLong, K.L., Polyak, V., Asmerom, Y. and Reeder, P.P., 2016. A mid-Holocene paleoprecipitation record from Belize. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 463, pp.103-111.

Pope, K.O., Pohl, M.E., Jones, J.G., Lentz, D.L., Von Nagy, C., Vega, F.J. and Quitmyer, I.R., 2001. Origin and environmental setting of ancient agriculture in the lowlands of Mesoamerica. *Science*, 292(5520), pp.1370-1373.

Rosenmeier, M.F., Hodell, D.A., Brenner, M., Curtis, J.H. and Guilderson, T.P., 2002a. A 4000-year lacustrine record of environmental change in the southern Maya lowlands, Peten, Guatemala. *Quaternary Research*, 57(2), pp.183-190.

Rosenmeier, M.F., Hodell, D.A., Brenner, M., Curtis, J.H., Martin, J.B., Anselmetti, F.S., Ariztegui, D. and Guilderson, T.P., 2002b. Influence of vegetation change on watershed hydrology: implications for paleoclimatic interpretation of lacustrine δ 18 O records. *Journal of Paleolimnology*, 27(1), pp.117-131.

Rue, D.J., 1987. Early agriculture and early Postclassic Maya occupation in western Honduras. *Nature*, 326(6110), pp.285-286.

Rue, D., Webster, D. and Traverse, A., 2002. Late Holocene fire and agriculture in the Copan Valley, Honduras. *Ancient Mesoamerica*, 13(2), pp.267-272.

Rushton, E.A., Metcalfe, S.E. and Whitney, B.S., 2013. A late-Holocene vegetation history from the Maya lowlands, Lamanai, Northern Belize. *The Holocene*, 23(4), pp.485-493.

Smyth, M.P., Dunning, N.P., Weaver, E.M., van Beynen, P. and Zapata, D.O., 2017. The perfect storm: climate change and ancient Maya response in the Puuc Hills region of Yucatán. *Antiquity*, 91(356), pp.490-509.

Stansell, N.D., Steinman, B.A., Abbott, M.B., Rubinov, M. and Roman-Lacayo, M., 2013. Lacustrine stable isotope record of precipitation changes in Nicaragua during the Little Ice Age and Medieval Climate Anomaly. *Geology*, 41(2), pp.151-154.

Schüpbach, S., Kirchgeorg, T., Colombaroli, D., Beffa, G., Radaelli, M., Kehrwald, N.M. and Barbante, C., 2015. Combining charcoal sediment and molecular markers to infer a Holocene fire history in the Maya Lowlands of Petén, Guatemala. *Quaternary Science Reviews*, 115, pp.123-131.

Torrescano, N. and Islebe, G.A., 2006. Tropical forest and mangrove history from southeastern Mexico: a 5000 yr pollen record and implications for sea level rise. *Vegetation History and Archaeobotany*, 15(3), pp.191-195.

Torrescano-Valle, N. and Islebe, G.A., 2015. Holocene paleoecology, climate history and human influence in the southwestern Yucatan Peninsula. *Review of Palaeobotany and Palynology*, 217, pp.1-8.

Urquhart, G.R., 2009. Paleoecological record of hurricane disturbance and forest regeneration in Nicaragua. *Quaternary International*, 195(1-2), pp.88-97.

Velez, M.I., Curtis, J.H., Brenner, M., Escobar, J., Leyden, B.W. and Popenoe de Hatch, M., 2011. Environmental and cultural changes in highland Guatemala inferred from Lake Amatitlán sediments. *Geoarchaeology*, 26(3), pp.346-364.

Webster, J.W., Brook, G.A., Railsback, L.B., Cheng, H., Edwards, R.L., Alexander, C. and Reeder, P.P., 2007. Stalagmite evidence from Belize indicating significant droughts at the time of Preclassic Abandonment, the Maya Hiatus, and the Classic Maya collapse. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 250(1-4), pp.1-17.

Wahl, D., Byrne, R., Schreiner, T. and Hansen, R., 2006. Holocene vegetation change in the northern Peten and its implications for Maya prehistory. *Quaternary Research*, 65(3), pp.380-389.

Wahl, D., Schreiner, T., Byrne, R. and Hansen, R., 2007a. A paleoecological record from a Late Classic Maya reservoir in the north Petén. *Latin American Antiquity*, 18(2), pp.212-222.

Wahl, D., Byrne, R., Schreiner, T. and Hansen, R., 2007b. Palaeolimnological evidence of late-Holocene settlement and abandonment in the Mirador Basin, Peten, Guatemala. *The Holocene*, 17(6), pp.813-820.

Wahl, D., Estrada-Belli, F. and Anderson, L., 2013. A 3400 year paleolimnological record of prehispanic human–environment interactions in the Holmul region of the southern Maya lowlands. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 379, pp.17-31.

Wahl, D., Byrne, R. and Anderson, L., 2014. An 8700 year paleoclimate reconstruction from the southern Maya lowlands. *Quaternary Science Reviews*, 103, pp.19-25.

Wahl, D., Hansen, R.D., Byrne, R., Anderson, L. and Schreiner, T., 2016. Holocene climate variability and anthropogenic impacts from Lago Paixban, a perennial wetland in Peten, Guatemala. *Global and Planetary Change*, 138, pp.70-81.

Walsh, M.K., Prufer, K.M., Culleton, B.J. and Kennett, D.J., 2014. A late Holocene paleoenvironmental reconstruction from Agua Caliente, southern Belize, linked to regional climate variability and cultural change at the Maya polity of Uxbenká. *Quaternary Research*, 82(1), pp.38-50.

3. The legacy of Pre-Columbian fire on the pine-oak forests of upland Guatemala

William J. Harvey[1], Sandra Nogué[2], Nathan Stansell[3], Gillian Petrokofsky[1], Byron Steinman[4], Katherine J. Willis[1]

[1]Long-Term Ecology Laboratory, Department of Zoology, University of Oxford, Oxford, UK

[2]School of Geography and Environmental Sciences, University of Southampton, Highfield, Southampton, UK

[3]Department of Geology and Environmental Geosciences, Northern Illinois University, De Kalb, IL, USA

[4]Large Lakes Observatory and Department of Earth and Environmental Sciences, University of Minnesota Duluth, Duluth, Minnesota, USA

Published in Frontiers in Forests and Global Change

3.1 Abstract

Mountain tropical forests of the Southern Maya Area (Pacific Chiapas and Guatemala, El Salvador and Northern Honduras) predominantly comprise pine and oak formations, which form intricate mosaics and complex successional interactions following large-scale fire. These forests have been transformed by the peoples of the Maya civilization through practices of horticulture, agriculture and architectural developments over thousands of years. Anthropogenic impacts and the extent of early human interaction with these upland forests are currently poorly understood. In this study I identify: (i) the natural baseline vegetation of the region; (ii) when human impact and agrarian practices began in the Maya uplands; and (iii) what impacts the Maya had on forest structure, composition, and successional regeneration. Past vegetation, anthropogenic use of fire, and herbivory presence were reconstructed using proxy analysis of fossil pollen, macroscopic charcoal, microscopic charcoal, and dung fungal spores (*Sporormiella*). Three phases of forest succession were identified over the past 6,000 years broadly pertaining to the well-defined archaeological periods of (i) the Archaic (10,000-2000B.C.E.); (ii) Pre-Classic (2000B.C.E. – 100C.E.); and (iii) Terminal Pre-Classic (100-250C.E.), Classic (250-950C.E.), and Post-Classic (950-1522C.E.). I present the earliest evidence for agriculture within the Southern Maya Area through presence of peppers (*Capsicum*) from 3850B.C.E. and the rise of maize cultivation (*Zea mays*) from 970B.C.E. Persistent high intensity burning driven by agricultural practices and lime production during the Late-PreClassic (400-100B.C.E.) to Classic Period resulted in a compositional change of forest structure c.150B.C.E. from oak (*Quercus*) dominated forests to pine (*Pinus*) dominated forests. The legacy of Pre-Columbian anthropogenically driven fire in these mountain tropical forests demonstrates the resilience and thresholds for fire driven succession. These findings are particularly relevant for addressing current land use and management strategies involving agriculture, fire and forest management in these upland areas.

3.2 Introduction

Unlike the Amazon or boreal regions, Central America does not have large tracts of intact forests (Watson et al. 2018), but reductions in extent of intact forests are a concern. It is calculated that forest cover reduced by 13.3% in Guatemala between 2000-2013C.E. according to Potapov et al. (2017). Mountain tropical forests (MTF) are important for the provision of ecosystem services particularly biodiversity and water (Martínez et al., 2009) and loss of intactness has serious implications for these ecosystem services. Given the current high international interest in the effects of human actions that cause degradation of forests and subsequent loss of ecological function, drawing on long-term ecological data could provide evidence of historical changes in forest composition and extent. This type of long-term data for this region is limited, and further, rarely considered in modern conservation discussions (Jeffers et al. 2015). This represents a key knowledge gap for understanding the function and protection of intact forests in this region and more generally.

The Middle to Late Holocene (6000-2000B.C.E.) vegetation history of the Central American uplands (>1000m.a.s.l.) is not well understood but is essential to our understanding of early human impacts and prehistoric land use across the Maya Area (Neff et al. 2006). Early human populations across Central America are suggested to have increasingly interacted with their surrounding environment from 6000B.C.E., aided by increasingly favourable climatic conditions (Turner & Miksicek 1984; Colunga-GaricaMartin & Zizumbo-Villareal 2004; Ford & Nigh, 2009).

The Maya occupied three separate areas: Southern, Central and Northern (Figure 3.1). The latter two are entirely within the lowlands (<1000m). Our research area lies within the Southern uplands, which includes the highlands of Guatemala and adjacent Chiapas (Coe, 1966). There are altitudinal gradients in temperature and precipitation, with annual mean temperatures ranging between 14-25 °C and annual rainfall rangingbetween 900-

3700mm yr^{-1} (Kappelle, 2006). The vegetation inhabiting this upland area is typically comprised of tropical and subtropical mixed deciduous and coniferous forests, known as MTF formations, which start in the Sierra Madre de Chiapas (southern Mexico) and extend down to Northern Nicaragua (Dinerstein et al. 2017).

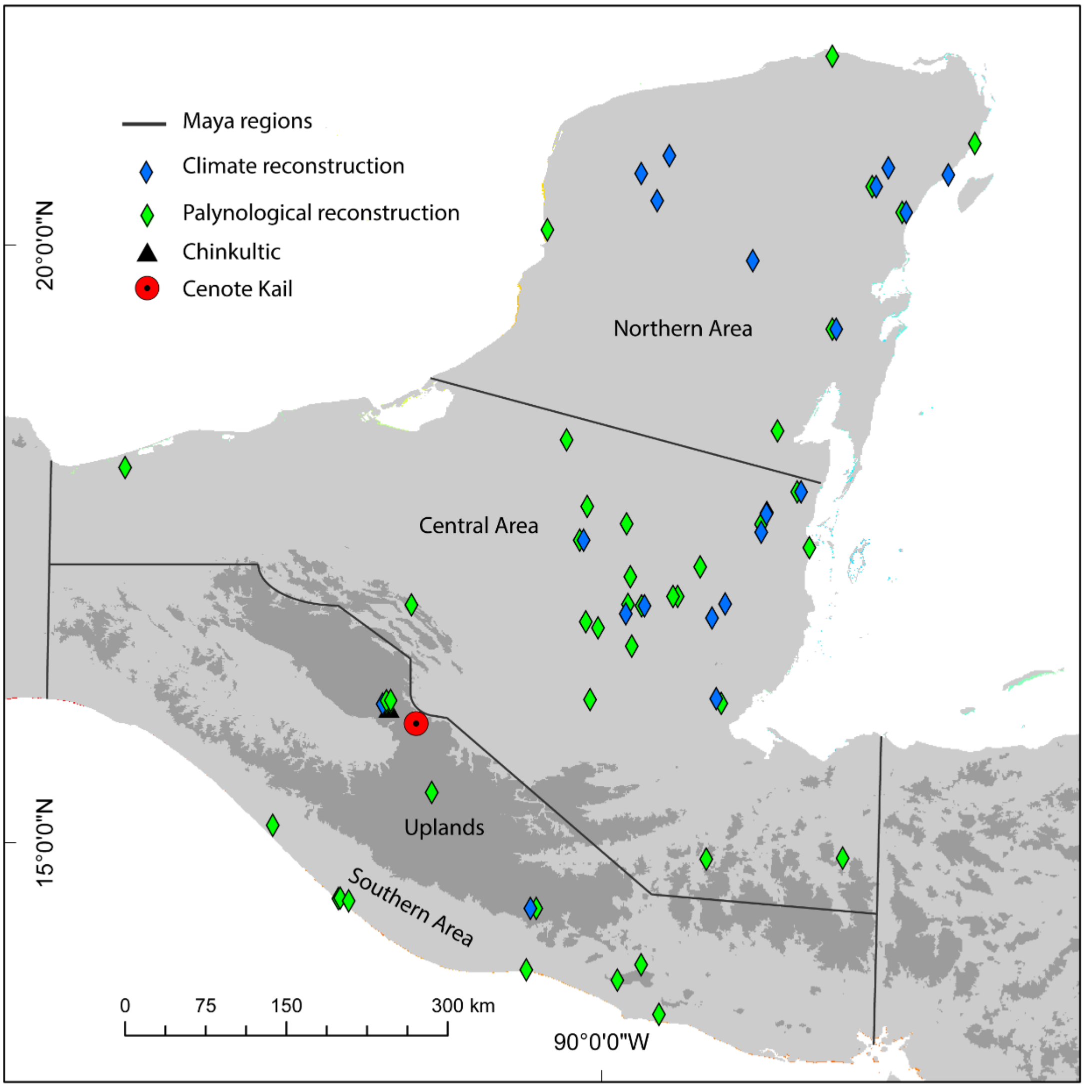


Figure 3.1 Topographic map of Central America depicting (i) Maya regions; (ii) independent climate proxies (blue diamond); (iii) Previous vegetation reconstructions in the Maya Area (green diamond); (iv) location of archaeological complex Chinkultic (black triangle); and (v) location of Cenote Kail (red circle) (see SI for sites).

Previous work in the Maya Area

In palaeoecology records from Maya sites, anthropogenic impacts to vegetation are typically inferred from the: (i) presence of known cultigens, such as *Capsicum* (peppers), Cucurbitaceae (gourds), *Maranta arundinacea* (arrowroot), *Phaseolus* (beans), and *Zea mays* (Maize) (White, 1999); (ii) presence of “weedy taxa”, such as, Amarathaceae, Compositae, and *Polygonum* (Dull, 2004a; Franco-Gaviria et al. 2018); (iii) reductions in all or select arboreal taxa, such as *Quercus* (Dull, 2004a; 2004b; 2007; Velez et al. 2011); and (iv) increases in local and regional burning (e.g. Dull, 2004a; 2004b; 2007; Anderson & Wahl, 2016).

Based on this existing work, Archaic (10,000-2000B.C.E.) anthropogenic impacts and the extent of early human interaction with the upland forests of the Maya Area are currently debated. There have been eleven palaeopalynological studies conducted in the southern Maya Area (Figures 3.1& 3.2) and only five of these reconstructions have been undertaken in the uplands (Dull, 2004a; Caffrey et al. 2011; Velez et al. 2011; Franco-Gaviria et al. 2018). Interpretations of fossil pollen and charcoal records from Laguna Verde (El Salvador) and Lago Amatitlan (Guatemala) identify extensive human alteration of the upland vegetation between 2550 - 625B.C.E. (Dull, 2004a; Velez et al. 2011). Likewise, records from Lake San Lorenzo and Lake Esmeralda (Chiapas) present evidence that anthropogenic and climatic impacts drove vegetation changes from c.450B.C.E. (Franco-Gaviria et al. 2018). In contrast, palynological evidence from Miqul Meadow (Guatemala) has led to the suggestion that climate is the sole driver of vegetation change (Caffrey et al. 2011). An issue with both of these interpretations however is that these records are largely low in resolution (more than 200 years between samples: e.g. Laguna Verde & Miqul Meadow) and poorly chronologically constrained (e.g. Miqul Meadow). Two higher resolution records from Lake San Lorenzo and Lake Esmeralda present evidence of anthropogenic and climatic impacts from c.450B.C.E. (Franco-

Gaviria et al. 2018). In order to reconstruct the impacts of disturbance events in MTFs and forest succession, palaeoecological records must present data sets at a resolution higher than that of rate of succession, which is up to 200 years in MTF (Kappelle, 2006).

The impacts of climate upon the vegetation reconstruction from Miqul Meadow & Laguna Verde are inferred from nearby lowland sites (e.g. La Yeguada, Panama: Bush et al. 1992; and Peten Itza, Guatemala: Islebe et al. 1996) and/or elsewhere in Central and South America (e.g. Lake Miragoane, Haiti: Hodell et al. 1991; and Peru: Thompson et al. 1995) as well as marine archives (e.g. Cariaco basin: Haug et al. 2001) although the latter records are problematic, due to the spatial heterogeneity of precipitation across the Central American Isthmus through time. It is therefore important to use independent climate proxies from each individual site.

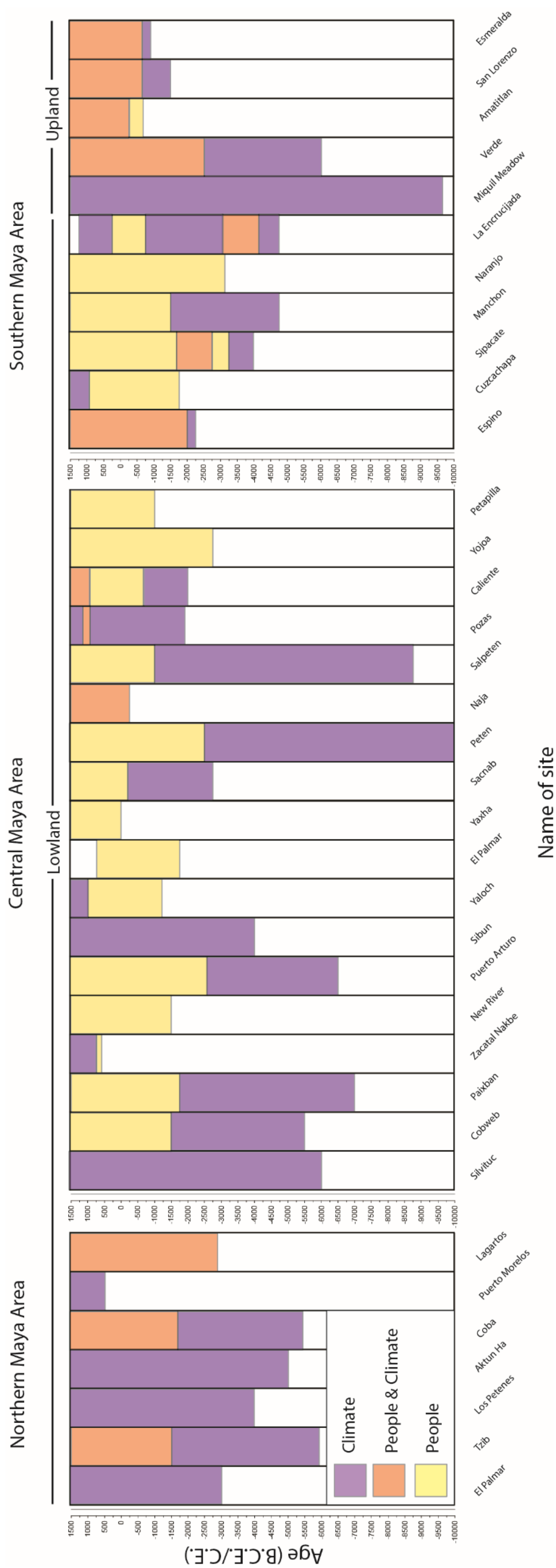


Figure 3.2 Summary of impacts upon vegetation from the Maya Area during the Pre-Columbian Holocene as reported by authors in the peer reviewed literature (see SI for sites).

Forest Succession

Currently the arboreal canopy of MTFs are predominantly comprised of a combination of coniferous forest taxa (e.g. *Pinus* and *Abies*) and mixed hard wood forest (MHWF) taxa (e.g. *Quercus*, *Alnus*, and *Liquidambar*), which are well adapted to variable climatic conditions and natural fires (Corrales et al. 2015). These MTF formations are a combination of pine forests (PF), pine-oak forests (POF), mountain-pine-oak forests (MPOF), oak forests (OF), pine-oak-*liquidambar* forests (POLF), mountain rain forests (MRF), and cloud forests (CF) (Kappelle, 2006). These typically overlap in floristic composition (PF, POF, MPOF, OF, POLF and MRF) but vary in species abundance (Miranda 1952; Breedlove 1981; Kappelle, 2006; Figueroa-Rangel et al. 2008; 2010; 2012). POF form intricate mosaics and complex successional interactions, especially at higher elevations, which extend up into the broad-leaved evergreen CF (Rzedowski, 2006). Altitudinally, MPOF in Chiapas are found above 1500m, while POF formations have an extensive range from 500-3400m, with strong turnovers between species along altitudinal gradients (Kappelle, 2006). There are over 150 species of *Pinus* and *Quercus* that can be found across the uplands of Guatemala (Muller, 1942; Kappelle, 2006). Only 47% of forest cover (1990-2000C.E.) remains and it is highly fragmented due to high human population densities and land modification for subsistence farming (Corrales et al. 2015).

Drivers of POF dynamics have been previously investigated in upland Guatemala (Velez et al. 2011), neighbouring Chiapas (Domínguez-Vázquez & Islebe, 2008), Pacific Mexico (Figueroa-Rangel et al. 2008; 2010; 2012) and Costa Rica (Islebe & Hooghiemstra, 1997) detailing the climatic and anthropogenic mechanisms that contribute towards changes in POF composition through time (Kappelle, 2006). In all these studies fire has been identified as the dominant driver of structural and successive turnover within POF systems, however there is disagreement as to what factors are driving these fires. Changes in burning are controlled by complex interactions of fire, fuel load, climate, and humans (Cochrane, 2009; Bowman et al., 2011; Anderson & Wahl, 2016). While it is not possible to truly differentiate between anthropogenic and naturally occurring fires (Anderson & Wahl, 2016), inferences can be made by combining multiple lines of evidence such as charcoal with the presence of known agricultural grains e.g. *Zea mays* (Dull, 2004a; 2004b; 2007); or with climatic proxy data to infer known shifts in precipitation impacting fuel loads and ignitions (Bowman et al., 2011).

Research conducted on the Pacific coast of Mexico (Figueroa-Rangel et al. 2008; 2010; 2012) and in Costa Rica (Islebe & Hooghiemstra, 1997), suggests that fire within POFs are primarily climatically driven; while, palynological work in Guatemala and Chiapas (Domínguez-Vázquez & Islebe, 2008; Velez et al. 2011) indicates a more intertwined relationship of climate and people. Other factors considered to affect the structure and successional regeneration of POFs are overall climate (temperature and precipitation), soil (type, nutrient availability), anthropogenic activities (timber extraction and agriculture) (Kappelle, 2006). In addition, herbivory can cause deviations in successional pathways through altering the amount of available biomass and seed dispersal (Baker et al. 2016; Arroyo- Rodríguez et al. 2017).

It has been suggested that without further disturbances natural recovery will return a fallow field to a POF within *c.*80 years (Figueroa-Rangel et al. 2008). Sustained low-intensity and long duration human disturbance leads to a deviation of this natural sequence resulting in slowed recovery and more intensive anthropogenic or climatic disturbances can reverse or reset recovery times (Kappelle, 2006). However, these are theoretical timelines and to date there is very little evidence on recovery rates from different types of disturbances (fire, human, climate) in this region and also how this varies according to altitude.

This study set out to identify (i) the natural baseline vegetation of the region: (ii) when human impact and agrarian practices began in the Maya uplands; and (iii) what impacts the Maya had on forest structure, composition, and successional regeneration. To address the potential impacts of anthropogenic influences and herbivory upon the biota of upland Guatemala, fossil proxies for vegetation, burning, and animal populations were reconstructed for the last 6,000 years and compared to local and regional climatic records and nearby archaeological sites. These proxies included fossil pollen, macroscopic charcoal (>150um), microscopic charcoal (<150um), and fossil dung fungal spores (*Sporormiella*), extracted from a cenote sediment core to explore these relationships.

3.3 Methods

Study Site: Cenote Kail

Cenote Kail is a small lake (150m diameter) and was identified within the uplands of the Southern Maya Area (N16°00'00.0" W91°33'14.4, 1534m.a.s.l.) situated 28km away from the well documented archaeological complex Chinkultic (Ball, 1980; Figure 3.1). This city was established sometime between 50B.C.E and 75C.E. and occupied until 300-350C.E. The city was then abandoned between 350-700C.E. before being occupied again from 700-1250C.E. (Ball, 1980). The lake is presently surrounded by a coniferous forest mosaic best described as POF or MPOF. Vegetation is distributed between densely populated mixed deciduous and coniferous forested patches, and large open shrub/grasslands.

In 2015 a 545cm sedimentary composite core, with overlapping sections, was extracted from Cenote Kail using a Livingstone piston corer (Livingstone, 1955). Forty-six samples (1g wet weight) were extracted at 10cm intervals for biological proxy analysis of macroscopic charcoal, microscopic charcoal, pollen, and coprophilous fungal spores (*Sporormiella*).

Chronology

An age depth model was constructed using thirty-eight calibrated radiocarbon dates obtained from charcoal and terrestrial leaf fragments (Reimer et al. 2013), which represent a single event or one-two seasons of growth, were carefully selected for radiocarbon dating (Table 3.1). Samples were pre-treated using standard acid-base-acid protocols (Abbott and Stafford, 1996). Radiocarbon dates were generated at the W.M. Keck Carbon Cycle Accelerator Mass Spectrometry Laboratory at the University of California, Irvine. The IntCal13 radiocarbon dataset (Reimer, 2013) was used to calibrate the measured radiocarbon dates and OxCal (v.4.3) was utilised to construct an age-depth model applying a Bayesian approach (Ramsey, 2009). Outliers were identified using the general outlier model implementing an outlier probability of 0.05 (Ramsey, 2008). Sedimentation rate was calculated using this age-depth model.

Table 3.1 Measured, calibrated and modelled radiocarbon ages for Cenote Kail. *Omitted dates identified by the general outlier model.

Lab #	Measured Age (C^{14} Cal yrs B.P.)		Depth	2σ Cal Age Range (B.C.E./ C.E.)		Median Age (B.C.E./ C.E.)	OxCal Modelled Age (B.C.E./ C.E.)		Median Modelled Age (B.C.E/ C.E.)	Model Agreement
146795	385	±20	106.5	1445	1620	1532.5	1560	1633	1596.5	99.9
209175	260	±20	118.75	1528	1797	1662.5	1515	1595	1555	99.2
209176	560	±25	138.75	1311	1425	1368	1312	1425	1368.5	105.7
209177	870	±20	160.75	1052	1220	1136	1061	1224	1142.5	102.3
146797	1080	±30	192	894	1018	956	895	1017	956	114.4
169170	1380	±80	229.8	433	865	649	431	767	599	107.3
146798/146799	1975/2115	±20/45	267	-44	53	4.5	-40	61	10.5	55.9
209178	2070	±30	299.25	-174	-1	-87.5	-188	-50	-119	85.5
209179	2235	±25	318.75	-385	-206	-295.5	-389	-210	-2995	103
209180	2515	±25	332.75	-791	-543	-667	-789	-543	-666	101.2
146800	2585	±20	342	-805	-772	-788.5	-806	-770	-788	64.8
209181	2990	±50	355.75	-1391	-1054	-1222.5	-1371	-1023	-1197	116.6
209182	3220	±20	378.75	-1527	-1439	-1483	-1596	-1436	-1516	130.8
209183	3350	±35	382.75	-1739	-1531	-1635	-1728	-1529	-1628.5	118.4
209184	3405	±20	387.75	-1749	-1642	-1695.5	-1745	-1654	-1699.5	102.9
209185	3415	±20	390.75	-1767	-1658	-1712.5	-1757	-1667	-1712	110.1
209186	3590	±20	394.5	-2018	-1889	-1953.5	-2015	-1886	-1950.5	106.8
209188	3700	±60	407.75	-2284	-1928	-2106	-2196	-1984	-2090	103.9
209189	3750	±40	412.75	-2286	-2035	-2160.5	-2270	-2046	-2158	95.6
209190	3750	±25	413.75	-2278	-2041	-2159.5	-2273	-2052	-2162.5	100.4
146802	3940	±25	428.5	-2561	-2345	-2453	-2466	-2310	-2388	98.9
209191	3875	±25	431.25	-2465	-2286	-2375.5	-2468	-2343	-2405.5	101.1
209193	4315	±30	467.25	-3013	-2888	-2950.5	-3011	-2888	-2949.5	96.1
209195	4475	±25	484.25	-3338	-3030	-3184	-3303	-3025	-3164	93
209196	4570	±25	498.25	-3491	-3119	-3305	-3361	-3118	-3239.5	92.6
193048	4545	±25	508.8	-3366	-3106	-3236	-3367	-3146	-3256.5	102.5
146803	4570	±20	519	-3485	-3126	-3305.5	-3659	-3194	-3426.5	100.8
193050	4900	±25	521.7	-3709	-3643	-3676	-3708	-3642	-3675	106.9
193051	4995	±25	532.9	-3927	-3704	-3815.5	-3913	-3705	-3809	100.7
193052	5100	±20	536.9	-3965	-3804	-3884.5	-3961	-3798	-3879.5	13.9
193054	5130	±30	543.7	-3990	-3804	-3897	-3989	-3811	-3900	66
***209187**	3485	±25	404.75	-1886	-1703	-1794.5	-2164	-1759	-1961.5	42
***209192**	4275	±25	438.25	-2916	-2879	-2897.5	-2916	-2369	-2642.5	28.1
***209194**	4185	±40	472.25	-2892	-2633	-2762.5	-3145	-2755	-2950	22.8
***209197**	5020	±60	499.25	-3958	-3674	-3816	-3386	-3116	-3251	6.9
***193049**	5090	±20	516.33	-3961	-3801	-3881	-3872	-3281	-3576.5	16.5
***193053**	5330	±25	541.3333	-4245	-4051	-4148	-4197	-3805	-4001	19.8

Fossil Pollen and *Sporormiella* Analysis

Fossil pollen was used to reconstruct the abundance and composition of past vegetation dynamics. Fossil pollen extraction and preparation followed standard palynological procedures applying the Oxford Long-Term Ecology Laboratories protocol (OxLEL, 2016). Silicone oil was used as the mounting agent to allow for the rotation of grains, easing identification. Samples were spiked with known concentrations of an exotic marker, *Lycopodium* spores (batch No. 20848 or 9666), to calculate pollen accumulation rates. Pollen influx was calculated using pollen accumulation rates and sedimentation rate (Bennett & Willis, 2001). Counting and identification of pollen grains were conducted at 400x and 1000x magnification. For each level a minimum of 300 terrestrial pollen grains were counted. Morphological identification was achieved using (i) pollen databases (Bush & Weng, 2007; APSA, 2007; Martin & Harvey, 2017); (ii) published plates: (Roubik & Moreno, 1991; Willard et al. 2004); and (iii) botanical reference materials from the OxLEL reference collection. In order to interpret the relative composition of the forest, coniferous and mixed-hard wood forest (MHWF) canopy taxa and were compared as a ratio. The abundance of *Sporormiella* spores were used to indicate herbivorous animal presence and abundance. *Sporormiella* spores were counted and morphologically identified on the same slides (Davis & Shafer, 2006; Baker et al. 2016).

Charcoal Analysis

Macroscopic fossil charcoal fragments (>150um) were used to infer past periods of burning where local is taken to represent burning within a 10km radius of the catchment area (see Gavin et al., 2003; Lynch et al., 2004; Peters and Higuera, 2007; Higuera et al., 2007; 2011; Anderson & Wahl, 2016). All fragments were counted in the 1g samples over 150um at 10x magnification.

Microscopic charcoal (<150um), representing a regional signal of up to 100km (see Clark, 1988), were also counted on the same slides applying the point counting method at 400x magnification (Clark, 1982). Microscopic charcoal counts were recorded until a minimum of 50 lycopodium grains and 200 fields of view were encountered for each level to allow for concentrations of macroscopic charcoal (cm^2yr^1) to be calculated. Weight was converted to volume using density measured from the loss on ignition. Point sampling charcoal for reconstructing fire variability is limited compared to continuous sediment sampling (Whitlock & Larson, 2001).

Data Handling

Pollen counts were converted to percentages, while the annual influx of S*porormiella*, macroscopic and microscopic charcoal were calculated as accumulation rates using the number of charcoal fragments or number of *Sporormiella*, the number of the exotic marker counted, and the sedimentation rate (Maher 1981; Bennett 1994; Bennett & Willis, 2001; Whitlock & Larson, 2002; Baker et al. 2016). To identify discrete zones in the resulting palynological diagrams, constrained hierarchical clustering upon the palynological assemblage was applied following the broken stick model (Bennett, 1996).

Before preforming all ordination analyses, I square-root transformed the percentage data to normalise the distribution (Bennett & Willis, 2001). A square root transform was chosen because it can be applied to data sets containing zero values. To check if it was appropriate to apply a linear or unimodal ordination method Detrended Correspondence Analysis (DCA) was conducted upon the palynological assemblage data (Ter Braak & Prentice 1988). To calculate the species turnover I extracted the site scores for the first axis of the DCA. Principal Component Analysis (PCA) was used to infer similarities between samples and the change in trajectories of composition of taxa through time applying a singular value decomposition of the centered but not scaled data matrix, this a linear relationship to the underlying gradient. Finally, I performed a Canonical Correspondence Analysis (CCA) to quantify the relationship between environmental variables (fire and herbivory) and the palynological assemblage data. Ellipse's representing the discreat Zones were calculated using standard parameterization (cos(theta + d/2), cos(theta - d/2)), where cos(d) is the correlation of the parameters was applied (see Murdoch & Chow, 1996). Statistical analysis and presentation of data was performed using packages Vegan (Oksanen et al. 2015) and Rioja (Juggins et al. 2009) in base R (R Core Team, 2012).

3.4 Results

Chronology and Resolution

The age-depth model indicates that the sedimentary core (545-105cm) spans the past 6000 years from between 4000B.C.E. to 1522C.E. There is no evidence for any hiatus in the sequence (Figure 3.3). The general outlier model (see Ramsey, 2008) identified six dates which did not converge with the sequence and thus were removed from the overall age-depth model (Table 3.1). Overall model agreement was high (96.7) and represented an average age range of 177 years surrounding the median modelled age (with a range of 36-465 years). The average age between radiocarbon samples is 183 years (with a range of 5-589 years).

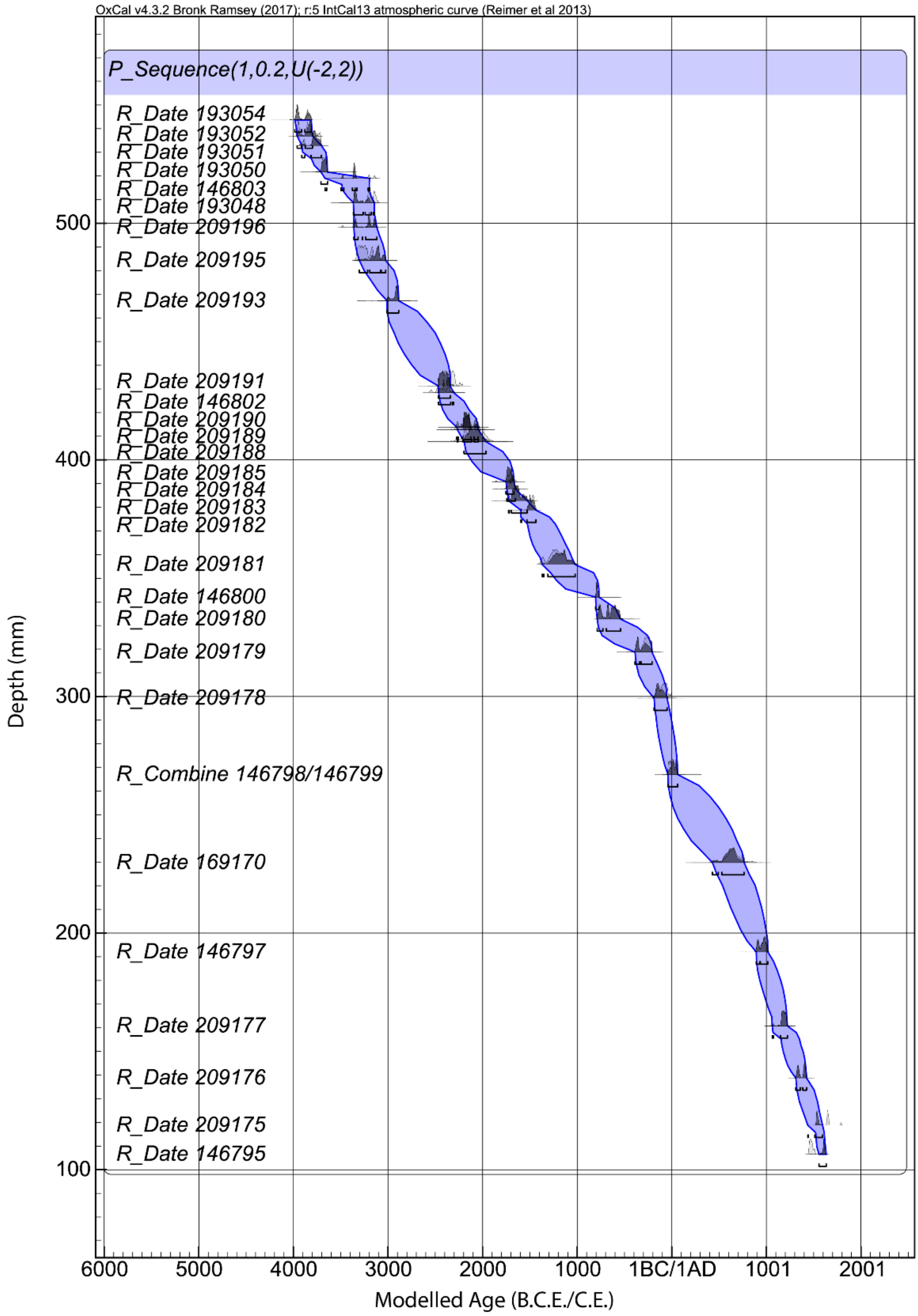


Figure 3.3 Age depth model for Cenote Kail.

Palaeoecological Trends

Three statistically significant Zones were identified using the broken stick model (Figures 3.4 & 3.5). Seventy-six taxa were recognised in the palynological sequence extracted from Cenote Kail. Throughout the sequence *Pinus, Quercus* and *Morella cerifera* dominate the arboreal component while Compositae and Poaceae are the most abundant herbaceous taxa (Figure 3.5). Temporal spacing between samples is as follows: (i) Zone 1 represents an average spacing of 130 years spanning 1800 years (with a range of 68-415 years); (ii) Zone 2 represents an average spacing of 137 years spanning 2300 years (with a range of 53-192 years); and, (iii) Zone 3 represents an average of 90 years spanning 1400 years (with a range of 68-160 years).

Results from the CCA show that microscopic and macroscopic charcoal are significant environmental variables most associated with Zones 2 & 3, while *Sporormiella* is most associated with Zone 1 and is not statistically significant (Figure 3.4a). The PCA displays a distinct gradient and several associations between taxa and samples (Figure 3.4b). The first axis represents 20.2% of the variation, while axis 2 represents 10.5% of the variation. The arch between samples suggests that there is only one clear gradient. To help visualise this gradient, when the independently calculated palynological Zones are superimposed upon these quadrants it is clear that the top and bottom right quadrants are most associated with Zone 1, the top left quadrant is most associated with Zone 2 and the bottom left quadrant is most associated with Zone 3 (Figure 3.4b). The first taxonomic association is comprised of canopy taxa *Quercus,* understory taxa Leguminosae, *Myrica,* Ericaceae and the herbaceous and agrarian taxa *Capsicum* which is most associated with Zone 1. The second taxonomic association is comprised of understory taxa *Juniperus* and *Cercocarpus* and herbaceous taxa Polygalaceae, Apiaceae, Compositae *Aphelandra* and agrarian taxa Capsicum most associated with Zone 2. The third taxonomic association is comprised of canopy taxa *Pinus, Alnus* and *Liquidambar* together with understory taxa

Morella cerifera and herbaceous taxa Poaceae and Campanulaceae which is most associated with Zone 3 (Figure 3.4b).

Zone 1 (545.75-421cm, 14 samples, 4000-2200B.C.E.) spans c.1800 years concurrent with the last 2000 years of the Archaic Period (10,000-2000B.C.E.) (Figure 3.5). This Zone is predominantly defined by POF taxa *Quercus* (25.9%) and *Pinus* (11%) alongside herbaceous taxa Compositae (27.6%). Between 4000-3300 B.C.E. there is evidence for a decline in canopy taxa (from 61.3-37.3% of the total pollen sum), particularly *Quercus* (18-9.7%). In contrast *Pinus* became abundant during this period rising from 4000B.C.E. (2.3%) through to 3300B.C.E. (16.7%). *Myrica* and *Alnus* are mostly present throughout this Zone notably peaking at 3100B.C.E. (15.3%). *Brosimum* (0-4.3%), Anacardiaceae (0.3-4.3%), Leguminosae (0-6.3%), *Morella cerifera* and Rubiaceae (0-9%) are present in low abundance and on average decrease from 4000-2200B.C.E.

The ratio of coniferous to MHWF is on average 30:70. The coniferous to MHWF ratio changes from 25:75 to 66:34 between 3700-3300B.C.E.. Compositae abundance increases between 4000-3200B.C.E. (17.3-35.3%) and peaks at 2900B.C.E. (53.3%) and 2700B.C.E. (47.3%). Amaranthaceae is present at 10.3% from 4000B.C.E. but subsequently declines leading up to 3700B.C.E. (1.3%). *Capsicum* enters the record and increases from 3850-3300 B.C.E. (0.3-5.3%). Polygalaceae follows an identical trend peaking at 3300B.C.E. (4.3%). Poaceae is stable and in low abundance (2.3-5.6%). Macroscopic and microscopic charcoal are relatively low decreasing between 4000-3000B.C.E. (macroscopic charcoal: 0.44-0.32 particles cm^2yr^1; and, microscopic charcoal: 552-86 particles cm^2yr^1) and then increasing through to 2300B.C.E (macroscopic: 1.2 particles cm^2yr^1; and, microscopic: 770 particles cm^2yr^1). Pollen influx is also low decreasing from 4000-3300B.C.E. (965-344 grains $x10^3$ cm^2yr^{-1}) and increasing after 2300B.C.E. (1,919 grains $x10^4$ cm^2yr^{-1}). *Sporomiella* abundance is relatively high and stable (2.6-10.5%) falling below 4% abundance at 3100B.C.E. (2.6%), 2700B.C.E. (2.9%) and 2320B.C.E. (3.8%). There is a sustained high abundance of >10% between 2600-2500B.C.E. (10.2-13.3%).

Zone 2 (412 –263.5cm, 17 samples, 2200B.C.E – 100C.E.) covers 2100 years, covering the Early, Middle and Late Pre-Classic Periods (2000-B.C.E. – 100C.E.) and is defined by arboreal taxa *Quercus*, *Pinus* and *Morella cerifera* and herbaceous taxa Compositae, Poaceae and *Zea mays* (Figure 3.5). *Quercus* continues to dominate the arboreal component (23%); however, decreases between 1550-970B.C.E. (34-6%). After 970B.C.E. (6%) *Quercus* recovers through to 550B.C.E. (43%) before decreasing rapidly by 350C.E. (17.3%) and stabilising by 100C.E. (13%). *Pinus* continues to be persistently present and in stable abundance with slight increases between 1550-650B.C.E. (4.6-17.7%) and a larger increase from 340B.C.E. – 100C.E. (6.3-28.3%). The ratio of coniferous to MHWF taxa continues to favour MHWF taxa, particularly *Quercus* (47:63) with a turnover to more coniferous taxa between 1150-970B.C.E. (17:83-74:26) and 230B.C.E. – 50C.E. (4:6-7:3). *Morella cerifera* first substantially enters the record from 970B.C.E. (10.3%) but does not establish until 230B.C.E. where it rises to the second most abundant forest taxa through to 100C.E. (19.7%). Prior to the arrival of *Zea mays* (c.1000B.C.E.), Amaranthaceae abundance briefly increases c.1150B.C.E. (5.3%).The rise of *Zea mays* from 970B.C.E. (8.6%) peaks at 930B.C.E. (17%) and is abundant until 650B.C.E. (4.6%). Polygalaceae re-establishes between 1350-750B.C.E. (4-3.3%). Poaceae begins to increase from 1150B.C.E (2%) through to 100C.E. (11.5%), while Compositae remains the dominant herbaceous taxa (33.1%).

Pollen influx is high during this Zone peaking at 1150B.C.E. (175 $x10^4$ grains cm^2yr^{-1}), and declining at 970B.C.E. (577 $x10^3$ grains cm^2yr^{-1}) and between 650-550B.C.E. (810 – 781 $x10^3$ grains cm^2yr^{-1}) and 340-130B.C.E. (881- 798 $x10^3$ grains cm^2yr^{-1}). Macroscopic charcoal rises substantially after 1150B.C.E. (1.25 particles cm^2yr^1) through to 50C.E. (24.9 particles cm^2yr^1). Microscopic charcoal follows a similar trend; however, begins to increase from the beginning of this Zone (1163 particles cm^2yr^1) and peaks at 970B.C.E. (4004 particles cm^2yr^1) increasing again from 650 B.C.E. – 50C.E. (911- 5660 particles cm^2yr^1). *Sporormiella* continues to be high in abundance and stable (0.6-8.8%) but on average is lower (4.4%) than in Zone 1 (7.2%). There are particularly high abundances of *Sporormiella* from 2100B.C.E. (7.4%) to 1750B.C.E. (8.8%), 930B.C.E (6.5%) and at 550B.C.E. (7.7%).

Zone 3 (254.5-114cm, 15 samples, 100-1522C.E.) encompasses c.1400 years and is defined by the arboreal components: *Pinus, Quercus, Morella cerifera,* and *Liquidambar,* and herbaceous components: Compositae and Poaceae (Figure 3.5). This zone is representative of the Terminal Preclassic (150-250C.E.), Classic (250-950C.E.) and Post-Classic Periods (950-1522C.E.). *Quercus* and *Morella cerifera* decline between 200-1070C.E. (30-4.7%) while *Pinus* increases (21.3-64%). *Liquidambar* establishes and rises from 1070C.E. (0.7%) through to 1522C.E. (9.3%). Of the remaining MHWF canopy taxa, *Alnus* increases after 850.C.E. (1.3%) through to 1150C.E. (6.3%) and then again from 1200-1522C.E. (0.7-6.3%). The coniferous to MHWF ratio is reversed between 100-1522C.E. (78:22) in favour of coniferous taxa. Compositae remains in high abundance (22.9%) but decreases after 850C.E. (45.3%) through to 1522C.E. (7.7%). Poaceae increases from 200-650C.E. (15.7-28%). Influx of macroscopic and microscopic charcoal decreases from 200-1000C.E. (macroscopic charcoal: 0.44-0.32 particles cm^2yr^1; and, microscopic charcoal: 552-86 particles cm^2yr^1)**.** Pollen Influx decreases from 200C.E. through to 1522C.E. (10-20 $x10^4$ grains cm^2yr^{-1}). *Sporormiella* abundance increases from 70B.C.E. (0.9%) through to 200C.E. (7.1%) then decreases down until the end of this Zone (4.1%). Overall *Sporormiella* abundance is comparatively lower (3.3%) than in Zone 2 (4.4%).

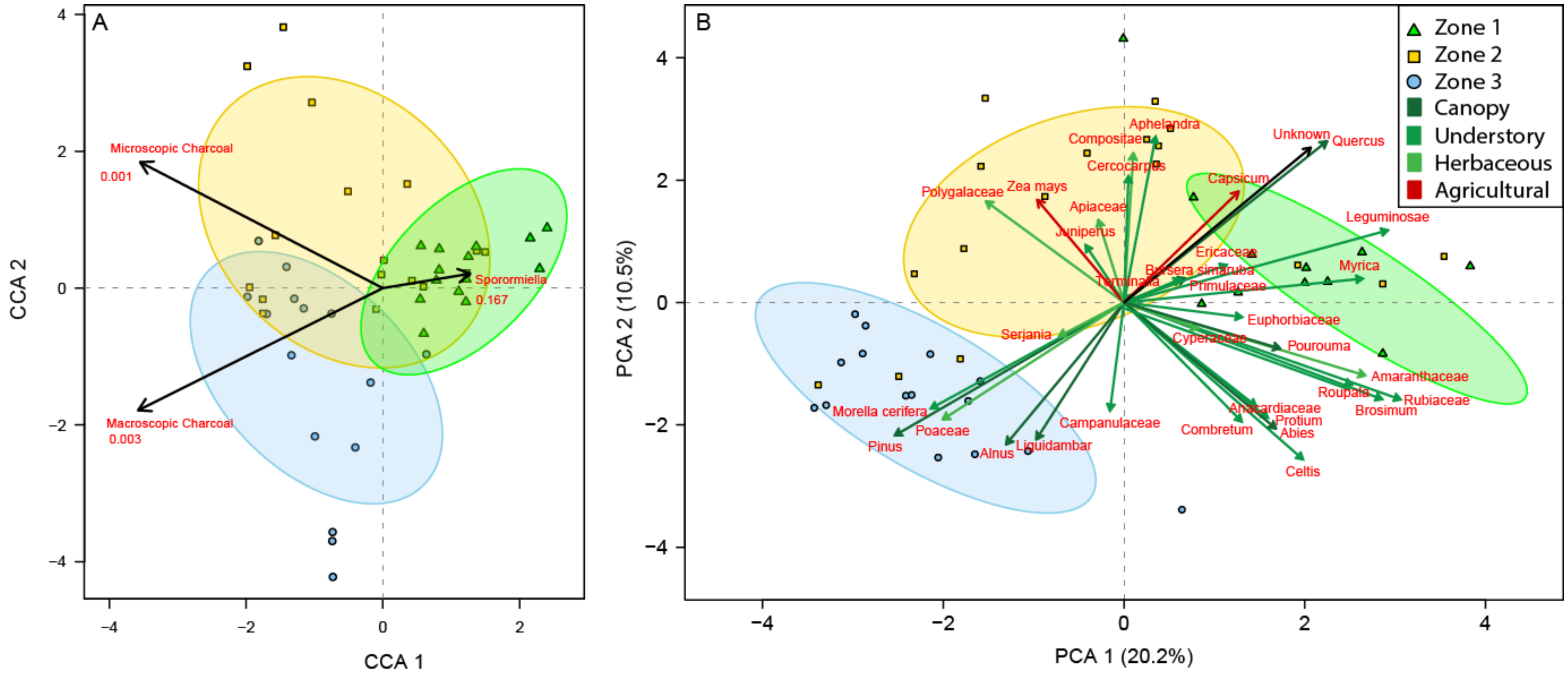


Figure 3.4 Canonical correspondence analysis of the palaeopalynological data set ordinated against independent environmental indicators of local fire (macroscopic charcoal), regional fire (microscopic charcoal), and herbivory (*Sporormiella*) (A). Principal component analysis of the palaeopalynological data set (B). Zones are derived from the broken stick model and are represented by ellipses at a confidence of 95%. Zone 1 = green triangles; Zone 2 = yellow squares; Zone 3 = blue circles.

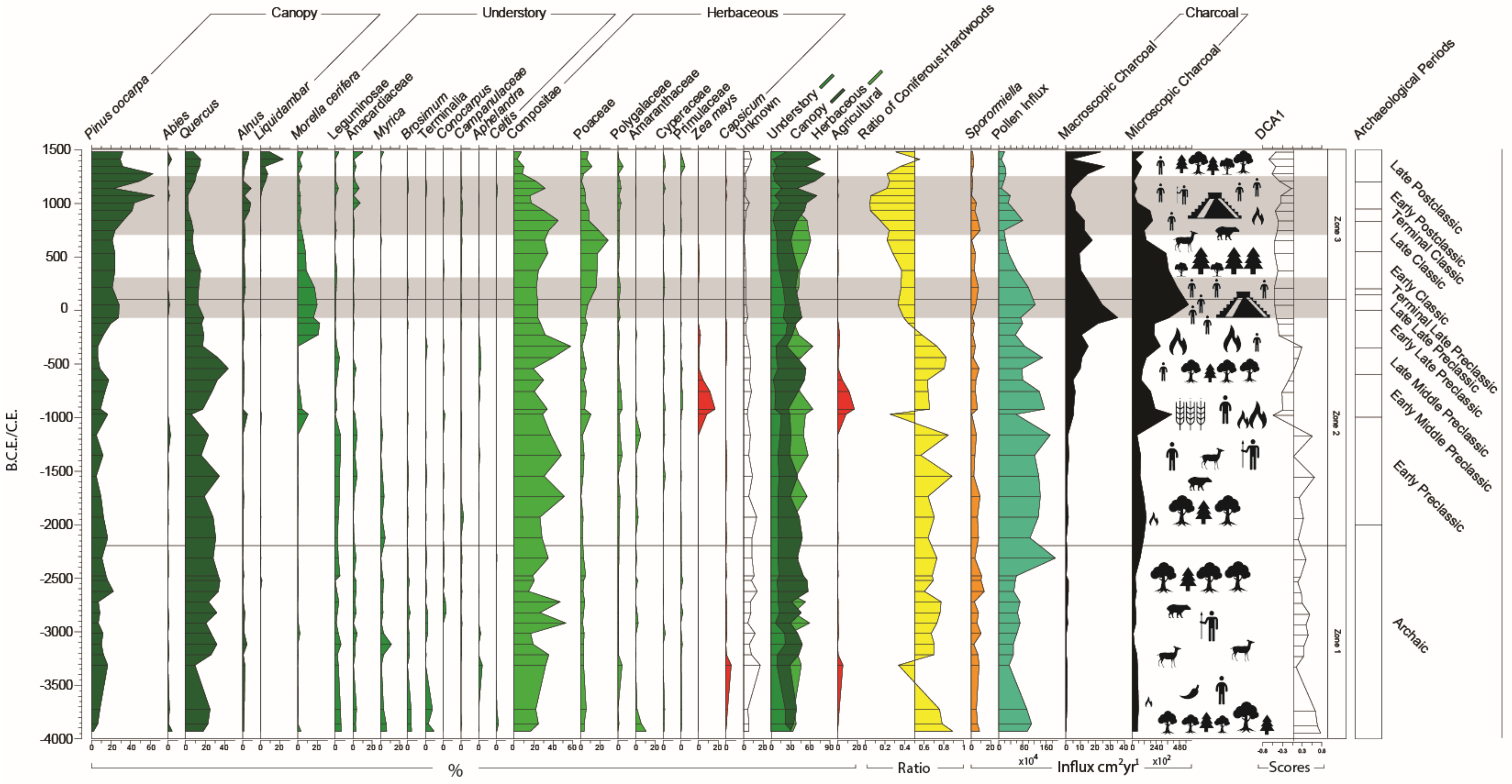


Figure 3.5 Palynological percentage diagram of taxa appearing in an abundance greater than 2%; forest structure; coniferous to hardwood ratio; pollen influx; macroscopic and microscopic influx; DCA axis 1; and Occupation of Chinkultic (dark bands). The palynological data are expressed as a percentage of total land pollen.

3.5 Discussion

The Natural Baseline Vegetation

This sequence represents the vegetation dynamics of the Maya uplands of Guatemala over the past 6000 years. Our data indicates that the natural baseline of this region is best described as OF to MPOF a finding also reported in Kappelle (2006). This deciduous coniferous mosaic of oak dominated forests largely persists from 4000-230B.C.E. after which, the vegetation assemblage deviates away from the natural baseline towards pine dominated forests. Deviation from the natural baseline was attributed to extensive and prolonged anthropogenic settlement and activities surrounding agrarian practices and architectural developments. While our record suggests that this region has been predominantly forested through time, there is clear evidence for compositional changes in flora as a direct result of anthropogenic activities particularly between 3700-3300B.C.E. and from 1000B.C.E.-1524C.E. (Figure 3.5). The transition from MPOFs in Zone 1 (4000-2200B.C.E.) through to PFs in Zone 3 (100-1522C.E.) is reflected in the taxonomic associations of the PCA and the environmental drivers presented in the CCA (Figure 3.4a & 3.4b).

Anthropogenic Impacts and Agrarian Practices

Archaeological records have widely found that after c.1800B.C.E. village farming became firmly established across the wider Maya Area (Neff et al. 2006). This is reflected in the interpretations of the reconstructed palynological assemblages for both the lowlands and the uplands (Figure 3.2). Disturbance driven by anthropogenic activities, such as: (i) agricultural practices (e.g. Dull, 2004a; 2004b; 2007); (ii) rearing livestock (Lovell, 1985); (iii) timber extraction (e.g. Dull, 2004a; 2004b; 2007; Velez et al. 2011); and (iv) lime production (Anderson & Wahl, 2016), can initiate or maintain local vegetation succession impacting: (i) forest composition, (ii) structure, and (iii) regeneration (Gonzalez-Espinosa et al. 1991).

Evidence from Cenote Kail suggests that people were manipulating the uplands of Guatemala from at least c.4000B.C.E. and practicing agriculture from c.3850B.C.E. This is the earliest palynological evidence for agriculture in the Southern Maya Area, preceding evidence from lowland Pacific Guatemala and from El Salvador, which all indicate agrarian practices established from c.3500B.C.E. (Dull, 2004a; Neff et al. 2006).

Evidence for agriculture from Centote Kail is first indicated by vegetation changes from 4000B.C.E. The observed changes include (i) a decline in canopy and understory taxa; (ii) increases in weedy disturbance taxa; (iii) a very small increase in local and regional burning; (iv) and the presence of cultivated taxa *Capsicum* (White, 1999), between c.3850-3300B.C.E. (Figure 3.5). Archaic populations from the Maya Area combined agriculture (e.g. pepper, beans, maize, squash and chili) with hunting and gathering from as early as 5200B.C.E. (Pope et al. 2001). A mixture of traditional hunter-gather practices combined with limited agriculture is exemplified by the abundance and variety of edible fruits and nuts (e.g. *Brosimum*, *Myrica* and Anacardiaceae) and high abundance of fauna as indicated by the influx of *Sporormiella*.

I hypothesise that agriculture started in and spread from the uplands to the lowlands driven by increasingly favourable climatic conditions in the lowlands, brought about after the Holocene Thermal Maximum (6000-3000BC.E.) (Ford & Nigh, 2009). Human populations dispersed with the expansion of the lowland forests (Rosenmeier et al. 2002; Hillesheim et al. 2005; Neff et al. 2006; Wahl et al. 2006; 2014; Bush et al. 2009; Mueller et al. 2009; Escobar et al. 2012), increasingly interacting with the tropical forest ecosystem and gaining ethnobotanical knowledge (Ford & Nigh, 2009). Little is known about the Pre-Columbian human habitation of the upland Maya Areas, particularly during the Archaic, due to a scant archaeological record (MacNeish, 1982; Clark & Cheetham, 2002; Lohse, 2006; 2009). Our results from Cenote Kail provide evidence for occupation of the uplands from c.4000B.C.E.; and suggest that agriculture was practiced in the uplands before it was brought to the lowlands.

The start of the Pre-Classic (2000B.C.E.) is marked by the first appearance of state level settlements and an increased reliance on domesticated crops, particularly *Zea mays* (Neff et al. 2006). Settlements and agriculture were concentrated around water bodies, such as Cenotes, which provided reliable access to fresh water for sustenance and agriculture (Lucero et al. 2014). Although pollen records have been used to document the spread of maize agriculture in the Maya Area, most of these records are in the lowlands (Figure 3.1). Consequently, our understanding of the initial arrival of maize in the uplands of Central America is poor. Traditional *Zea mays* agriculture is evident in the record extracted from Cenote Kail from 970B.C.E. This is late compared to the uplands of El Salvador, c.2500B.C.E. (Dull, 2004a); however, the relative palynological abundance of *Zea mays* found in Cenote Kail, suggests that the expanse of agriculture was much greater. Agriculture in this region precedes the development of the nearest archaeological temple complex, Chinkultic, by c.900 years and culminated c.400 years before the settlement was established (Ball, 1980). This could be interpreted as a migration of upland populations, to lowland settlement and state level societal establishment.

Zea mays agriculture is typically associated with Milpa (e.g. Dull, 2004a; 2004b; 2007). Milpa entails a five to ten year cycle between periods of cultivation and fallow (Cowgill, 1962). Intensification of Milpa cycling due to increasing human populations commonly lead to the depletion of nutrients in the soil (Ford & Nigh, 2009). After 550B.C.E I suggest that the agricultural settlement surrounding Cenote Kail was abandoned in favour of more productive soils nearby.

By c.350B.C.E. large pyramids were being built across the Maya Area including the establishment of Chinkultic c.50B.C.E. (Ball, 1980). These pyramids were typically covered in plaster for architectural as well as decorative purposes (Anderson & Wahl, 2016). The production of this lime plaster involved the burning of powdered limestone (Oates, 2008). Monuments built during the Pre-Classic period were covered in this plaster (Hansen, 2001; 2012; Anderson & Wahl, 2016). Hansen (2012) reports that floor thickness alone could exceed 13cm, which is far more than was structurally necessary. Anderson & Wahl (2016) explore the amount of fuel required to produce sufficient lime to meet the demands of this monument building and the impact that this might have had on the forest environment. They calculate 192km^2 of forest would have been required for burning to create enough plaster for the construction of El Mirador in the central Maya Area. While Chinkultic is significantly smaller than El Mirador, the required plaster to create the complex of temples and ball courts would have been extensive. I suggest that the large increase of macroscopic and microscopic charcoal from c.200B.C.E. relates to the production of lime plaster at Chinkultic, coinciding with its founding and absence of evidence for agriculture. The extraction of wood from the surrounding forests for burning is reflected in the structure of these POFs as well as patterns for local and regional burning.

Forest structure, composition, and successional regeneration

Relatively equal abundances of canopy, understory, and herbaceous taxa from 4000-3700B.C.E. indicate a diverse and stratified forest structure comprised of at least three vegetative levels. The high diversity of taxa, particularly in the understory (e.g Leguminosae, Anacardiaceae, *Myrica* and Rubiaceae), suggests a relatively low and open canopy allowing light through onto the forest floor (Bush, 2000). This structure is typical of middle succession in mixed POF after a large clearance event (Peterson & Reich, 2001).

Anthropogenic impacts, as indicated by agricultural grains and reductions in forest taxa in Zone 1 occur between c.4000-3300B.C.E. Disturbance to the natural vegetation baseline was likely caused by settlement and agrarian practices directly surrounding Cenote Kail. After 3300B.C.E. cultivation ceases and arboreal taxa (understory and canopy) re-establish within c.100 years (3200-3100B.C.E.). This follows the expected recovery time of c.80 years for POFs (Kappelle, 2006; Figueroa-Rangel et al. 2008).

By 2600B.C.E. the mature structure of the POF are well established and persist in relative equilibrium until further anthropogenic disturbance from 1150C.E. Weedy disturbance taxa (e.g. Amaranthaceae), reductions in canopy taxa (e.g. *Quercus*) and the creation of more open habitats exemplify anthropogenic disturbance prior to the agrarian establishment of *Zea mays* (e.g. Dull, 2004a; 2004b; 2007). Deforestation, agrarian cultivar, and increased regional burning surrounding Cenote Kail all coincide from c.1000B.C.E. (Figure 3.5) and are attributed to the expansion and development of the Pre-Classic Maya (e.g. Neff et al. 2006). Increases in local and regional burning from the onset of Pre-Classic agriculture marks the sustained decline and eventual transition of POFs to pine dominated forests.

Plant community composition after burning is strongly dictated by: (i) the sprouting ability of dominant species; (ii) the ability of subdominant species to increase in numbers; and (iii) the failure of invasive species to become established (Elliot 1999, McDonald 2003). Many species of oak rapidly sprout from their root collar after burning (e.g. *Quercus insignis*, *Q. skinneri*), dominating early successional stands (Barnes & Van Lear, 1980; Kirby & Watkins, 2015); however, several species of pine have also adapted to cope with fires through the development of thick bark, serotiny, rapid growth, and sprouting, including *Pinus teocote* and *P. pseudostrobus* (Richardson, 2000; Rodriguez-Trejo & Fule, 2003). The early successional formation of oak dominance is evident between 970-550B.C.E. (Figure 5). As the forest becomes more established oak abundance typically diminishes under faster growing conifers (Sheffer, 2012).

Extraction of wood, sustained land clearance, and most importantly burning has changed the structure of the POF from oak dominated to Pine dominated (Figure 3.5). Additionally, herbivores, such as the white tailed deer (*Odocoileus virginianus*) may have also impacted forest composition and regeneration through selective browsing on young saplings and individual species (Vera, 2000; Kirby & Watkins, 2015). The coppice systems created by the Maya are particularly vulnerable to browsing from medium and large sized herbivores such as the white-tailed deer (Joyce & Dolman, 2004). Pines have been found to be preferentially browsed compared to other arboreal taxa (Blair & Brunett, 1980). While overall herbivore abundance decreases through time their browsing impacts upon forest structure may have been particularly important to recovery after prolonged disturbance (Joyce & Dolman, 2004). The negative correlation between the Sporormiella and charcoal may also be explained by fuel limitations following grazing.

The pine dominated forests become increasingly established between 150B.C.E. - 1070C.E. (Figure 3.5). When coniferous forests form closed stands they drastically change the environment beneath them. The most substantial changes involve the greater uptake of soil water and decrease of light that can reach the ground (Jucker et al. 2014). The combination of these factors makes it almost impossible for other arboreal taxa to reproduce and grow (Kapple, 2006). For example, most species of Oak suffer increased reproductive failure under closed canopy conditions (Jucker et al. 2014) relying on the dispersal of acorns to forest edges or clearings through animal transport (Lopez-Barrera, 2003; Kapple, 2006). Large herbivores, such as the Baird tapir (*Tapirus bairdii*), are important to the structure and diversity of recovering POFs due to their role as long distance seed dispersers, ingesting whole seeds and dropping them intact with their faeces (Bodmer, 1991; Rodriques et al. 1993; Fragoso, 1997; Olmos 1997; Lawton, 2000). The reduction of herbivore abundance during the transition of Oak dominated POFs to Pine dominated POFs (c.220B.C.E.) is likely to have contributed to the established rise in Pine.

Coniferous forest stands remain dominant until they are removed through felling or die of disease, insect attack or old age (Jones, 1974). The transition from pine dominated coniferous forests to MHWF's is gradual and relies upon the breakup of the coniferous forest canopy to allow for secondary canopy taxa to rise through (Jones, 1974). The establishment of *Quercus*, *Liquidambar* and *Alnus* after c.850C.E. demonstrates this final transition back to MHWF dominance (Figure 3.5).

Results from this study indicate that fire has been the most important driver of vegetative change in this ecosystem throughout the last 6000 years, particularly during the Pre-Classic and Classic periods (2000B.C.E. - 950C.E.). Fire driven change from MHWF (oak-dominated) to coniferous forests (pine-dominated) has previously been attributed to climate driven aridity (e.g. Figueroa-Rangel et al. 2008; 2010; 2012); however, our study suggests that anthropogenic activity is the most likely source of burning and overall vegetative change. The predominantly anthropogenic signal for burning represented in Cenote Kail is inferred through the combined evidence of: (i) agricultural practices; (ii) reduction of MHWF taxa; and (iii) rapid increase of burning coinciding with the establishment and expansion of nearby Maya temples and settlements (e.g. Chinkultic).

Terrestrial hydroclimatic reconstructions from the upland Maya Area suggest that only modest changes in precipitation amounts occurred over the last several millennia. Climatic evidence from Lago Amatitlan indicates lower lake levels from 250B.C.E.-125C.E. and 875-1375C.E. which has been attributed to a decline in water level resulting from either a drier climate and/or reforestation after anthropogenic abandonment (Velez et al. 2011), while evidence from San Lorenzo (Chiapas) indicates periods of drought from c.700-500B.C.E. and c.850-1200C.E. (Franco-Gaviria et al. 2018).

Further, these records suggest that although climate may have played an abetting role in driving forest dynamics, anthropogenic activities ultimately drove the observed forest changes. Our findings suggest that anthropogenic activities revolving around agriculture and architectural developments, have initiated and maintained successive regeneration of vegetation from mixed oak dominated forests to pine dominated forests; however, further work investigating past hydroclimate changes for this region will be required to fully understand the role of climate as an independent driver of this system.

3.6 Conclusions

The POFs within the Southern Maya area were transformed by Pre-Columbian human populations through practices of agriculture and architectural developments over thousands of years extending back into the Archaic Period (Betz 1997; Piperno & Pearsall 1998; Smith 1998; Dull, 2004a; Neff et al. 2006). Three successional phases can be discerned following a combination of natural and anthropogenically modified successional pathways. The Archaic period is defined by light anthropogenic disturbance, centred around some land clearance for agriculture. I present the earliest evidence for agriculture in the southern Maya Area, preceding neighbouring upland and lowland sites by c.350 years. *Zea mays* cultivation is prevalent from 970-550B.C.E. after which time sedentary agriculture does not appear to be widely practiced. Herbivorous animals, such as deer and tapir, are likely to have played an important role in forest recovery after disturbance; however, discerning their individual impacts would require further research applying emerging techniques in Ancient DNA (Meltzer, 2015). Persistent high intensity burning for lime production during the Late-PreClassic to Classic Period are suggested to have resulted in a turnover of forest structure c.150B.C.E. from oak dominated POF to pine dominated POF. Climax succession towards MHWF after 850C.E. indicates that land use dramatically changed after the initial abandonment at Chinkultic to allow for a complete successional recovery.

Evidence for the fragmentation, degradation and subsequent recovery of these MTFs over the past 6000 years provides a valuable comparison for the present-day anthropogenic activities that are driving current changes in this region. To protect the remaining intact fragments of these MTFs and to encourage the recovery of areas that have suffered past compositional or structural shifts, fire needs to be carefully managed.

3.7 Acknowledgements

The authors would like to thank both reviews and the editor for their thoughtful, constructive and insightful comments. This research was funded by the Natural Environment Research Council of the United Kingdom NE/L002612/1, US National Science Foundation EAR-1502989 and St Edmund Hall, University of Oxford. Gillian Petrokofsky is funded by a European Commission LIFE+ grant.

3.8 References

Abbott, M.B. and Stafford, T.W., 1996. Radiocarbon geochemistry of modern and ancient Arctic lake systems, Baffin Island, Canada. *Quaternary Research*, *45*(3), pp.300-311.

Anderson, L. and Wahl, D., 2016. Two Holocene paleofire records from Peten, Guatemala: Implications for natural fire regime and prehispanic Maya land use. *Global and Planetary Change*, *138*, pp.82-92.

Arroyo- Rodríguez, V., Melo, F.P., Martínez- Ramos, M., Bongers, F., Chazdon, R.L., Meave, J.A., Norden, N., Santos, B.A., Leal, I.R. and Tabarelli, M., 2017. Multiple successional pathways in human- modified tropical landscapes: new insights from forest succession, forest fragmentation and landscape ecology research. *Biological Reviews*, 92(1), pp.326-340.

APSA, 2007. The Australasian Pollen and Spore Atlas V1.0. Australian National University, Canberra. Available at: http://apsa.anu.edu.au/ [Accessed 13/06/2018].

Baker, A.G., Cornelissen, P., Bhagwat, S.A., Vera, F.W. and Willis, K.J., 2016. Quantification of population sizes of large herbivores and their long- term functional role in ecosystems using dung fungal spores. Methods in Ecology and Evolution, 7(11), pp.1273-1281.

Ball J.W., 1980. The Archaeological Ceramics of Chinkultic, Chiapas, Mexico. *New World Archaeological Foundation*, (43).

Barnes, T.A. and Van Lear, D.H., 1998. Prescribed fire effects on advanced regeneration in mixed hardwood stands. *Southern Journal of Applied Forestry*, *22*(3), pp.138-142.

Bennett, J.P., 1974. Concepts of mathematical modeling of sediment yield. *Water Resources Research*, *10*(3), pp.485-492.

Bennett, K.D., 1994. Confidence intervals for age estimates and deposition times in late-Quaternary sediment sequences. *The Holocene*, *4*(4), pp.337-348.

Bennett, K.D. and Humphry, R.W., 1995. Analysis of late-glacial and Holocene rates of vegetational change at two sites in the British Isles. *Review of Palaeobotany and Palynology*, *85*(3-4), pp.263-287.

Bennett, K.D., 1996. Determination of the number of zones in a biostratigraphical sequence. *New Phytologist*, *132*(1), pp.155-170.

Bennett, K.D. and Willis, K.J., 2001. Pollen. Tracking Environmental Change Using Lake Sediements. Volume 3: Terrestrial, Algal, and Siliceous Indicators.

Betz, V. 1997. Early plant domestication in Mesoamerica. Athena Review 2:24–31.

Blair, R.M. and Brunett, L.E., 1980. Seasonal browse selection by deer in a southern pine-hardwood habitat. *The Journal of Wildlife Management*, pp.79-88.

Bodmer, R.E., 1991. Strategies of seed dispersal and seed predation in Amazonian ungulates. *Biotropica*, pp.255-261.

Bowman, D.M., Balch, J., Artaxo, P., Bond, W.J., Cochrane, M.A., D'antonio, C.M., DeFries, R., Johnston, F.H., Keeley, J.E., Krawchuk, M.A. and Kull, C.A., 2011. The human dimension of fire regimes on Earth. *Journal of biogeography*, *38*(12), pp.2223-2236.

Breedlove, D. E. 1981. Flora of Chiapas, Part 1: Introduction to the Flora of Chiapas. The California Academy of Sciences, San Francisco.

Burleigh, R., 1974. Radiocarbon dating: some practical considerations for the archaeologist. *Journal of Archaeological Science*, *1*(1), pp.69-87.

Bush, M.B., 2000. Deriving response matrices from Central American modern pollen rain. *Quaternary Research*, *54*(1), pp.132-143.

Bush, M.B., Correa-Metrio, A.Y., Hodell, D.A., Brenner, M., Anselmetti, F.S., Ariztegui, D., Mueller, A.D., Curtis, J.H., Grzesik, D.A., Burton, C. and Gilli, A., 2009. Re-evaluation of climate change in lowland Central America during the Last Glacial Maximum using new sediment cores from Lake Petén Itzá, Guatemala. In *Past Climate Variability in South America and Surrounding Regions* (pp. 113-128). Springer, Dordrecht.

Bush, M.B. and Weng, C., 2007. Introducing a new (freeware) tool for palynology. *Journal of Biogeography*, *34*(3), pp.377-380.

Caffrey, M.A., Taylor, M.J. and Sullivan, D.G., 2011. A 12,000-year record of vegetation and climate change from the Sierra de Los Cuchumatanes, Guatemala. *Journal of Latin American Geography*, pp.129-151.

Clark, R.L., 1982. Point count estimation of charcoal in pollen preparations and thin sections of sediments. *Pollen et spores*.

Clark, J.S., 1988. Particle motion and the theory of charcoal analysis: source area, transport, deposition, and sampling. *Quaternary Research*, *30*(1), pp.67-80.

Clark, J.E., and Cheetham D. 2002. Mesoamerica's Tribal Foundations. In The Archaeology of Tribal Societies, edited by William A. Parkinson, pp. 278-339.

Cochrane, M.A. and Barber, C.P., 2009. Climate change, human land use and future fires in the Amazon. *Global Change Biology*, *15*(3), pp.601-612.

Colunga-GarcíaMarín, P. and Zizumbo-Villarreal, D., 2004. Domestication of plants in Maya LowlandsDomesticacion de plantas en las tierras bajas Mayas. *Economic Botany*, *58*(1), pp.101-S110.

Coe, M.D. and Houston, S.D., 1966. *The Maya*. London: Thames and Hudson.

Corrales, L., Bouroncle, C. and Zamora, J.C., 2015. An overview of forest biomes and ecoregions of Central America. In *Climate Change Impacts on Tropical Forests in Central America* (pp. 33-54). Routledge.

Cowgill, U.M., 1962. An agricultural study of the southern Maya lowlands. *American Anthropologist*, *64*(2), pp.273-286.

Davis, O.K. and Shafer, D.S., 2006. *Sporormiella* fungal spores, a palynological means of detecting herbivore density. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *237*(1), pp.40-50.

Dinerstein, E., Olson, D., Joshi, A., Vynne, C., Burgess, N.D., Wikramanayake, E., Hahn, N., Palminteri, S., Hedao, P., Noss, R. and Hansen, M., 2017. An ecoregion-based approach to protecting half the terrestrial realm. *BioScience*, *67*(6), pp.534-545.

Dull, R.A., 2004a. An 8000-year record of vegetation, climate, and human disturbance from the Sierra de Apaneca, El Salvador. *Quaternary Research*, *61*(2), pp.159-167.

Dull, R.A., 2004b. A Holocene record of Neotropical savanna dynamics from El Salvador. Journal of Paleolimnology, 32(3), pp.219-231.

Dull, R.A., 2007. Evidence for Forest Clearance, Agriculture, and Human- Induced Erosion in Precolumbian El Salvador. *Annals of the Association of American Geographers*, *97*(1), pp.127-141.

Elliott, K.J., Hendrick, R.L., Major, A.E., Vose, J.M. and Swank, W.T., 1999. Vegetation dynamics after a prescribed fire in the southern Appalachians. *Forest Ecology and Management*, *114*(2-3), pp.199-213.

Escobar, J., Hodell, D.A., Brenner, M., Curtis, J.H., Gilli, A., Mueller, A.D., Anselmetti, F.S., Ariztegui, D., Grzesik, D.A., Pérez, L. and Schwalb, A., 2012. A∼ 43-ka record of paleoenvironmental change in the Central American lowlands inferred from stable isotopes of lacustrine ostracods. Quaternary Science Reviews, 37, pp.92-104.

Ford, A. and Nigh, R., 2009. Origins of the Maya forest garden: Maya resource management. *Journal of Ethnobiology*, *29*(2), pp.213-236.

Foster, D.R. and Lindbladh, M., 2010. Dynamics of Long-lived Foundation Species: The History of Quercus in Southern Scandinavia.

Figueroa-Rangel, B.L., Willis, K.J. and Olvera-Vargas, M., 2008. 4200 years of pine-dominated upland forest dynamics in west- central Mexico: human or natural legacy. *Ecology*, *89*(7), pp.1893-1907.

Figueroa-Rangel, B.L., Willis, K.J. and Olvera-Vargas, M., 2010. Cloud forest dynamics in the Mexican neotropics during the last 1300 years. *Global Change Biology*, *16*(6), pp.1689-1704.

Figueroa-Rangel, B.L., Willis, K.J. and Olvera-Vargas, M., 2012. Late-Holocene successional dynamics in a transitional forest of west-central Mexico. *The Holocene*, *22*(2), pp.143-153.

Franco-Gaviria, F., Correa-Metrio, A., Cordero-Oviedo, C., López-Pérez, M., Cárdenes-Sandí, G.M. and Romero, F.M., 2018. Effects of late Holocene climate variability and anthropogenic stressors on the vegetation of the Maya highlands. Quaternary Science Reviews, 189, pp.76-90.

Gavin, D.G., Brubaker, L.B. and Lertzman, K.P., 2003. An 1800-year record of the spatial and temporal distribution of fire from the west coast of Vancouver Island, Canada. *Canadian Journal of Forest Research*, *33*(4), pp.573-586.

González- Espinosa, M., Quintana- Ascencio, P.F., Ramírez- Marcial, N. and Gaytán-Guzmán, P., 1991. Secondary succession in disturbed Pinus- Quercus forests in the highlands of Chiapas, Mexico. *Journal of Vegetation Science*, *2*(3), pp.351-360.

Hansen, R.D., 2001. The first cities: The beginnings of urbanization and state formation in the Maya Lowlands. *Maya: divine kings of the rain forest*, pp.50-65.

Hansen, R.D., 2012. The beginning of the end: conspicuous consumption and environmental impact of the Preclassic lowland Maya. *An Archaeological Legacy: Essays in honor of Ray T. Matheny*, pp.243-291.

Haug, G.H., Hughen, K.A., Sigman, D.M., Peterson, L.C., Rohl, U., 2001. Southward migration of the Intertropical Convergence Zone through the Holocene. Science 293, 1304 – 1308.

Higuera, P.E., Peters, M.E., Brubaker, L.B. and Gavin, D.G., 2007. Understanding the origin and analysis of sediment-charcoal records with a simulation model. *Quaternary Science Reviews*, *26*(13-14), pp.1790-1809.

Higuera, P.E., Gavin, D.G., Bartlein, P.J. and Hallett, D.J., 2011. Peak detection in sediment–charcoal records: impacts of alternative data analysis methods on fire-history interpretations. *International Journal of Wildland Fire*, *19*(8), pp.996-1014.

Hillesheim, M.B., Hodell, D.A., Leyden, B.W., Brenner, M., Curtis, J.H., Anselmetti, F.S., Ariztegui, D., Buck, D.G., Guilderson, T.P., Rosenmeier, M.F. and Schnurrenberger, D.W., 2005. Climate change in lowland Central America during the late deglacial and early Holocene. *Journal of Quaternary Science*, *20*(4), pp.363-376.

Hodell, D.A., Curtis, J.H., Jones, G.A., Heguera-Gundy, A., Brenner, M., Binford, M.W., Dorsey, K.T., 1991. Reconstruction of Caribbean climate over the past 10,500 years. Nature 352, 790 – 793.

Ingersoll, C.A., 1826. A view of South America and Mexico. H. Huntington, JB., New York.

Islebe, G.A., Hooghiemstra, H., Brenner, M., Curtis, J.H., 1996. A Holocene vegetation history from lowland Guatemala. The Holocene 6, 265 – 271.

Islebe, G.A. and Hooghiemstra, H., 1997. Vegetation and climate history of montane Costa Rica since the last glacial. *Quaternary Science Reviews*, *16*(6), pp.589-604.

Jeffers, E.S., Nogué, S. and Willis, K.J., 2015. The role of palaeoecological records in assessing ecosystem services. *Quaternary Science Reviews*, *112*, pp.17-32.

Jones, J.R., 1974. Silviculture of southwestern mixed conifers and aspen: the status of our knowledge. Res. Pap. RM-122. Fort Collins, CO: US Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station. 44 p, 122.

Joys, A.C., Fuller, R.J. and Dolman, P.M., 2004. Influences of deer browsing, coppice history, and standard trees on the growth and development of vegetation structure in coppiced woods in lowland England. *Forest Ecology and Management*, *202*(1-3), pp.23-37.

Jucker, T., Bouriaud, O., Avacaritei, D., Dănilă, I., Duduman, G., Valladares, F. and Coomes, D.A., 2014. Competition for light and water play contrasting roles in driving diversity–productivity relationships in Iberian forests. *Journal of Ecology*, *102*(5), pp.1202-1213.

Juggins, S., Juggins, M.S., WA, W. and IKFA, M., 2009. Package ‘rioja’.

Kappelle, M., 2006. Neotropical montane oak forests: overview and outlook. In *Ecology and conservation of neotropical montane oak forests* (pp. 449-467). Springer, Berlin, Heidelberg.

Keever, C., 1950. Causes of succession on old fields of the Piedmont, North Carolina. *Ecological Monographs*, *20*(3), pp.229-250.

Kirby, K. and Watkins, C., 2015. Europe's changing woods and forests: from wildwood to managed landscapes. CABI.

Lawton, R.O., 2000. Baird’s tapir. Monteverde: ecology and conservation of a tropical cloud forest, pp.242-243.

Lawton, R.O., Nair, U.S., Pielke, R.A. and Welch, R.M., 2001. Climatic impact of tropical lowland deforestation on nearby montane cloud forests. Science, 294(5542), pp.584-587.

Livingstone, D.A., 1955. A lightweight piston sampler for lake deposits. *Ecology*, *36*(1), pp.137-139.

Lohse, J.C., J. Awe, C. Griffith, R. Rosenswig, and F. Valdez. 2006 Preceramic Occupations in Belize: Updating the Paleoindian and Archaic record. Latin American Antiquity 17: 209–226.

Lohse, J.C. 2009 The Archaic to Preclassic transition in Belize: What We Know and Why We Don't Know More. Research Reports in Belizean Archaeology 6:141–150.

Lopez-Barrera. 2003. Edge effects in a forest mosaic: Implications for Oak regeneration in the Highlands of Chiapas, Mexico.PhD Thesis. University of Edinburgh, Edinburgh.

Lucero, L.J., Fedick, S.L., Dunning, N.P., Lentz, D.L. and Scarborough, V.L., 2014. 3 Water and Landscape: Ancient Maya Settlement Decisions. *Archeological Papers of the American Anthropological Association*, *24*(1), pp.30-42.

Lynch, J.A., Clark, J.S. and Stocks, B.J., 2004. Charcoal production, dispersal, and deposition from the Fort Providence experimental fire: interpreting fire regimes from charcoal records in boreal forests. *Canadian Journal of Forest Research*, *34*(8), pp.1642-1656.

MacNeish, R.S. 1982 Third Annual Report of the Belize Archaic Archaeological Reconnaissance. Robert S. Peabody Foundation for Archaeology, Andover.

Maher, L.J., 1981. Statistics for microfossil concentration measurements employing samples spiked with marker grains. *Review of Palaeobotany and Palynology*, *32*(2-3), pp.153-191.

Martin, A.C. and Harvey, W.J., 2017. The Global Pollen Project: a new tool for pollen identification and the dissemination of physical reference collections. *Methods in Ecology and Evolution*, *8*(7), pp.892-897.

Martínez, M.L., Pérez-Maqueo, O., Vázquez, G., Castillo-Campos, G., García-Franco, J., Mehltreter, K., Equihua, M. and Landgrave, R., 2009. Effects of land use change on biodiversity and ecosystem services in tropical montane cloud forests of Mexico. *Forest Ecology and management*, 258(9), pp.1856-1863.

McDonald, R.I., Peet, R.K. and Urban, D.L., 2003. Spatial pattern of Quercus regeneration limitation and Acer rubrum invasion in a Piedmont forest. *Journal of Vegetation Science*, *14*(3), pp.441-450.

Meltzer, D.J., 2015. Pleistocene overkill and North American mammalian extinctions. *Annual Review of Anthropology*, *44*, pp.33-53.

Metcalfe, S.E., Barron, J.A. and Davies, S.J., 2015. The Holocene history of the North American Monsoon:'known knowns' and 'known unknowns' in understanding its spatial and temporal complexity. Quaternary Science Reviews, 120, pp.1-27.

Miranda, F., 1952. *La vegetación de Chiapas, primera parte*. Ediciones Del Gobierno Del Estado Seccion Autografica Departmento De Prensa Y Turismo.

Mueller, A.D., Islebe, G.A., Hillesheim, M.B., Grzesik, D.A., Anselmetti, F.S., Ariztegui, D., Brenner, M., Curtis, J.H., Hodell, D.A. and Venz, K.A., 2009. Climate drying and associated forest decline in the lowlands of northern Guatemala during the late Holocene. Quaternary Research, 71(2), pp.133-141.

Muller, C.H., 1942. *The Central American species of Quercus*(No. 477). US Government Printing Office.

Neff, H., Pearsall, D.M., Jones, J.G., Arroyo, B., Collins, S.K. and Freidel, D.E., 2006. Early Maya adaptive patterns: Mid-late Holocene paleoenvironmental evidence from Pacific Guatemala. Latin American Antiquity, 17(3), pp.287-315.

Oates, J.A., 2008. Lime and limestone: chemistry and technology, production and uses. John Wiley & Sons.

Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Wagner, H. and Oksanen, M.J., 2015. Package 'vegan'.

Olmos, F., 1997. Tapirs as seed dispersers and predators. *Tapirs: status survey and conservation action plan*, pp.3-9.

OxLEL, 2016. Pollen Preparation Procedure. Oxford Long-Term Ecology Lab. Protocols. Available at: https://oxlel.zoo.ox.ac.uk/wp-content/uploads/2016/10/OxLEL-Fossil-pollen-extraction-protocol.pdf [Accessed 13/06/2018].

Peters, M.E. & Higuera, P.E., 2007. Quantifying the source area of macroscopic charcoal with a particle dispersal model. *Quaternary Research*, *67*(2), pp.304-310.

Peterson, D.W. and Reich, P.B., 2001. Prescribed fire in oak savanna: fire frequency effects on stand structure and dynamics. *Ecological Applications*, *11*(3), pp.914-927.

Piperno, D.R. and D.M. Pearsall. 1998 The Origins of Agriculture in the Lowland Neotropics. Academic Press, San Diego.

Pope, K.O., Pohl, M.E., Jones, J.G., Lentz, D.L., Von Nagy, C., Vega, F.J. and Quitmyer, I.R., 2001. Origin and environmental setting of ancient agriculture in the lowlands of Mesoamerica. Science, 292(5520), pp.1370-1373.

Potapov, P., Hansen, M.C., Laestadius, L., Turubanova, S., Yaroshenko, A., Thies, C., Smith, W., Zhuravleva, I., Komarova, A., Minnemeyer, S. and Esipova, E., 2017. The last frontiers of wilderness: Tracking loss of intact forest landscapes from 2000 to 2013. *Science Advances*, 3(1), p.e1600821.

R Core Team (2012). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Ramsey, C. B. (2008). Deposition models for chronological records. *Quaternary Science Reviews*, *27*(1-2), 42-60.

Ramsey, C.B., 2009. Bayesian analysis of radiocarbon dates. *Radiocarbon*, *51*(1), pp.337-360.

Reimer, P.J., Bard, E., Bayliss, A., Beck, J.W., Blackwell, P.G., Ramsey, C.B., Buck, C.E., Cheng, H., Edwards, R.L., Friedrich, M. and Grootes, P.M., 2013. IntCal13 and Marine13 radiocarbon age calibration curves 0–50,000 years cal BP. *Radiocarbon*, *55*(4), pp.1869-1887.

Richardson, D.M. ed., 2000. *Ecology and biogeography of Pinus*. Cambridge University Press.

Rodríguez-Trejo, D.A. and Fulé, P.Z., 2003. Fire ecology of Mexican pines and a fire management proposal. *International Journal of Wildland Fire*, *12*(1), pp.23-37.

Rodrigues, M., Olmos, F. and Galetti, M., 1993. Seed dispersal by tapir in southeastern Brazil. *Mammalia*, *57*(3), pp.460-461.

Rosenmeier, M.F., Hodell, D.A., Brenner, M., Curtis, J.H., 2002a. A 4000-year lacustrine record of environmental change in the Southern Maya Lowlands, Peten, Guatemala. Quat. Res. 57, 183-190.

Roubik, D.W. and Moreno, P., 1991. Pollen and spores of Barro Colorado Island [Panama]. *Pollen and spores of Barro Colorado Island [Panama].*, *36*.

Rzedowski, J., 2006. Vegetación de México. 1ra. Edición digital, Comisión Nacional para el Conocimiento y Uso de la Biodiversidad, México, 504.

Sheffer, E., 2012. A review of the development of Mediterranean pine–oak ecosystems after land abandonment and afforestation: are they novel ecosystems?. *Annals of Forest Science*, *69*(4), pp.429-443.

Smith, B.D., 1998. Between foraging and farming. *Science*, *279*(5357), pp.1651-1652.

Ter Braak, C.J. and Prentice, I.C., 1988. A theory of gradient analysis. In Advances in ecological research (Vol. 18, pp. 271-317). Academic Press.

Thompson, L.G., Mosley-Thompson, E., Davis, M.E., Lin, P.-N., Henderson, K.A., Cole-Dai, J., Bolzan, J.F., Liu, K.-b., 1995. Late Glacial Stage and Holocene tropical ice core records from Huascara´n, Peru. Science 269, 46 – 50.

Turner, B.L. and Miksicek, C.H., 1984. Economic plant species associated with prehistoric agriculture in the Maya lowlands. *Economic botany*, *38*(2), pp.179-193.

Velez, M.I., Curtis, J.H., Brenner, M., Escobar, J., Leyden, B.W. and Popenoe de Hatch, M., 2011. Environmental and cultural changes in highland Guatemala inferred from Lake Amatitlán sediments. Geoarchaeology, 26(3), pp.346-364.

Vera, F.W.M., 2000. *Grazing ecology and forest history*. CABI publishing.

Wahl, D., Byrne, R., Schreiner, T. and Hansen, R., 2006. Holocene vegetation change in the northern Peten and its implications for Maya prehistory. *Quaternary Research*, *65*(3), pp.380-389.

Wahl, D., Byrne, R. and Anderson, L., 2014. An 8700 year paleoclimate reconstruction from the southern Maya lowlands. *Quaternary Science Reviews*, *103*, pp.19-25.

Watson, J.E., Evans, T., Venter, O., Williams, B., Tulloch, A., Stewart, C., Thompson, I., Ray, J.C., Murray, K., Salazar, A. and McAlpine, C., 2018. The exceptional value of intact forest ecosystems. *Nature Ecology & Evolution*, pp.1.

White, C.D., 1999. Reconstructing Ancient Maya Diet. University of Utah Press.

Whitlock, C. and Larsen, C., 2002. Charcoal as a fire proxy. In *Tracking environmental change using lake sediments* (pp. 75-97). Springer, Dordrecht.

Willard, D.A., Bernhardt, C.E., Weimer, L., Cooper, S.R., Gamez, D. and Jensen, J., 2004. Atlas of pollen and spores of the Florida Everglades. *Palynology*, *28*(1), pp.175-227.

3.9 Supplementary Information

Table 3.2 Sites represented on Figures 3.1 & 3.2.

Vegetation			
Name of Site	Longitude	Latitude	References
Agua Caliente	16.16667	-89	Walsh et al. 2014
Aguada Chilonche	16.8	-90.0333	Brenner et al. 1990
Aguada Chimj	16.85	-90.1333	Brenner et al. 1990
Aguada Petapilla	14.867	-89.125	Rue et al. 2002; McNeil et al. 2010
Aguada Zacatal Nakbe	17.66907	-89.7928	Wahl et al. 2007
Biosphere Reserve of Los Petenes	20.13125	-90.4546	Gutiérrez-Ayala et al. 2012
Cenote Aktun Ha	20.27429	-87.4862	Gabriel et al. 2009
Coba	20.49151	-87.7387	Leyden et al. 1998
Cobweb Swamp	17.93772	-88.3664	Jone, 1994; Pohl et al. 1996
El Palmar	17.22809	-89.7615	Torrescano & Islebe, 2006; Luzzadder-Beach et al. 2017
La Encrucijada Biosphere Reserve	15.14967	-92.751	Joo-Chang et al. 2015
Lago Amatitlan	14.45639	-90.5661	Velez et al. 2011
Lago Naja	16.991	-91.5916	Domínguez-Vázquez & Isleb, 2008
Lago Oquevix	16.64869	-89.7502	Brenner et al. 1990
Lago Paixban	17.81556	-90.1208	Anderson & Wahl, 2016; Wahl et al. 2016
Lago Peten Itza	16.998	-89.779	Islebe et al. 1996; Curtis et al. 1998; Hillesheim et al. 2005; Mueller et al. 2009; 2010; Correa-Metrio et al. 2012
Lago Puerto Arturo	17.53333	-90.1833	Wahl et al. 2006; 2007; 2014; Anderson & Wahl, 2016
Lago Sacnab	17.06141	-89.3636	Deevey, 1979
Lago Salpeten	16.98333	-89.6667	Leyden, 1987
Lago Silvituc	18.372	-90.2948	Torrescano-Valle & Islebe, 2015
Lago Tzib	19.29693	-88.0701	Carrillo-Bastos et al. 2010
Lago Yaxha	17.06255	-89.4053	Deevey et al. 1979
Lago Yojoa	14.87372	-87.9838	Rue, 1987
Laguana las Pozas	16.2	-90.1	Johnston et al. 2001
Laguna Cuzcachapa	13.98323	-89.6713	Dull, 2007
Laguna del Espino	13.57	-89.52	Dull, 2004a
Laguna Verde	13.85417	-89.8856	Dull, 2004b
Laguna Yaloch	17.30972	-89.1747	Wahl et al. 2013
Lower Rio Naranjo	14.53871	-92.2023	Neff et al. 2006
Manchon	14.51711	-92.1188	Neff et al. 2006
Miqul Meadow	15.42344	-91.4387	Caffrey et al. 2011

New River Lagoon	17.66667	-88.6667	Rushton et al. 2013
Puerto Morelos	20.84907	-86.8784	Islebe & Sánchez, 2002
Ria Lagartos Biosphere Reserve	21.57944	-88.0722	Aragón-Moreno et al. 2012
San Andres	18.14063	-93.9886	Pope et al. 2001
Sibun River	17.47205	-88.2609	Monacci et al. 2011
Sipacate	13.94102	-90.6297	Neff et al. 2006
Hydroclimate			
Aguada X'caamal	20.60167	-89.7025	Hodell et al. 2005
Cenote Aktun Ha	20.27429	-87.4862	Gabriel et al. 2009
Chen Ha Cave	17	-89	Pollock et al. 2016
Coba	20.49151	-87.7387	Whitmore et al. 1996
Hillbank	17.59937	-88.6992	Metcalfe et al. 2009
La Vaca Perdida	20.37297	-89.5692	Smyth et al. 2017
Laberinto del Fauno	20.5874	-87.134	Medina-Elizalde et al. 2016
Lago Amatitlan	14.45639	-90.5661	Velez et al. 2011
San Lorenzo	16.146739	-91.770819	Franco-Gaviria et al. 2018
Esmeralda	16.118323	-91.725880	Franco-Gaviria et al. 2018
Lago Chichancanab	19.87	-88.77	Hodel et al. 1995; 2001
Lago Peten Itza	16.91667	-89.8333	Curtis et al. 1998; Hillesheim et al. 2005; Mueller et al. 2009; Pérez et al. 2010; Escobar et al. 2012
Lago Puerto Arturo	17.53333	-90.1833	Wahl et al. 2014; Anderson & Wahl, 2016
Lago Salpeten	16.98567	-89.6744	Rosenmeier et al. 2002a; 2002b
Lago Tzib	19.29693	-88.0701	Carrillo-Bastos et al. 2010
Lamanai	17.76333	-88.6519	Metcalfe et al. 2009
Macal Chasm	16.883	-89.108	Webster et al. 2007; Akers et al. 2016
Outpost	17.75195	-88.653	Metcalfe et al. 2009
Punta Laguna	20.64849	-87.6372	Curtis et al. 1996; Hodel et al. 2007
Tzabnah	20.75	-89.4667	Medina-Elizalde et al. 2010
Yok Balum	16.20833	-89.0733	Kennett et al. 2012

References

Akers, P.D., Brook, G.A., Railsback, L.B., Liang, F., Iannone, G., Webster, J.W., Reeder, P.P., Cheng, H. and Edwards, R.L., 2016. An extended and higher-resolution record of climate and land use from stalagmite MC01 from Macal Chasm, Belize, revealing connections between major dry events, overall climate variability, and Maya sociopolitical changes. *Palaeogeography, palaeoclimatology, palaeoecology*, *459*, pp.268-288.

Anderson, L. and Wahl, D., 2016. Two Holocene paleofire records from Peten, Guatemala: Implications for natural fire regime and prehispanic Maya land use. Global and Planetary Change, 138, pp.82-92.

Aragón-Moreno, A.A., Islebe, G.A. and Torrescano-Valle, N., 2012. A~ 3800-yr, high-resolution record of vegetation and climate change on the north coast of the Yucatan Peninsula. Review of palaeobotany and palynology, 178, pp.35-42.

Brenner, M., Leyden, B. and Binford, M.W., 1990. Recent sedimentary histories of shallow lakes in the Guatemalan savannas. Journal of Paleolimnology, 4(3), pp.239-252.

Caffrey, M.A., Taylor, M.J. and Sullivan, D.G., 2011. A 12,000-year Record of Vegetation and Climate Change from the Sierra de Los Cuchumatanes, Guatemala. Journal of Latin American Geography, 10(2), pp.129-151.

Carrillo-Bastos, A., Islebe, G.A., Torrescano-Valle, N. and González, N.E., 2010. Holocene vegetation and climate history of central Quintana Roo, Yucatán Península, Mexico. Review of Palaeobotany and Palynology, 160(3-4), pp.189-196.

Correa-Metrio, A., Bush, M.B., Cabrera, K.R., Sully, S., Brenner, M., Hodell, D.A., Escobar, J. and Guilderson, T., 2012. Rapid climate change and no-analog vegetation in lowland Central America during the last 86,000 years. Quaternary Science Reviews, 38, pp.63-75.

Curtis, J.H., Hodell, D.A. and Brenner, M., 1996. Climate variability on the Yucatan Peninsula (Mexico) during the past 3500 years, and implications for Maya cultural evolution. Quaternary Research, 46(1), pp.37-47.

Curtis, J.H., Brenner, M., Hodell, D.A., Balser, R.A., Islebe, G.A. and Hooghiemstra, H., 1998. A multi-proxy study of Holocene environmental change in the Maya lowlands of Peten, Guatemala. Journal of paleolimnology, 19(2), pp.139-159.

Deevey, E., Rice, D.S., Rice, P.M., Vaughan, H.H., Brenner, M. and Flannery, M.S., 1979. Mayan urbanism: impact on a tropical karst environment. Science, 206(4416), pp.298-306.

Domínguez-Vázquez, G. and Islebe, G.A., 2008. Protracted drought during the late Holocene in the Lacandon rain forest, Mexico. Vegetation History and Archaeobotany, 17(3), pp.327-333.

Dull, R.A., 2004a. A Holocene record of Neotropical savanna dynamics from El Salvador. Journal of Paleolimnology, 32(3), pp.219-231.

Dull, R.A., 2004b. An 8000-year record of vegetation, climate, and human disturbance from the Sierra de Apaneca, El Salvador. Quaternary Research, 61(2), pp.159-167.

Dull, R.A., 2007. Evidence for Forest Clearance, Agriculture, and Human- Induced Erosion in Precolumbian El Salvador. Annals of the Association of American Geographers, 97(1), pp.127-141.

Escobar, J., Hodell, D.A., Brenner, M., Curtis, J.H., Gilli, A., Mueller, A.D., Anselmetti, F.S., Ariztegui, D., Grzesik, D.A., Pérez, L. and Schwalb, A., 2012. A∼ 43-ka record of paleoenvironmental change in the Central American lowlands inferred from stable isotopes of lacustrine ostracods. Quaternary Science Reviews, 37, pp.92-104.

Franco-Gaviria, F., Correa-Metrio, A., Cordero-Oviedo, C., López-Pérez, M., Cárdenes-Sandí, G.M. and Romero, F.M., 2018. Effects of late Holocene climate variability and anthropogenic stressors on the vegetation of the Maya highlands. Quaternary Science Reviews, 189, pp.76-90.

Gabriel, J.J., Reinhardt, E.G., Peros, M.C., Davidson, D.E., van Hengstum, P.J. and Beddows, P.A., 2009. Palaeoenvironmental evolution of Cenote Aktun Ha (Carwash) on the Yucatan Peninsula, Mexico and its response to Holocene sea-level rise. Journal of Paleolimnology, 42(2), pp.199-213.

Gutiérrez-Ayala, L.V., Torrescano-Valle, N. and Islebe, G.A., 2012. Reconstrucción paleoambiental del Holoceno tardío de la reserva Los Petenes, Península de Yucatán, México. Revista mexicana de ciencias geológicas, 29(3), pp.749-763.

Hillesheim, M.B., Hodell, D.A., Leyden, B.W., Brenner, M., Curtis, J.H., Anselmetti, F.S., Ariztegui, D., Buck, D.G., Guilderson, T.P., Rosenmeier, M.F. and Schnurrenberger, D.W., 2005. Climate change in lowland Central America during the late deglacial and early Holocene. Journal of Quaternary Science, 20(4), pp.363-376.

Hodell, D.A., Curtis, J.H. and Brenner, M., 1995. Possible role of climate in the collapse of Classic Maya civilization.

Hodell, D.A., Brenner, M., Curtis, J.H. and Guilderson, T., 2001. Solar forcing of drought frequency in the Maya lowlands. Science, 292(5520), pp.1367-1370.

Hodell, D.A., Brenner, M., Curtis, J.H., Medina-Gonzalez, R., Can, E.I.C., Albornaz-Pat, A. and Guilderson, T.P., 2005. Climate change on the Yucatan Peninsula during the little ice age. Quaternary Research, 63(2), pp.109-121.

Hodell, D.A., Brenner, M. and Curtis, J.H., 2007. Climate and cultural history of the northeastern Yucatan Peninsula, Quintana Roo, Mexico. Climatic Change, 83(1), pp.215-240.

Islebe, G.A., Hooghiemstra, H., Brenner, M., Curtis, J.H. and Hodell, D.A., 1996. A Holocene vegetation history from lowland Guatemala. The Holocene, 6(3), pp.265-271.

Islebe, G. and Sánchez, O., 2002. History of late Holocene vegetation at Quintana Roo, Caribbean coast of Mexico. Plant Ecology, 160(2), pp.187-192.

Johnston, K.J., Breckenridge, A.J. and Hansen, B.C., 2001. Paleoecological evidence of an Early Postclassic occupation in the southwestern Maya lowlands: Laguna Las Pozas, Guatemala. Latin American Antiquity, 12(2), pp.149-166.

Jones, J.G., 1994. Pollen evidence for early settlement and agriculture in northern Belize. Palynology, 18(1), pp.205-211.

Joo-Chang, J.C., Islebe, G.A. and Torrescano-Valle, N., 2015. Mangrove history during middle-and late-Holocene in Pacific south-eastern Mexico. The Holocene, 25(4), pp.651-662.

Kennett, D.J., Breitenbach, S.F., Aquino, V.V., Asmerom, Y., Awe, J., Baldini, J.U., Bartlein, P., Culleton, B.J., Ebert, C., Jazwa, C. and Macri, M.J., 2012. Development and disintegration of Maya political systems in response to climate change. Science, 338(6108), pp.788-791.

Leyden, B.W., 1987. Man and climate in the Maya lowlands. Quaternary Research, 28(3), pp.407-414.

Leyden, B.W., Brenner, M. and Dahlin, B.H., 1998. Cultural and Climatic History of Cobá, a Lowland Maya City in Quintana Roo, Mexico 1. Quaternary Research, 49(1), pp.111-122.

Luzzadder- Beach, S., Beach, T., Garrison, T., Houston, S., Doyle, J., Román, E., Bozarth, S., Terry, R., Krause, S. and Flood, J., 2017. Paleoecology and Geoarchaeology at El Palmar and the El Zotz Region, Guatemala. Geoarchaeology, 32(1), pp.90-106.

McNeil, C.L., Burney, D.A. and Burney, L.P., 2010. Evidence disputing deforestation as the cause for the collapse of the ancient Maya polity of Copan, Honduras. Proceedings of the National Academy of Sciences, 107(3), pp.1017-1022.

Medina-Elizalde, M., Burns, S.J., Lea, D.W., Asmerom, Y., von Gunten, L., Polyak, V., Vuille, M. and Karmalkar, A., 2010. High resolution stalagmite climate record from the Yucatán Peninsula spanning the Maya terminal classic period. Earth and Planetary Science Letters, 298(1-2), pp.255-262.

Medina-Elizalde, M., Burns, S.J., Polanco-Martínez, J.M., Beach, T., Lases-Hernández, F., Shen, C.C. and Wang, H.C., 2016. High-resolution speleothem record of precipitation from the Yucatan Peninsula spanning the Maya Preclassic Period. Global and Planetary Change, 138, pp.93-102.

Metcalfe, S., Breen, A., Murray, M., Furley, P., Fallick, A. and McKenzie, A., 2009. Environmental change in northern Belize since the latest Pleistocene. Journal of Quaternary Science, 24(6), pp.627-641.

Monacci, N.M., Meier-Grünhagen, U., Finney, B.P., Behling, H. and Wooller, M.J., 2011. Paleoecology of mangroves along the Sibun River, Belize. Quaternary Research, 76(2), pp.220-228.

Mueller, A.D., Islebe, G.A., Anselmetti, F.S., Ariztegui, D., Brenner, M., Hodell, D.A., Hajdas, I., Hamann, Y., Haug, G.H. and Kennett, D.J., 2010. Recovery of the forest ecosystem in the tropical lowlands of northern Guatemala after disintegration of Classic Maya polities. Geology, 38(6), pp.523-526.

Mueller, A.D., Islebe, G.A., Hillesheim, M.B., Grzesik, D.A., Anselmetti, F.S., Ariztegui, D., Brenner, M., Curtis, J.H., Hodell, D.A. and Venz, K.A., 2009. Climate drying and associated forest decline in the lowlands of northern Guatemala during the late Holocene. Quaternary Research, 71(2), pp.133-141.

Mueller, A.D., Islebe, G.A., Hillesheim, M.B., Grzesik, D.A., Anselmetti, F.S., Ariztegui, D., Brenner, M., Curtis, J.H., Hodell, D.A. and Venz, K.A., 2009. Climate drying and associated forest decline in the lowlands of northern Guatemala during the late Holocene. Quaternary Research, 71(2), pp.133-141.

Neff, H., Pearsall, D.M., Jones, J.G., Arroyo, B., Collins, S.K. and Freidel, D.E., 2006. Early Maya adaptive patterns: Mid-late Holocene paleoenvironmental evidence from Pacific Guatemala. Latin American Antiquity, 17(3), pp.287-315.

Pérez, L., Bugja, R., Massaferro, J., Steeb, P., Geldern, R.V., Frenzel, P., Brenner, M., Scharf, B. and Schwalb, A., 2010. Post-Columbian environmental history of Lago Petén Itzá, Guatemala. Revista Mexicana de Ciencias Geológicas, 27(3).

Pohl, M.D., Pope, K.O., Jones, J.G., Jacob, J.S., Piperno, D.R., Lentz, D.L., Gifford, J.A., Danforth, M.E. and Josserand, J.K., 1996. Early agriculture in the Maya lowlands. Latin American Antiquity, 7(4), pp.355-372.

Pope, K.O., Pohl, M.E., Jones, J.G., Lentz, D.L., Von Nagy, C., Vega, F.J. and Quitmyer, I.R., 2001. Origin and environmental setting of ancient agriculture in the lowlands of Mesoamerica. Science, 292(5520), pp.1370-1373.

Pollock, A.L., van Beynen, P.E., DeLong, K.L., Polyak, V., Asmerom, Y. and Reeder, P.P., 2016. A mid-Holocene paleoprecipitation record from Belize. Palaeogeography, Palaeoclimatology, Palaeoecology, 463, pp.103-111.

Rosenmeier, M.F., Hodell, D.A., Brenner, M., Curtis, J.H. and Guilderson, T.P., 2002a. A 4000-year lacustrine record of environmental change in the southern Maya lowlands, Peten, Guatemala. Quaternary Research, 57(2), pp.183-190.

Rosenmeier, M.F., Hodell, D.A., Brenner, M., Curtis, J.H., Martin, J.B., Anselmetti, F.S., Ariztegui, D. and Guilderson, T.P., 2002b. Influence of vegetation change on watershed hydrology: implications for paleoclimatic interpretation of lacustrine δ 18 O records. Journal of Paleolimnology, 27(1), pp.117-131.

Rue, D.J., 1987. Early agriculture and early Postclassic Maya occupation in western Honduras. Nature, 326(6110), pp.285-286.

Rue, D., Webster, D. and Traverse, A., 2002. Late Holocene fire and agriculture in the Copan Valley, Honduras. Ancient Mesoamerica, 13(2), pp.267-272.

Rushton, E.A., Metcalfe, S.E. and Whitney, B.S., 2013. A late-Holocene vegetation history from the Maya lowlands, Lamanai, Northern Belize. The Holocene, 23(4), pp.485-493.

Smyth, M.P., Dunning, N.P., Weaver, E.M., van Beynen, P. and Zapata, D.O., 2017. The perfect storm: climate change and ancient Maya response in the Puuc Hills region of Yucatán. antiquity, 91(356), pp.490-509.

Torrescano, N. and Islebe, G.A., 2006. Tropical forest and mangrove history from southeastern Mexico: a 5000 yr pollen record and implications for sea level rise. Vegetation History and Archaeobotany, 15(3), pp.191-195.

Torrescano-Valle, N. and Islebe, G.A., 2015. Holocene paleoecology, climate history and human influence in the southwestern Yucatan Peninsula. Review of Palaeobotany and Palynology, 217, pp.1-8.

Velez, M.I., Curtis, J.H., Brenner, M., Escobar, J., Leyden, B.W. and Popenoe de Hatch, M., 2011. Environmental and cultural changes in highland Guatemala inferred from Lake Amatitlán sediments. Geoarchaeology, 26(3), pp.346-364.

Wahl, D., Byrne, R., Schreiner, T. and Hansen, R., 2006. Holocene vegetation change in the northern Peten and its implications for Maya prehistory. Quaternary Research, 65(3), pp.380-389.

Wahl, D., Schreiner, T., Byrne, R. and Hansen, R., 2007. A paleoecological record from a Late Classic Maya reservoir in the north Petén. Latin American Antiquity, 18(2), pp.212-222.

Wahl, D., Estrada-Belli, F. and Anderson, L., 2013. A 3400 year paleolimnological record of prehispanic human–environment interactions in the Holmul region of the southern Maya lowlands. Palaeogeography, Palaeoclimatology, Palaeoecology, 379, pp.17-31.

Wahl, D., Byrne, R. and Anderson, L., 2014. An 8700 year paleoclimate reconstruction from the southern Maya lowlands. Quaternary Science Reviews, 103, pp.19-25.

Wahl, D., Hansen, R.D., Byrne, R., Anderson, L. and Schreiner, T., 2016. Holocene climate variability and anthropogenic impacts from Lago Paixban, a perennial wetland in Peten, Guatemala. Global and Planetary Change, 138, pp.70-81.

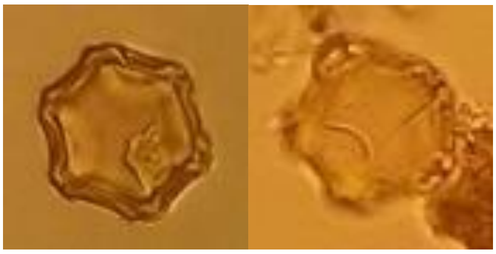
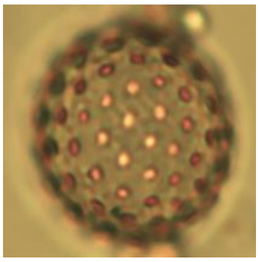
Walsh, M.K., Prufer, K.M., Culleton, B.J. and Kennett, D.J., 2014. A late Holocene paleoenvironmental reconstruction from Agua Caliente, southern Belize, linked to regional climate variability and cultural change at the Maya polity of Uxbenká. Quaternary Research, 82(1), pp.38-50.

Webster, J.W., Brook, G.A., Railsback, L.B., Cheng, H., Edwards, R.L., Alexander, C. and Reeder, P.P., 2007. Stalagmite evidence from Belize indicating significant droughts at the time of Preclassic Abandonment, the Maya Hiatus, and the Classic Maya collapse. Palaeogeography, Palaeoclimatology, Palaeoecology, 250(1-4), pp.1-17.

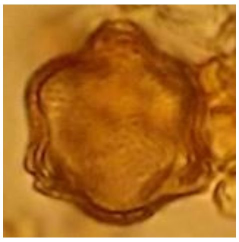
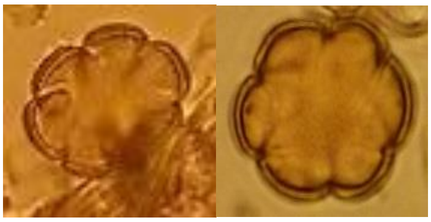
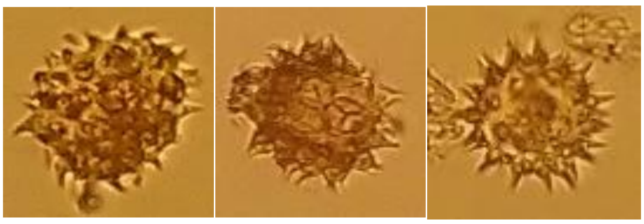
Whitlock, C. and Larsen, C., 2001. 2001: Charcoal as a fire proxy. In Smol, JP, Birks, HJB and Last, WM., editors, Tracking environmental change using lake sediments. Volume 3: terrestrial, algal, and siliceous indicators. Kluwer Academic Publishers, 75-97.

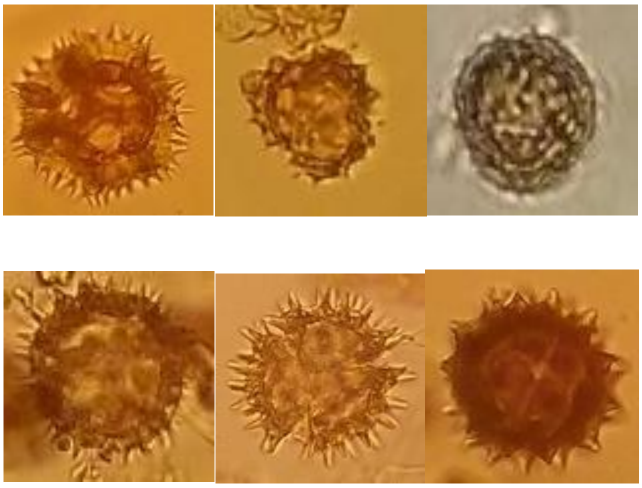
Whitmore, T.J., Brenner, M., Curtis, J.H., Dahlin, B.H. and Leyden, B.W., 1996. Holocene climatic and human influences on lakes of the Yucatan Peninsula, Mexico: an interdisciplinary, palaeolimnological approach. The Holocene, 6(3), pp.273-287.

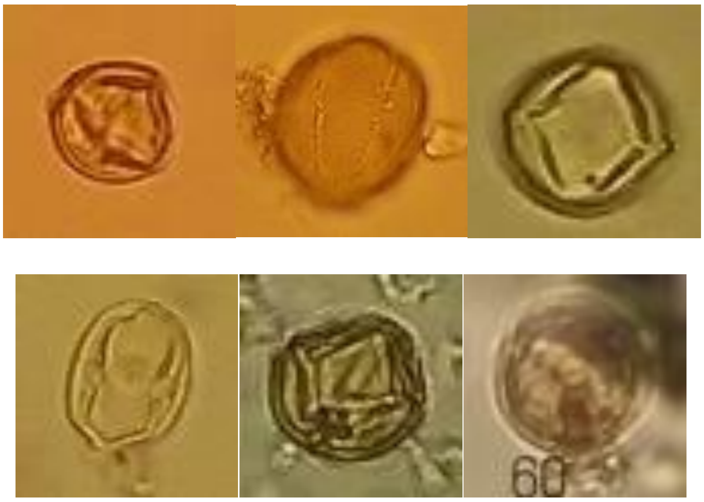
Table 3.3 Images of palynological taxa at 400x magnification identified from Cenote Kail.

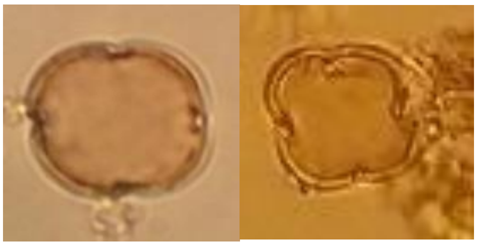
Name	**Image (not to scale)**
Abies	
Alnus	 
Amaranthaceae	 

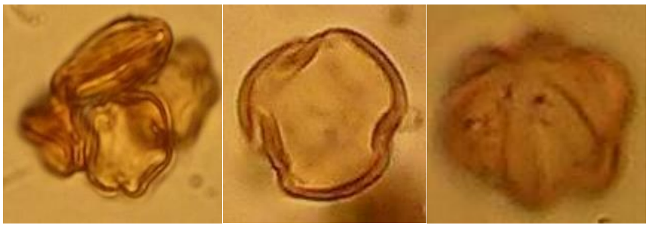
Anacardiaceae	
Aphelandra	
Apiaceae	
Brassicaceae	
Brosimum	

Bursera simaruba	
Campanulaceae	
Capsicum	
Celtis	
Cercocarpus	
Combretum	
Compositae	

	
Cyperaceae	
Ericaceae	
Euphorbiaceae	
Juniperus	

Liquidambar	
Leguminosae	
Morella cerifera	
Myrica	
Pinus oocarpa	

Poaceae	
Polygalaceae	
Pourouma	
Primulaceae	
Protium	
Quercus	

Roupala	
Rubiaceae	
Serjania	
Terminalia	
Zea mays	
Unknown	

4. A PALYNOLOGICAL PERSPECTIVE ON THE IMPACTS OF EUROPEAN CONTACT: HISTORIC DEFORESTATION, RANCHING AND AGRICULTURE SURROUNDING THE CUCHUMATANES HIGHLANDS, GUATEMALA

William J. Harvey[1], Sandra Nogué[2], Nathan Stansell[3], Carole Adolf[1], Peter Long[1], Kathy Willis[1]

[1]Long-Term Ecology Laboratory, Department of Zoology, University of Oxford, Oxford, UK

[2]School of Geography and Environmental Sciences, University of Southampton, Highfield, Southampton, UK

[3]Department of Geology and Environmental Geosciences, Northern Illinois University, De Kalb, IL, USA

To be submitted to Vegetation History and Archaeobotany

4.1 Abstract

The Spanish conquest of the Cuchumatanes highlands (1524-1541C.E.) lead to dramatic land use changes adhering to colonial practices and values, which included the rearing of livestock, agriculture, timber extraction, mining, and the relocation of indigenous populations to new settlements. These changes are often recorded in historical accounts and official records; however, these are sparse, incomplete, and have been lost over the passage of time. Here, I present a high-resolution palaeoenvironmental reconstruction for Cenote Kail (Guatemala) since the Spanish Conquest, to provide additional evidence of land use changes from an integrated multi-proxy perspective. I analysed: (i) fossil pollen; (ii) macroscopic and microscopic charcoal; and (iii) dung fungal spores (*Sporormiella*) from a lake sediment core extracted from Cenote Kail in the Cuchumatanes highlands and remotely sensed satellite data. I reconstructed: (i) forest composition and dynamics; (ii) burning, (iii) fauna abundance, and (iv) agriculture activities. High resolution age-depth modelling was conducted using a combination of Pb^{210} and C^{14} dates. The high temporal resolution enabled a novel integrated validation of the charcoal data sets with remotely sensed satellite data and the historical record. Three stages of floral compositional change were discerned from the palynological assemblage data encompassing: (i) the decline of mountain hard wood forests (MHWF), associated with the building of new settlements, agriculture and timber extraction for fuel (1550-1675C.E.); (ii) pastoral expansions involving the rearing of livestock (1700-1800C.E.); and (iii) the expansions of urban settlements and increasing management of the land (1821-2015C.E.). Bovid seed predation was identified as the dominant factor preventing MHWF from re-establishing in the Cuchumatanes highlands over the past 500 years. Burning, locally and regionally is limited and in line with the modern regime, which suggests that fire has been managed and controlled since European contact.

4.2 Introduction

After European contact and the Spanish conquest of the territory representing modern Guatemala (1524-1541C.E.) the anthropogenic use of land was drastically altered to facilitate the rearing of livestock, agriculture, large scale timber extraction, mining, and new settlements. These were heterogenous across the uplands and lowlands varying in extent, duration and intensity (Thompson, 1958). These practices initially attained to Spanish colonial aspirations following three important ideologies: (i) the church; (ii) the state; and (iii) the ambition of individuals to attain and generate wealth (Lovell, 1985). The Cuchumatanes highlands (Figure 4.1) were subject to drastic land use changes under colonial rule documented in various historical accounts (e.g. Ingersoll, 1826; Thompson, 1958) and official records (e.g. Cortez y Larraz, 1958). In the absence of chronicled accounts or direct measures of land use change, palaeoenvironmental reconstructions of proxy measures can be used to infer impacts and the mechanistic responses of anthropogenic practices across space and through time (e.g. Dull et al. 2004a; 2004b; 2007; Velez et al. 2011).

In this study I apply a multi-proxy approach to independently reconstruct the land use history of the area surrounding the Cuchumatanes highlands after European contact, with the aim to identify how and when anthropogenic practices involving different types of land use change impacted vegetation composition during the past 500 years, and independently validate the catchment area for burning represented by macroscopic and microscopic charcoal using satellite earth observation data.

Integration of remotely sensed satellite data with palaeoecological records is often challenging and rarely attempted due to the resolution of palaeolimnological records and their associated age-depth uncertainties (Metcalfe et al. 2015). Lakes with high sedimentation rates may be precisely dated using ^{210}Pb measurements to give annually resolved sedimentary sequences going back up to 200 years (Oldfield et al. 1984).

Precision dating of lake sediments allows for palaeoecological data and satellite data to be directly compared enabling contemporary validation of the palaeoecological proxy data (e.g. charcoal representing burning) for as long as the satellite instrument has been active (e.g. MODIS since 2000C.E.). I present the first sub-decadal dated palaeolimnological record from this region enabling a high-resolution integrated reconstruction of land-use history since the Spanish Conquest (1524C.E.).

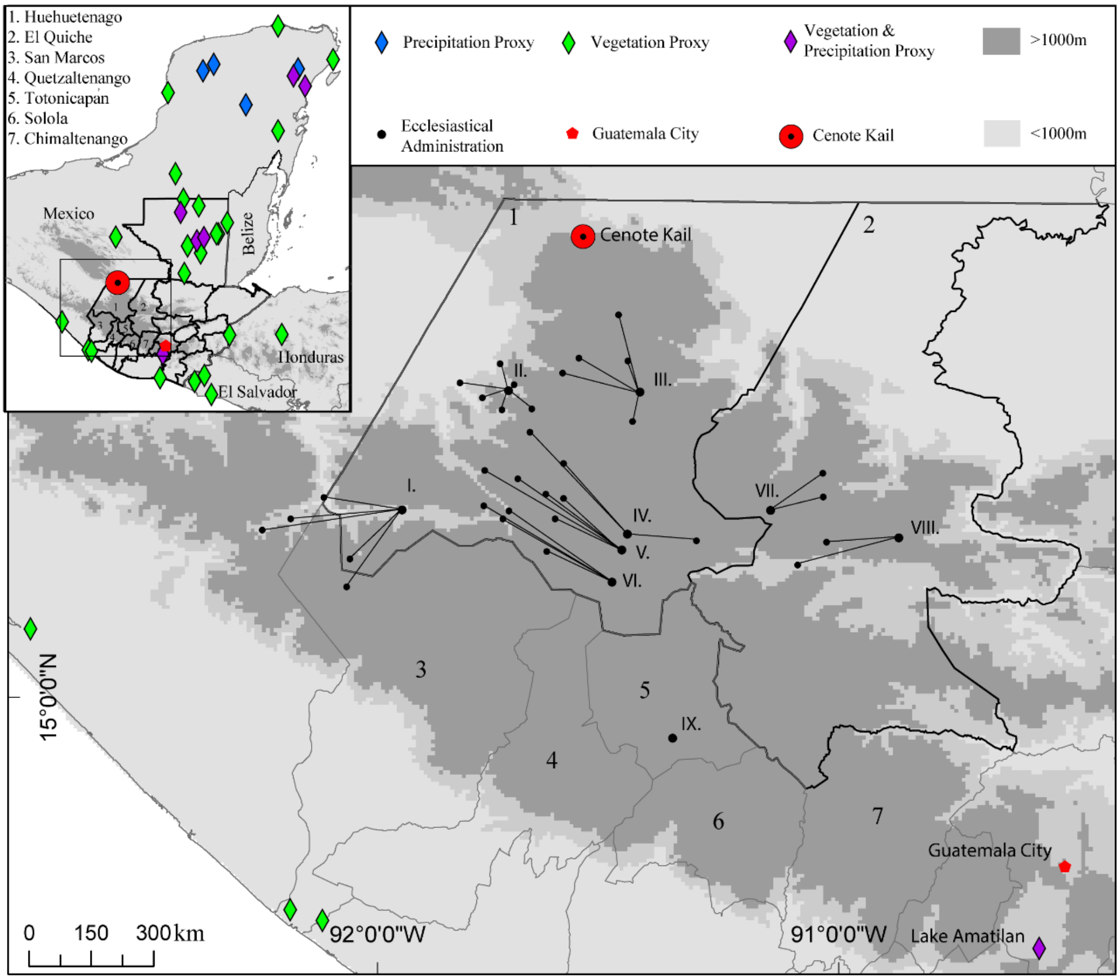


Figure 4.1 Regional Map of the Maya area depicting: (i) Columbian palaeo-climatic and palynological records; (ii) the current departments for the Cuchumatan Highlands; and (iii) colonial ecclesiastical administrative areas and churches: (I) San Andres Cuilco; (II) San Marcos; (III) San Pedro Soloma; (IV) Chiantla; (V) Huehuetenango; (VI) Santa Ana Malacatan; (VII) Santa Maria Nebaj; (VIII) San Miguel Uspantan; and (IX) Totonicapan.

Climate

In the uplands of Guatemala climate (precipitation and temperature) is highly variable and is primarily determined by the altitude rather than latitude (Ingersoll, 1826). Mean annual temperatures range between 14-25 °C, while average rainfall lies between 900-3700mm (Kappelle, 2006). The region is defined as being within the Central American Dry Corridor (CADC), a region of Central America defined by its high rainfall variability between the wet and dry seasons (Bouroncle et al. 2017). Drivers of centennial to decadal scale climate change include a combination of the position of the Inter Tropical Convergence Zone, the North Atlantic Oscillation, and the El Niño Southern Oscillation (ENSO) (Metcalfe et al. 2015). While there are currently no palaeoclimatic precipitation reconstructions for the Cuchumatan highlands, a nearby diatom record from Lake Amatitlán suggests that conditions became increasingly wetter during the Little Ice Age (*c.*1400-1850C.E.) (Velez et al. 2011). The only other palaeoenvironmental precipitation record to have been produced from within the CADC is a $\delta^{18}O$ lake record from lowland Central Pacific Nicaragua (Stansell et al. 2013). This record presents increasingly drier conditions for the LIA. Little else is known about the spatial and temporal dynamics of precipitation for this upland region and therefore further research is warranted to determine if precipitation patterns are homogenous with the northern lowland regions (Figure 4.1) or respond variably (Metcalfe et al. 2015).

Vegetation

The vegetation response to landscape disturbance over the past *c.*500 years is particularly important for understanding the response and resilience of the mixed hard wood forests (MHWFs) and coniferous forests (CF), e.g. pine forests (PFs) and mixed pine-oak forests (POFs), to past and current management practices, particularly those involving natural regeneration and municipal-communal management (Ewel, 1979; Miles, 1987; Focacci et al. 2011; Holder & Chase, 2012). To assess the status of these forests, it is essential to distinguish the stages of succession that have led to its current state (Figueroa-Rangel et al. 2012).

Forest cover across the whole of Guatemala is reported to have declined at an annual rate of 1.2% between 1990 – 2005C.E. (Holder & Chase, 2012). There are very few remaining primary forests outside of the cloud forests in the Sierra de las Minas and several regions in the Petén district (Veblen 1976; Holder, 2006; Holder & Chase, 2012). Secondary forests account for more than 40% of the total forest area in the tropics (Brown & Lugo 1990; Corlett 1995; Willis et al. 2004) forming complex successional groups as they have expanded to recolonise former agricultural landscapes (Tucker 2008; Brady 2009; Redo et al. 2009; Bass 2010). In Guatemala, most of these secondary forests occur on municipal and communal lands, which the local human populations depend on for timber and fuel (Urrea 1995; Reyes 1998; Pira et al. 1999; Gibson 2001; Van Kempen et al. 2009; Holder & Chase, 2012). While the high expense of transporting timber out of the Cuchumatanes highlands has previously precluded this area for commercial logging (Veblen, 1974), a history of deforestation for agrarian expansion has led to many hectares of forests being felled.

Today, the vegetation surrounding the Cuchumatan highlands is comprised of PF, POF, cloud forests (CF), and agricultural/pastoral grasslands (Ramirez-Marcial et al., 2001; Breedlove, 1981; Rzedowski, 2006; Chiabai, 2015; Franco-Gaviria et al. 2018). Of these three vegetation types the PF's are the most widespread, dominated by *Pinus oocarpa* at the canopy level and *Acacia pennatula*, *Myrica cerifera*, and *Vernonia canescens* at the understory level (Franco-Gaviria et al. 2018). The formation of these PF's are most associated with sustained anthropogenic disturbance relating to anthropogenic use of fire and extensive grazing (Ramirez-Marcial et al., 2001).

The impact of European contact

The legacy left by the Maya caused widespread changes to the forests within the Maya Area through burning, for lime production (Hansen, 2001; 2012; Anderson & Wahl, 2016), and agrarian practices involving *Milpa* cycling (Wilken 1971; 1987; Nigh, 2008; Ford & Nigh, 2009), particularly during the Late Pre-Classic (350B.C.E.-250C.E.) and Classic Periods (250-950C.E.) which is when the Maya civilization expanded towards its climax (Chapter 3; Ford & Nigh, 2009). Accompanying the Spanish conquest (1524C.E.), European diseases, slavery and warfare drastically reduced the native population resulting in reduced indigenous anthropogenic pressure on the upland forests (Dull, 2004a; 2007; Velez et al. 2011); however, this was counterbalanced by new pressures of colonial settlements (Jaiuregui, 1894; Remesal, 1932; Lovell, 1985; Van Oss, 1986), grazing (Carranza, 1897; Vasquez, 1944; Veblen, 1976) and resource extraction (Recinos, 1954; Sherman, 1979; Lovell, 1983) as indicated by historical records and accounts. In the Cuchumatanes highlands the native population was reduced from 260,000 to 73,000 between 1520-1550C.E. (Lovell, 1985).

Previous palynological reconstructions linking European contact to the environmental changes in the Maya area are limited; most available records are of low temporal resolution, greater than 200 years between samples (e.g. Deevey et al. 1979; Curtis et al. 1998; Mueller et al. 2009) or are missing sediment from the last c.500 years (e.g. Neff et al. 2006; Caffrey et al. 2011). One palynological study has been previously conducted south of the Cuchumatan highlands (Lago Amatitlán), which reports evidence for deforestation and increased agriculture from c.1600C.E., and greater tree diversity after 1875C.E., including increasing abundance of *Alnus*, *Eugenia*, and *Morella* (Velez et al. 2011).

Across the wider Maya area (Yucatan Peninsula, Belize, Guatemala, El Salvador, and Northern Honduras), 29 sites have been previously investigated presenting palynological reconstructions spanning from c.1500C.E. through to present (Figure 4.1). Evidence for widespread forest recovery is supported after the initial arrival of the Spanish (c.1500-1600C.E.) across lowland Guatemala (Brenner et al. 1990; Wahl, 2016; Anderson & Wahl, 2016), Mexico (Leyden, 1987), and El Salvador (Dull, 2004a; 2007). However, greater land clearance and deforestation are reported from Belize at this time (Walsh et al. 2014). This widely reflects the reductions of indigenous populations and corresponds to reduced burning across the larger Maya area (Dull, 2004; 2007; Walsh et al. 2014; Anderson & Wahl, 2016). After initial forest recovery, few palynological studies report upon vegetation changes during the past 500 years (e.g. Velez et al. 2011); however, Dull (2007) comments upon the reductions of *Quercus* during the 19th and 20th Centuries, which is supported by palynological evidence from Laguna del Espino (Dull, 2004a), Laguna Cuzachapa (Dull 2007), and Lago Amatitlan (Velez, 2011). By integrating high resolution proxy data for vegetation, burning and herbivory with the historical record and modern remote sensing data this study aimed to determine the long-term ecological implications of anthropogenic forcing upon the vegetation of the areas surrounding the Cuchumatan Highlands since the Spanish Conquest (1524C.E.).

4.3 Methods

Field and sampling techniques

Cenote Kail is situated in the uplands of Guatemala (N16°00'00.0" W91°33'14.4, 1534m.a.s.l.). surrounded by a mixed coniferous forest mosaic, ranches, agricultural fields and mines (Figure 4.2). In 2015 a 105cm composite core, with overlapping sections, was extracted from Cenote Kail using a Livingstone piston corer (Livingstone, 1955). The uppermost 20 cm of sediment were collected separately using a piston corer with polycarbonate tubing. The surface sediments were sampled in the field at 0.25 cm intervals into plastic Whirlpak® bags in order to preserve the sediment-to-water interface.

Thirty lake sediment samples (1g wet weight) were extracted for biological proxy analysis of fossil pollen, *Sporormiella*, and macroscopic charcoal (>150µm) and microscopic charcoal (<150µm) based upon information inferred from the age depth model. The upper 36cm were sampled at a resolution of 2cm representing 2-13 years between samples. This enabled a high-resolution comparison of the palaeoecological data to satellite derived data covering the past *c.*20 years. The lower half of the core (41-105cm) was sampled at 5-10cm resolutions representing 25-50 years between samples.

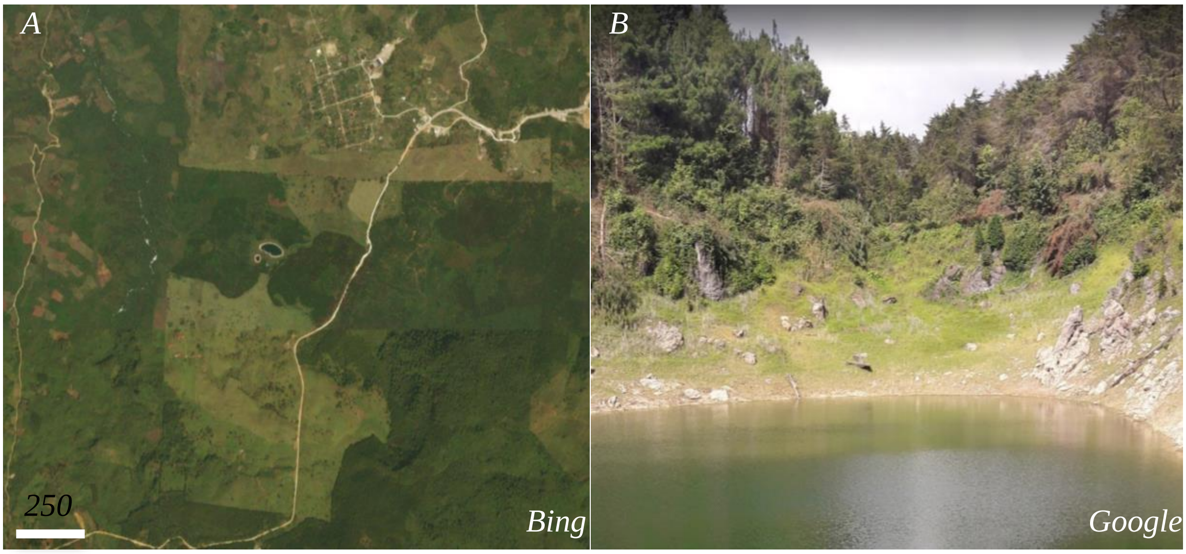


Figure 4.2 Aerial view of Cenote Kail depicting land cover: forests, agriculture and pastures 'A' (Bing Maps, 2019). Photograph looking over Cenote Kail exemplifying contemporary vegetation assemblage and anthropogenically modified land cover 'B' (Google Maps, 2019).

Chronology

A high-resolution age depth model was constructed using ten ^{210}Pb dates and four calibrated C^{14} dates and (Table 4.1). Charcoal fragments were carefully selected for radiocarbon dating (Reimer, 2013). Samples were pre-treated using standard acid-base-acid protocols (Abbott & Stafford, 1996). Radiocarbon dates were generated at the W.M. Keck Carbon Cycle Accelerator Mass Spectrometry Laboratory at the University of California, Irvine. The IntCal13 radiocarbon dataset (Reimer, 2013) was used to calibrate the measured radiocarbon dates and OxCal (v.4.3) was utilised to construct an age-depth model applying a Bayesian approach (Ramsey, 2009). Outliers were identified using the general outlier model implementing an outlier probability of 0.05 (Ramsey, 2008). Sedimentation rate was calculated using this age-depth model. Years C.E. were assigned to the sediment subsamples based upon this age depth model.

Table 4.1 Measured, calibrated and modelled ^{210}Pb and ^{14}C ages for Cenote Kail.

Lab #	**Measured Age (B.P.)**		**Depth (cm)**	**2σ Calibrated Age Range (C.E.)**		**Median Calibrated Age**	**OxCal Modelled Age (C.E.)**		**Median Modeled Age**	**Model Agreement**
Pb2101	-62	3.8	0.9	2004	2019	2011.5	2007	2019	2013	74.7
*Pb2102_*	-61	3.9	2.9	2003	2019	2011	2005	2015	2010	97.9
Pb2103	-59	4	4.9	2001	2017	2009	2003	2013	2008	58.1
Pb2104	-57	4.2	6.9	1998	2015	2006.5	2001	2011	2006	106.7
Pb2105	-54	4.4	8.9	1995	2013	2004	1998	2009	2003.5	92.9
Pb2106	-51	4.7	10.9	1991	2010	2000.5	1994	2006	2000	109.7
Pb2107	-47	5	12.9	1987	2007	1997	1988	2005	1996.5	120.2
Pb2108	-43	5.6	14.9	1981	2004	1992.5	1984	2001	1992.5	121.3
Pb2109	-40	6	16.9	1978	2002	1990	1977	1998	1987.5	122.7
Pb21010	-22	5.7	18.7	1960	1983	1971.5	1963	1988	1975.5	124.2
169169	60	150	80	1516	…	…	1636	1830	1733	97.9
209173	165	20	99.75	1665	…	…	1485	1738	1611.5	74.7
209174	345	20	100.75	1467	1635	1551	1483	1680	1581.5	124.6
146795	385	20	106.5	1445	1620	1532.5	1455	1629	1542	115.8

Fossil Pollen and *Sporormiella* Analysis

Fossil pollen was used to reconstruct the abundance and composition of past vegetation dynamics. Fossil pollen extraction followed standard palynological procedures applying the Oxford Long-Term Ecology Laboratories protocol (OxLEL, 2016). Silicone oil was used to mount pollen grains on slides to allow for rotation, easing identification. Samples were spiked with known concentrations of an exotic marker, *Lycopodium* Spores (batch No. 20848 or 9666), to calculate pollen influx and accumulation rates (Stockmarr 1971). Counting and identification of pollen grains were conducted at 400x and 1000x magnification. For each level a minimum of 300 terrestrial pollen grains were counted. Morphological identification was achieved using: (i) pollen databases (Bush & Weng, 2007; APSA, 2007; Martin & Harvey, 2017); (ii) published plates (Roubik & Moreno, 1991; Willard et al. 2004); and (iii) botanical reference materials from the Oxford Long-Term Ecology Lab. reference collection. To interpret the relative composition of the forest (deciduous/coniferous), coniferous and mixed-hard-wood forest (MHWF) canopy taxa and were compared as a ratio.

The abundance of coprophilous fungal spores (*Sporormiella*) was used to indicate herbivorous animal presence and abundance. *Sporormiella* spores were counted and morphologically identified on the same slides (Davis & Shafer, 2006; Baker et al. 2016). The abundance of spores in sediments was calculated as accumulation rates (spore cm^{-2} $year^{-1}$) using the spore concentration (spore cm^{-2}) and the sedimentation rate (cm $year^{-1}$) (Maher 1981; Bennett 1994; Bennett & Willis, 2001; Baker et al. 2016).

Pollen counts were converted to percentages, while the annual influx of *Sporormiella*, macroscopic and microscopic charcoal were calculated as accumulation rates using the number of charcoal fragments or number of *Sporormiella*, the exotic marker, sample volume, and the sedimentation rate (Maher 1981; Bennett 1994; Bennett & Willis, 2001;

Whitlock & Larson, 2002; Baker et al. 2016). To identify discrete zones in the resulting palynological diagrams, constrained hierarchical clustering upon the palynological assemblage was applied following the broken stick model (Bennett, 1996). Before preforming all ordinations analysis, I square-root transformed the percentage data to normalise the distribution. A square root transform was chosen because it can be applied to data sets containing zero values (Malik & Piepho, 2014). To check if it was appropriate to apply a linear ordination method (e.g. Principal Component Analysis) or unimodal ordination method (e.g. Correspondence Analysis) detrended correspondence analysis (DCA) was conducted upon the palynological assemblage data (Ter Braak & Prentice 1988). To calculate the species turnover I extracted the site scores for the first axis of the DCA. Principal component analysis (PCA) was used to infer similarities between samples and the change in trajectories of composition of taxa through time applying a singular value decomposition of the centered but not scaled data matrix. The PCA applied a singular value decomposition of the centered but not scaled data matrix. This method of ordination was deemed appropriate to infer assosiations between taxa; however, limitations for the application of this method upon data sets containing zero values should be noted (Ter Braak & Prentice 1988). Finally, I performed a canonical correspondence analysis (CCA) to quantify the relationship between environmental variables (macroscopic charcoal, microscopic charcoal and *Sporormiella*) and the palynological assemblage data. Ellipse's representing the discreat Zones were calculated using standard parameterization (cos(theta + d/2), cos(theta - d/2)), where cos(d) is the correlation of the parameters (Murdoch & Chow, 1996). Statistical analysis and presentation of data was performed using packages Vegan (Oksanen et al. 2015) and Rioja (Juggins et al. 2009) in base R (R Core Team, 2012).

Fire Analysis: integrating fossil charcoal with satellite images.

Past fire was quantified by counting and analysing fossil charcoal fragments. Microscopic charcoal (<150μm) fragments were counted on the same slides applying the point counting method at 400x magnification and counts were recorded until a minimum of 50 *Lycopodium* spores and 200 fields of view were encountered for each level (Clark, 1982). Macroscopic fossil charcoal fragments were counted from the >150μm fraction of each 1g sample at 10x magnification. Charcoal volume was calculated from loss on ignition density and weight of each sample. This data was presented as charcoal influx as well as concentration. Macroscopic charcoal is typically used to infer local burning (Gavin et al., 2003; Lynch et al., 2004; Peters and Higuera, 2007; Higuera et al., 2007; 2011; Anderson & Wahl, 2016), while microscopic charcoal is typically used to infer more regional burning (Clark, 1988); however, I attempt to independently validate this assumption by comparing the fossil charcoal data to modern remotely sensed satellite data representing number of fires within a radius of up to 200km of Cenote Kail. This data was downloaded from MODIS (Moderate Resolution Imaging Spectroradiometer) for the years 2000-2015C.E. (MCD14ML version 6.1 Global monthly fire product, Justice et al. 2002; 2006). A MODIS active fire location represents the centre of a 1km pixel that is flagged by the algorithm as containing one or more fires within the pixel size of fire detected (Giglio et al. 2003).

To link past fire number and intensity to modern day burning regimes I applied the transfer function from Adolf et al. (2018a) to the fossil macroscopic and microscopic charcoal influx rates in order to calculate a modern fire number. To validate this approach in Central America I compared through correlation these reconstructed fire numbers to the MODIS derived fire numbers for overlapping years (MCD14ML version 6.1 Global monthly 1 km fire product, Justice et al. 2002; 2006). MODIS data was taken at 3 year averaged moving windows to account for age-depth uncertainty in the sedimentary record. Filtering of MODIS fire time series data was conducted using R to remove false fires (e.g. hot factory roofs) using an urban fire filter from Globcover 2009 (Arino et al. 2012). Spatial and temporal autocorrelations in the MCD14ML product were removed following Giglio, (2013); Oliveiras (2014); and Adolf et al. (2018a).

4.4 Results

Chronology and Resolution

The age-depth model indicates that the recovered composite core (105cm) covers the past 500 years in continuous time (Figure 4.3). The general outlier model did not identify any dates to be removed from the sequence. Overall model agreement was high (Index = 143.6) and represented an average age range of 206 years for the radiocarbon dates and 15.1 years for the Pb^{210} dates surrounding the median modelled age.

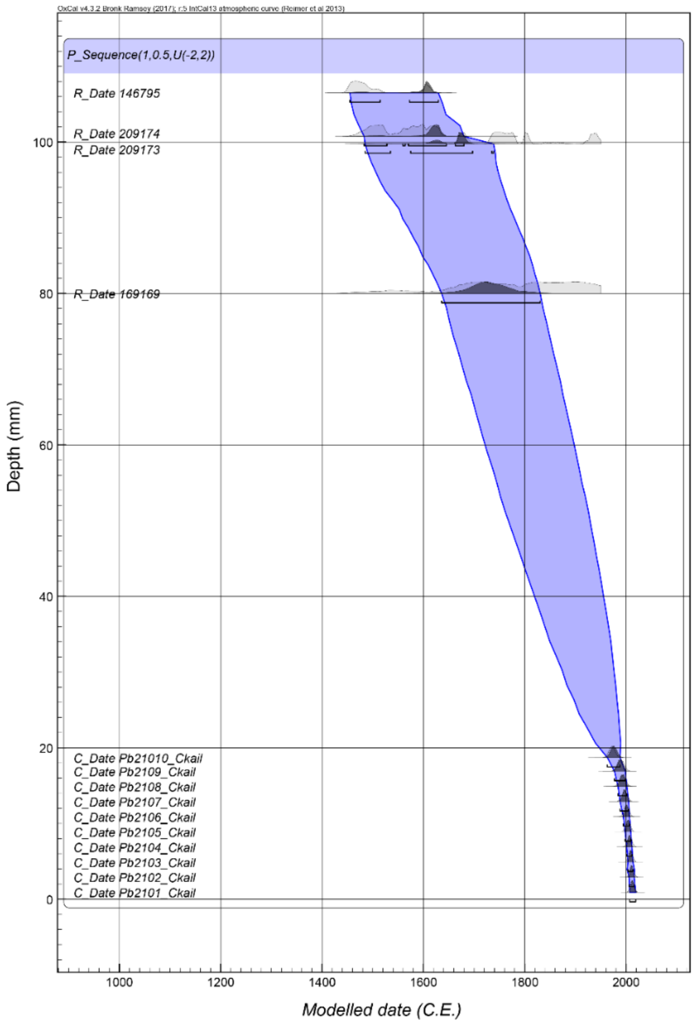


Figure 4.3: Age depth model of Cenote Kail post European contact.

Palaeoecological Trends

Three statistically significant Zones were identified from the broken stick model. Zone 1 (1550-1725C.E.) represents an average temporal resolution of 50 years between samples spanning 225 years (with a range of 49-50 years), Zone 2 (1725-1940C.E.) has an average resolution of 17 years spanning 215 years (with a range of 3-50 years) and the temporal resolution of Zone 3 (1940-2015C.E.) represents an average of 5 years spanning 75 (with a range of 2-11 years). Seventy-six taxa were recognised in the palynological sequence, which were grouped based upon their lowest identifiable common taxonomic denomination. *Pinus, Liquidambar*, *Quercus*, *Morella cerifera,* Anacardiaceae, and Leguminosae dominate the tree component while Compositae, Poaceae, and Cyperaceae are the most abundant herbaceous taxa.

The PCA displays several gradients and associations between samples and taxa (Figure 4.4). The first axis represents 16.3% of the variation, while axis 2 represents 14.1% of the variation. To help visualise the most distinctive gradient I superimposed the independently calculated palynological Zones upon the quadrants of the PCA. Zone 1 is most associated with the bottom left quadrant along with canopy taxa *Quercus*, *Liquidambar* and *Bursera simaruba* and understory taxa Anacardiaceae, Leguminaceae and *Roupala*. Zone 2 spans the right top and right bottom quadrants represented by canopy taxa *Alnus*; understory taxa *Myrica* and *Pourouma*; and herbaceous taxa Poaceae, Brassicaceae, Cyperaceae, Apiaceae and Primulaceae. Zone 3 is best represented by the top left quadrant associated with canopy taxa *Abies*; understory taxa *Terminalia*, Rubiaceae, *Aphelandra* and *Juniperus*; and herbaceous taxa Compositae. Results from the CCA show that microscopic charcoal and *Sporormiella* are significant environmental variables most associated with Zone 2 (Figure 4.4). Macroscopic charcoal is most associated with Zone 3 but is not a statistically significant.

Zone 1 (105-74cm, 4 samples, 1550-1725C.E.) spans 175 years and is defined by Canopy taxa *Pinus* (14-27.7%) *Liquidambar* (1.3-30.7%), and *Quercus* (0-13%). Total tree cover is very high (69.3-86.3%) with a dominance of canopy taxa from 1550C.E. (82.7%); however, this dramatically decreases towards 1700C.E. (28%) with understory (44.7%) and herbaceous (23.3%) taxa becoming more abundant from 1600C.E. (Figure 4.4). The reduction of *Liquidambar* (30.7-10.3%) from 1550-1600C.E. followed by *Quercus* (12-0%) and a further reduction in *Liquidambar* (10.3-1.3%) from 1600-1700C.E. marks the end of MHWF dominance in this sequence (Figure 4.5). Leguminosae (35.7%) becomes prevalent around 1600C.E. after which Anacardiaceae steadily increases through to 1700C.E. (8.3-18.7%). From 1650C.E. *Morella cerifera* rises to fill the tree component (5-17%) along with *Pinus* (14-20.3%). *Alnus* establishes in low abundance from 1700C.E. (6.3%). Compositae (7.6-12.3%) and Poaceae (3.3-7.3%) increase from c.1600-1700C.E. *Capsicum* is present in low abundances at 1550C.E. (1.3%) and 1600C.E. (2.7%). *Sporormiella* influx is in low and stable abundance (0.8-1.5cm2 year-1) until 1650C.E. (0cm^{2} year^{-1}). Macroscopic charcoal influx remains low (0.6-2.1particles cm-2 year-1) and microscopic charcoal influx decreases from 1550-1700C.E. (481.8-59.8 cm^{-2} year^{-1}). Microscopic charcoal particularly decreases between 1550-1600C.E. (481.8-154 cm^{-2} year^{-1}). Pollen influx is highest between 1550-1650C.E., (201,170-173,958 grains cm^{-2} year^{-1}) decreasing towards 1700C.E. (80,513 grains cm^{-2} year^{-1}).

Zone 2 (65-26cm, 12 samples, 1725-1942C.E.) covers 193 years and is characterised by Canopy taxa *Pinus* (16-28.3%), increasing abundances of understory taxa *Morella cerifera* (18.6-32%) and Anacardiaceae (0.6-8%) as well as herbaceous taxa Compositae (3.3-11.3%), Poaceae (3.3-16.3%) and Cyperaceae (0.7-7.7%). Total tree cover continues to slowly decline between 1750-1938C.E. (73.3-68.7%). Increases in Euphorbiaceae (0-3.3%) and *Myrica* from 1860-1938C.E. (0-3.7%) are joined by increases in Cyperaceae between 1860-1910C.E. (0.7-7.7%). *Zea mays* punctuates the sequence at 1900C.E.

(0.3%), while *Capsicum* appears at 1910C.E. (0.7%) and 1938C.E. (0.3%). *Sporormiella* influx is very high between 1750-1800C.E. (7.5-8.6 spores cm^{-2} $year^{-1}$), absent between 1800-1900C.E. (0%), and then high again between 1900-1938C.E. (0-8.5cm^{-2} $year^{-1}$). Macroscopic charcoal (1.9-4.6cm^{-2} $year^{-1}$) and microscopic charcoal (115.2-160.5cm^{-2} $year^{-1}$) increase from 1700-1800C.E. and both decrease between 1800-1900C.E. (macroscopic: 4.6-1cm^{-2} $year^{-1}$; microscopic 160.5-75.6cm^{-2} $year^{-1}$) Pollen influx remains stable (c.174,6046cm^{-2} $year^{-1}$).

Zone 3 (24-cm, 14 samples, 1942-2014C.E.) encompasses 67 years and is defined by herbaceous taxa Compositae (17-26.3%), understory taxa *Morella cerifera* (9.6-33%), and the sustained prevalence of Canopy taxa *Pinus* (10.6-29%). Total tree cover reduces from 1948-2014C.E. (65.3-53%). Canopy (28.9%), understory (31%) and herbaceous (33.2%) taxa are, on average, in equal abundance. *Morella cerifera* decreases in abundance after 1997C.E. (20-12.3%), while *Liquidambar* (0.6.3%) and Anacardiaceae (2-9.3%%) increase from 1948-2003C.E. Macroscopic charcoal remains in low abundance; however, increases from 1988-2006C.E. (0.2-3.2cm^{-2} $year^{-1}$) and also peaks in 2010C.E. (2.1cm^{-2} $year^{-1}$). Microscopic charcoal decreases from 1948-1988C.E. (201.5-2.4cm^{-2} $year^{-1}$) and is almost absent from 1988-2014C.E. (2.4-0.01cm^{-2} $year^{-1}$). *Sporormiella* remains in high abundance from 1948-1968C.E. (1.8-6.5cm^{-2} $year^{-1}$) after which influx decreases and is absent after 2008C.E. Pollen influx also decrease after 1968-2014C.E. (196,916-5,855cm^{-2} $year^{-1}$).

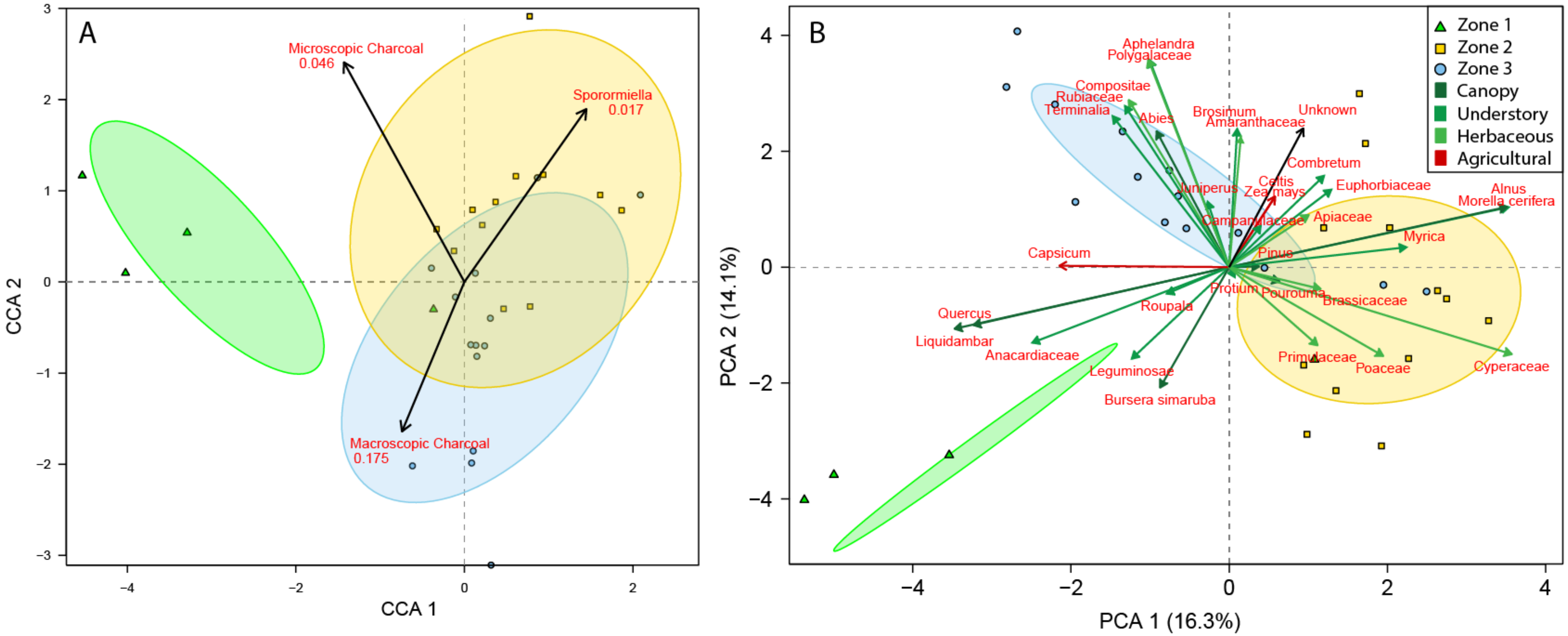


Figure 4.4 Canonical correspondence analysis (A). Principal component analysis (B). Zones derived from the broken stick model represented by ellipses at a confidence of 95%. Zone 1 = green triangles; Zone 2 = yellow squares; Zone 3 = blue circles.

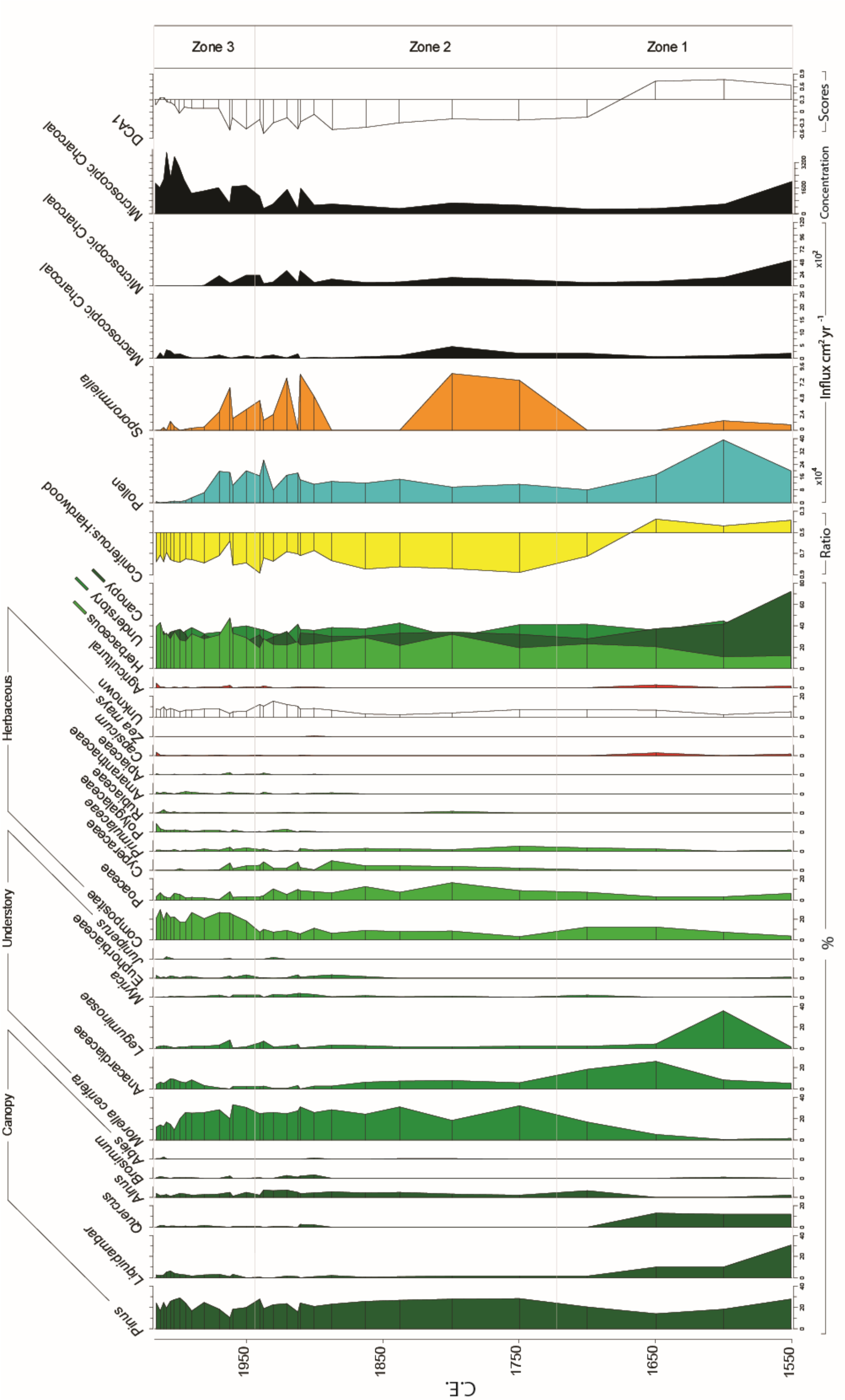


Figure 4.5: (i) Palynological percentage diagram of taxa appearing in an abundance greater than 2%; (ii) forest structure; (iii) coniferous to hardwood ratio; (iv) pollen influx; (v) *Sporormiella* Influx; (vi) macroscopic and microscopic influx; and (vii) DCA axis 1.

Charcoal Area Validation

The transfer function from Adolf et al. (2018a) that linked the past fire number and intensity to modern day burning regimes showed that the source lag for macroscopic and microscopic charcoal is estimated to be 16km for macroscopic charcoal and 180km for microscopic charcoal assuming that distance is indicated by the strongest correlations between charcoal and satellite data (Figure 4.6 & 4.7). The strongest correlations between charcoal influx and the MODIS product are slightly stronger for microscopic charcoal (r: 0.76) compared to macroscopic charcoal (r: 0.72). Microscopic (p-value: 0.1) and macroscopic (p-value: 0.3) charcoal are not significantly correlated between charcoal data sets supporting the two different source areas.

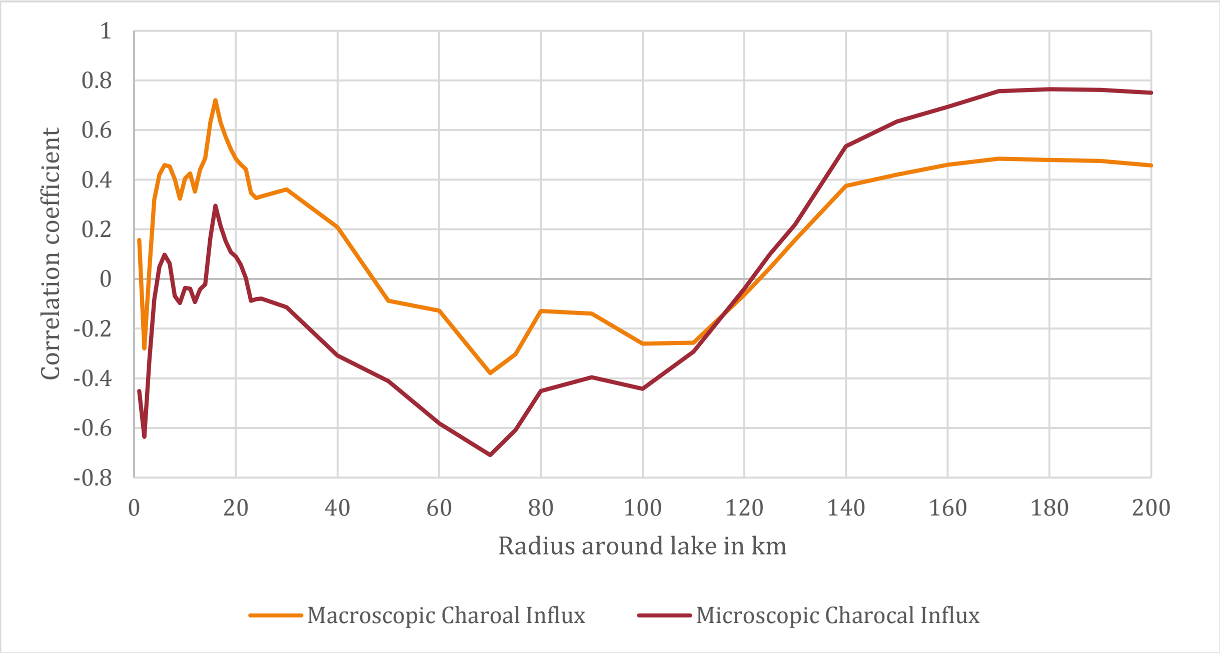


Figure 4.6 Calibration of macroscopic, microscopic and remote sensed data sets for fire.

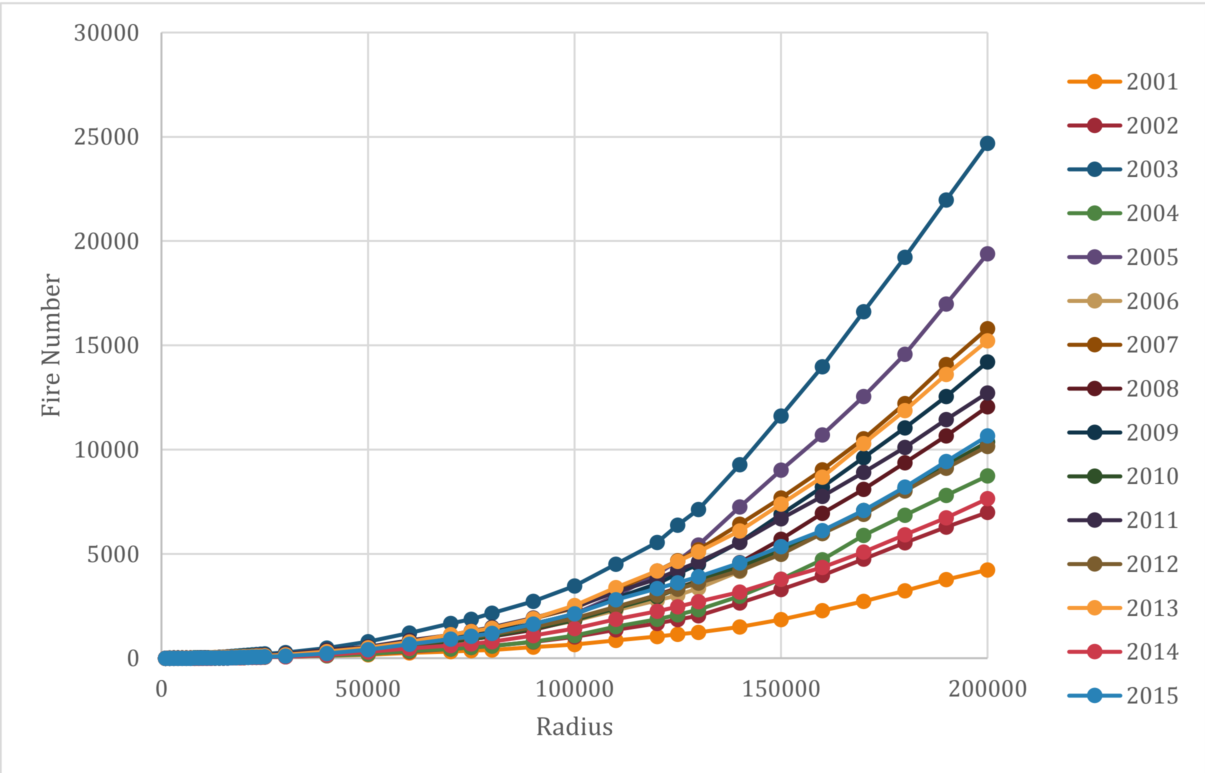


Figure 4.7 Remote sensed fire by number and area.

4.5 Discussion

How and when did anthropogenic practices involving different types of land use change impact floral assemblage changes around the Cuchumatan Highlands?

Three stages of compositional change can be discerned from the palynological assemblage since European contact in 1524C.E. These changes represent responses to anthropogenic activities in the Cuchumatan highlands corresponding to pastoral activities, agriculture, timber extraction, mining, and new settlements. These three phases encompass: (i) the decline of MHWF, associated with the building of new settlements, agriculture and timber extraction for fuel (1550-1675C.E.); (ii) pastoral expansions involving the rearing of livestock (1700-1800C.E.); and (iii) the expansions of urban settlements and the increasing anthropogenic management of the surrounding land (1821-2015C.E.).

Colonial Settlement Construction

Evidence from Cenote Kail indicates that land clearance for the establishment of new settlements around the Cuchumatan Highlands began from at least 1550C.E. and by 1650-1675C.E. most hard wood taxa (*Liquidambar* and *Quercus*) had been removed from the landscape (Figures 4.4 & 4.5). The palynological evidence suggests that hard-wood-taxa were removed due to land clearing for new settlements under a regime called ‘congregación’ or ‘reducción’ from 1537C.E. (Van Oss, 1986), which involved forced removal of indigenous peoples from their villages into colonial settlements (Figure 4.1). Historical records report that these settlements were mandated to have a church and administrative buildings, for which substantial amounts of timber were required (Jaiuregui, 1894; Remesal, 1932). Administrative towns, such as Purification Jacaltenango (meaning “wall of cabins” in Nahuatl) located 40km from the study site would have required even larger quantities of timber for both construction and for fuel (Lovell, 1985).

By the late-16th/early-17th century, historical (Thompson, 1958) and palynological accounts (Velez et al. 2011) report rapid deforestation across Guatemala to meet the needs of these towns. Timber was extracted for buildings reporting a combination of pine (Thompson, 1958) and oak (Dull, 2004a; Velez et al. 2011); however, it would appear from the historical records that timber extraction was non-discriminatory (Thompson, 1958). For example, the forests surrounding Lake Amatitlan (Figure 4.1) were rapidly being felled to meet the needs of Antigua for which evidence is presented is reported from historical chronicles (Thompson, 1958) and from a palynological record from Lake Amatitlan (Velez et al. 2011).

Pastoral Activities: Ranching

It is likely that as well as being preferentially extracted for wood, the increasing pressures of pastoral activities damaged the reproductive success of taxa such as *Quercus* through the consumption of acorns by cattle and sheep (van Wieren, 1996; Kappelle, 2006). Bovid's (including cattle, sheep and pigs) can digest fibrous content and plant lignin (van Wieren, 1996) meaning that predation of seeds such as acorns, would have dramatically increased with pastoral expansions. This would prevent further reproduction and recovery of the MHWF in this area (Kappelle, 2006; Wallace et al. 2015). During the Pre-Columbian era *Sporormiella* influx into Cenote Kail was found to be higher than most of the Colonial and Post-Colonial Periods (Harvey et al. 2019). This is thought to be due to the higher abundance of native herbivores such as, white tailed deer (*Odocoileus virginianus*), the Baird tapir (*Tapirus bairdii*), and peccary (*Tayassuidae*), which were reduced through habitat loss and hunting after European contact.

During the early 17th century Spanish settlers began to expand into the countryside (MacLeod, 1973), and by the end of the century the damage caused to the forests and soils were evident though the practices of excessive forest clearing and overgrazing (Veblen, 1976). In 1699C.E. and 1701C.E., the villages surrounding Antigua were forbidden from grazing or cultivating the surrounding hillsides by royal decree to attempt to preserve the depleted soils (MacLeod, 1973). These edicts are suggested to be the first conservation laws to be implemented anywhere in Latin America (Veblen, 1976). Substantial degradation to the underlying soil is first reported in the 19th century for the north-eastern half of the Department of Totonicapan (Carranza, 1897), which was the leading sheep-rearing district of Guatemala over the previous two centuries (Vasquez, 1944).

Evidence from Cenote Kail suggests that pastoral activities expanded from 1700-1800C.E. around the Cuchumatan highlands, and while no clear change in the overall vegetation structure can be discerned, sustained absence of *Liquidambar* and *Quercus* is evident (Figure 4.5). This could indicate the translocation of cattle and sheep from a neighbouring province such as the Department of Totonicapan over to the Department of Huehuetenango (Figure 4.1). Between 1800-1870C.E. the influx of *Sporormiella* diminished which could indicate a similar edict of land conservation as that recorded for the north-eastern half of the Department of Totonicapan (Carranza, 1897). One other such explanation could revolve around civil unrest pertaining to the Act of Independence of Central America 1821C.E. which led to land use change and abandonment due to war.

Land-use Management

Burning, locally and regionally is limited and in line with the modern regime, which suggests that fire has been managed and controlled at least since European contact (Figure 4.5). During the Pre-Columbian era (before 1524C.E.) fire was identified as a significant driver of forest turnover in this region (Chapter 3); however, land-use change to incorporate extensive ranching may have reduced natural burning regimes and/or previous anthropogenic uses of fire, such as burning for *Milpa* or lime production.

The conservation of the MHWF taxa around the Cuchumatan Highlands may therefore be achieved by continuing to limit the presence of fire in these forests, and by controlling or removing domestic bovids. This would allow for MHWF taxa such as *Quercus* and *Liquidambar* to re-establish over the course of 80-200 years (Kappelle, 2006).

There is no evidence of current mining activities directly surrounding Cenote Kail; however, some open cast quarries are evident upon the landscape. I found no evidence of land use change based upon mining activities within the palaeolimnological record from Cenote Kail. The possibility that the Cuchumatanes highlands might contain significant mineral wealth led to open-cast mines opening in Pichiquil, San Francisco Motozintla and Chiantla shortly after the Spanish conquest (Recinos, 1954; Sherman, 1979; Lovell, 1983). The gold mines of Pichiquil and San Francisco Motozintla did not prove successful (Recinos, 1954); however, success at Chiantla led to silver and lead extraction from 1537C.E. (Sherman, 1979). The mines of Chiantla produced modest quantities of silver and lead throughout the colonial period (Lovell, 1983).

What is Cenote Kail's charcoal source area?

The size of the source area for macroscopic charcoal and microscopic charcoal into a depositional environment is contentious. Macroscopic charcoal is widely suggested to reflect burning from a local to sub-regional source area between 0-10km (Gavin et al., 2003; Lynch et al., 2004; Peters and Higuera, 2007; Higuera et al., 2007; 2011; Anderson & Wahl, 2016), while microscopic charcoal is suggested to primarily reflect regional burning within a radius of up to several hundred kilometres (Clark, 1988); however, recent validation of charcoal dispersal across Europe linked both macroscopic and microscopic charcoal influx to a regional source area of around 40km radius (Adolf et al. 2018b). Our results from Cenote Kail indicate that the catchment area for macroscopic charcoal and microscopic charcoal varied by a degree of magnitude. Validation through the comparative integration of the charcoal records with MODIS-derived fire time series suggests two distinct biomass burning histories, the first reflecting extra-local to sub-regional burning at a radius of 16 km, and secondly a clearly regional burning signal from up to 180km. The direct distance of Cenote Kail to the Pacific coast is around 160km suggesting that the regional charcoal signal is indicative of burning inclusive of this wider region, encompassing anthropogenic settlements built in the Cuchumatan Highlands as well as lowland activities. The macroscopic charcoal signal is likely to reflect a more local signal, encompassing the modern pastoral, agricultural and mining towns of Aguacate, Yalambojoch and Yulaurel. The subtle differences between the correlation scores of macroscopic and miscroscopic charcoal are likely not enough to truly discriminate between local vs regional fire; however, do provide a best case scenario estimate.

4.6 Conclusions

The integrated approach of palaeoenvironmental techniques with historical records and remotely sensed satellite data has enabled a unique and high-resolution reconstruction of the flora, fire, and animal abundance of the areas surrounding the Cuchumatanes highlands over the past 500 years detailing anthropogenic impacts since European contact.

The high sedimentation rate and precise ^{210}Pb dating of Cenote Kail has enabled a rare validation of the palaeolimnological catchment area through cross comparisons of satellite data with the charcoal proxy data. This approach has enabled a calibration of the charcoal data sets to allow for a quantitative analysis of burning, comparable to modern day observations. Radial burning was identified at 16km for macroscopic charcoal and 180km for microscopic charcoal. To properly interpret the signals represented in the palaeolimnological record I recommend that all future palaeolimnological work should attempt to fully understand the catchment area for each proxy represented using this sort of quantitative approach.

The establishment of colonial settlements is evident from the palynological record from Cenote Kail as well as nearby Lake Amatitlan indicating that around 150 years of intensive logging lead to the permanent decline of the MTHF's. The recovery of these forests shows evidence of suppression since by the expansion of pastoral practices. Bovid seed predation is suggested to be the dominant factor preventing MHWF's from re-establishing in the Cuchumatanes highlands during the past 500 years. Evidence for edicts of conservation can be inferred from the *Sporormiella* record for different parts of the Cuchumatanes highlands during the 18th and 19th centuries. No direct evidence for the impacts of mining have been inferred from our data sets.

4.7 Acknowledgements

This research was funded by the Natural Environment Research Council of the United Kingdom NE/L002612/1, US National Science Foundation EAR-1502989 and St Edmund Hall, University of Oxford.

4.8 References

Abbott, M.B. and Stafford, T.W., 1996. Radiocarbon geochemistry of modern and ancient Arctic lake systems, Baffin Island, Canada. *Quaternary Research*, *45*(3), pp.300-311.

Adolf, C., Wunderle, S., Colombaroli, D., Weber, H., Gobet, E., Heiri, O., van Leeuwen, J.F., Bigler, C., Connor, S.E., Gałka, M. and La Mantia, T., 2018a. The sedimentary and remote- sensing reflection of biomass burning in Europe. *Global Ecology and Biogeography*, *27*(2), pp.199-212.

Adolf, C., Doyon, F., Klimmek, F. and Tinner, W., 2018b. Validating a continental European charcoal calibration dataset. *The Holocene*, 28(10), pp.1642–1652.

Anderson, L. and Wahl, D., 2016. Two Holocene paleofire records from Peten, Guatemala: Implications for natural fire regime and prehispanic Maya land use. *Global and Planetary Change*, *138*, pp.82-92.

Arino, O., Ramos Perez, J. J., Kalogirou, V., Bontemps, S., Defourny, P., & Van Bogaert, E. (2012). Global land cover map for 2009 (GlobCover 2009). PANGAEA. Retrieved from http://doi.org/10.1594/PANGAEA. 787668.

APSA, 2007. The Australasian Pollen and Spore Atlas V1.0. Australian National University, Canberra. Available at: http://apsa.anu.edu.au/ [Accessed 13/06/12018].

Baker, A.G., Cornelissen, P., Bhagwat, S.A., Vera, F.W. and Willis, K.J., 2016. Quantification of population sizes of large herbivores and their long- term functional role in ecosystems using dung fungal spores. Methods in Ecology and Evolution, 7(11), pp.1273-1281.

Bass, J. O., 2010. Learning landscape change in Honduras: Repeat photography and discovery. In R. H. Webb, D. E. Boyer, & R. M. Turner (Eds.), Repeat photography: Methods and applications in the natural sciences (pp. 275–288). Washington, DC: Island Press.

Bennett, J.P., 1974. Concepts of mathematical modelling of sediment yield. *Water Resources Research*, *10*(3), pp.485-492.

Bennett, K.D., 1996. Determination of the number of zones in a biostratigraphical sequence. *New Phytologist*, *132*(1), pp.155-170.

Bennett, K.D. and Willis, K.J., 2001. Pollen. Tracking Environmental Change Using Lake Sediements. Volume 3: Terrestrial, Algal, and Siliceous Indicators.

Bing Maps, 2019. Bing Maps [online]. Available at: https://www.bing.com/maps [Accessed 12/03/2019].

Brenner, M., Leyden, B. and Binford, M.W., 1990. Recent sedimentary histories of shallow lakes in the Guatemalan savannas. *Journal of Paleolimnology*, 4(3), pp.239-252.

Bouroncle, C., Imbach, P., Rodríguez-Sánchez, B., Medellín, C., Martinez-Valle, A. and Läderach, P., 2017. Mapping climate change adaptive capacity and vulnerability of smallholder agricultural livelihoods in Central America: ranking and descriptive approaches to support adaptation strategies. Climatic Change, 141(1), pp.123-137.

Brady, S. (2009). Revisiting a Honduran landscape described by Robert West: An experiment in repeat geography. Journal of Latin American Geography, 8, 7–27.

Brown, S., & Lugo, A. E., 1990. Tropical secondary forests. Journal of Tropical Ecology, 6, 1–32.

Bush, M.B. and Weng, C., 2007. Introducing a new (freeware) tool for palynology. *Journal of Biogeography*, *34*(3), pp.377-380.

Caffrey, M.A., Taylor, M.J. and Sullivan, D.G., 2011. A 12,000-year record of vegetation and climate change from the Sierra de Los Cuchumatanes, Guatemala. *Journal of Latin American Geography*, pp.129-151.

Carranza, J. E., 1897. Un pueblo de los altos. Quezaltenango, Establecimiento Tipogalfico Popular.

Chiabai, A., (ed.) 2015. Climate change impacts on tropical forests in Central America: an ecosystem service perspective. Routledge.

Clark, R.L., 1982. Point count estimation of charcoal in pollen preparations and thin sections of sediments. *Pollen et spores*.

Clark, J.S., 1988. Particle motion and the theory of charcoal analysis: source area, transport, deposition, and sampling. *Quaternary Research*, *30*(1), pp.67-80.

Corlett, R. T., 1995. Tropical secondary forests. Progress in Physical Geography, 19, 159–172.

Cortez y Larraz, P., 1958. Descripción geográfico-moral de la diócesis de Guatemala. *Guatemala: Biblioteca 'Goathemala'de la Sociedad de Geografía e Historia de Guatemala*.

Curtis, J.H., Brenner, M., Hodell, D.A., Balser, R.A., Islebe, G.A. and Hooghiemstra, H., 1998. A multi-proxy study of Holocene environmental change in the Maya Lowlands of Peten, Guatemala. *Journal of paleolimnology*, *19*(2), pp.139-159.

Davis, O.K. and Shafer, D.S., 2006. *Sporormiella* fungal spores, a palynological means of detecting herbivore density. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *237*(1), pp.40-50.

Deevey, E.S., Rice, D.S., Rice, P.M., Vaughan, H.H., Brenner, M. and Flannery, M.S. 1979: Mayan urbanism: impact on a tropical karst environment. *Science* 206, 298-306.

Dull, R.A., 2004a. An 8000-year record of vegetation, climate, and human disturbance from the Sierra de Apaneca, El Salvador. *Quaternary Research*, *61*(2), pp.159-167.

Dull, R.A., 2004b. A Holocene record of Neotropical savanna dynamics from El Salvador. *Journal of Paleolimnology*, 32(3), pp.219-231.

Dull, R.A., 2007. Evidence for Forest Clearance, Agriculture, and Human- Induced Erosion in Precolumbian El Salvador. *Annals of the Association of American Geographers*, *97*(1), pp.127-141.

Ewel, J. J. 1979. Secondary forests: the tropical wood resource of the future. In: Chavarria, M. (ed.) Simposio Internacional sobre las Ciencias Forestales y su Contribucian al Desarrollo de la America Tropical Concit/Interciencia/ SCITEC, San Jose.

Figueroa-Rangel, B.L., Willis, K.J. and Olvera-Vargas, M., 2012. Late-Holocene successional dynamics in a transitional forest of west-central Mexico. *The Holocene*, *22*(2), pp.143-153.

Gavin, D.G., Brubaker, L.B. and Lertzman, K.P., 2003. An 1800-year record of the spatial and temporal distribution of fire from the west coast of Vancouver Island, Canada. *Canadian Journal of Forest Research*, *33*(4), pp.573-586.

Gibson, C. C., 2001. Forest resources: Institutions for local governance in Guatemala. In J. Burger, E. Ostrom, R. B. Norgaard, D. Policansky, & B. D. Goldstein (Eds.), Protecting the commons: A framework for resource management in the Americas (pp. 71–89). Washington, DC: Island Press.

Giglio L, Descloitres J, Justice CO, Kaufman Y., 2003. An enhanced contextual fire detection algorithm for MODIS. Remote Sensing of Environment 87: 273-282.

Giglio, L., 2013. MODIS collection 5 active fire product user's guide (version 2.5). Retrieved from https://cdn.earthdata.nasa.gov/conduit/upload/907/MODIS_Fire_Users_Guide_2.5.pdf

Gogole Maps, 2019. Google Maps [online]. Available at: https://www.google.com/maps/ [Accessed 12/03/2019].

Harvey, W. J., Nogué, S., Stansell, N., Petrokofsky, G., Steinman, B., & Willis, K. J., 2019. The Legacy of Pre-Columbian Fire on the Pine-oak Forests of Upland Guatemala. *Frontiers In Forests and Global Change*, 2, 34.

Hicks, S., 2006. When no pollen does not mean no trees. *Vegetation History and Archaeobotany*, 15(4), pp.253-261.

Higuera, P.E., Peters, M.E., Brubaker, L.B. and Gavin, D.G., 2007. Understanding the origin and analysis of sediment-charcoal records with a simulation model. *Quaternary Science Reviews*, *26*(13-14), pp.1790-1809.

Higuera, P.E., Gavin, D.G., Bartlein, P.J. and Hallett, D.J., 2011. Peak detection in sediment–charcoal records: impacts of alternative data analysis methods on fire-history interpretations. *International Journal of Wildland Fire*, *19*(8), pp.996-1014.

Holder, C.D., 2006. The hydrological significance of cloud forests in the Sierra de las Minas Biosphere Reserve, Guatemala. *Geoforum*, *37*(1), pp.82-93.

Holder, C.D. and Chase, G., 2012. The role of remittances and decentralization of forest management in the sustainability of a municipal-communal pine forest in eastern Guatemala. *Environment, development and sustainability*, *14*(1), pp.25-43.

Ingersoll, C.A., 1826. A view of South America and Mexico. H. Huntington, JB., New York.

Jáuregui, A.B., 1894. Los Indios: Su historia y su civilizacion. Tip. la Unión.

Juggins, S., Juggins, M.S., WA, W. and IKFA, M., 2009. Package 'rioja'.

Justice, C. O., Giglio, L., Korontzi, S., Owens, J., Morisette, J. T., Roy, D., ... Kaufman, Y. J. (2002). The MODIS fire products. *Remote Sensing of Environment*, 83(1–2), 244–262.

Justice, C., Giglio, L., Boschetti, L., Roy, D., & Csiszar, I. (2006). MODIS fire products. Retrieved from https://modis.gsfc.nasa.gov/data/atbd/ atbd_mod14.pdf

Kappelle, M., 2006. Neotropical montane oak forests: overview and outlook. In *Ecology and conservation of neotropical montane oak forests* (pp. 449-467). Springer, Berlin, Heidelberg.

Leyden, B.W., Brenner, M. and Dahlin, B.H., 1998. Cultural and Climatic History of Cobá, a Lowland Maya City in Quintana Roo, Mexico 1. *Quaternary Research*, 49(1), pp.111-122.

Livingstone, D.A., 1955. A lightweight piston sampler for lake deposits. *Ecology*, *36*(1), pp.137-139.

Lovell, W.G., 1983. Landholding in Spanish Central America: Patterns of ownership and activity in the Cuchumatán highlands of Guatemala, 1563-1821. *Transactions of the Institute of British Geographers*, pp.214-230.

Lovell, W. G, 1985. Conquest and Survival in Colonial Guatemala, A Historical Geography of the Cuchumatán Highlands, 1500–1821. McGill-Queen's University Press.

Lynch, J.A., Clark, J.S. and Stocks, B.J., 2004. Charcoal production, dispersal, and deposition from the Fort Providence experimental fire: interpreting fire regimes from charcoal records in boreal forests. *Canadian Journal of Forest Research*, *34*(8), pp.1642-1656.

Maher, L.J., 1981. Statistics for microfossil concentration measurements employing samples spiked with marker grains. *Review of Palaeobotany and Palynology*, *32*(2-3), pp.153-191.

Malik, W.A. and Piepho, H.P., 2016. On a new family of shifted logarithmic transformations. Journal of Statistical Computation and Simulation, 86(9), pp.1697-1708.

Martin, A.C. and Harvey, W.J., 2017. The Global Pollen Project: a new tool for pollen identification and the dissemination of physical reference collections. *Methods in Ecology and Evolution*, *8*(7), pp.892-897.

Metcalfe, S.E., Barron, J.A. and Davies, S.J., 2015. The Holocene history of the North American Monsoon:'known knowns' and 'known unknowns' in understanding its spatial and temporal complexity. *Quaternary Science Reviews*, 120, pp.1-27.

Miles, J. 1987. Vegetation succession: past and present perceptions. In: Gray, A. J., Crawley, M. J. & Edwards, P. J. (eds.) Colonization, succession and stability, pp. 1- 29. Blackwell, Oxford.

Mueller, A.D., Islebe, G.A., Hillesheim, M.B., Grzesik, D.A., Anselmetti, F.S., Ariztegui, D., Brenner, M., Curtis, J.H., Hodell, D.A. and Venz, K.A., 2009. Climate drying and associated forest decline in the lowlands of northern Guatemala during the late Holocene. *Quaternary Research*, *71*(2), pp.133-141.

Neff, H., Pearsall, D.M., Jones, J.G., Arroyo, B., Collins, S.K. and Freidel, D.E., 2006. Early Maya adaptive patterns: Mid-late Holocene paleoenvironmental evidence from Pacific Guatemala. *Latin American Antiquity*, 17(3), pp.287-315.

Odgaard, B.V., 1999. Fossil pollen as a record of past biodiversity. *Journal of Biogeography*, *26*(1), pp.7-17.

Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Wagner, H. and Oksanen, M.J., 2015. Package 'vegan'.

Oldfield, F. and Appleby, P.G., 1984. Empirical testing of 210 Pb-dating models for lake sediments. In Lake sediments and environmental history.

Oliveras, I., Anderson, L. O., & Malhi, Y. (2014). Application of remote sensing to understanding fire regimes and biomass burning emissions of the tropical Andes. *Global Biogeochemical Cycles*, 28(4), 480–496.

OxLEL, 2016. Pollen Preparation Procedure. Oxford Long-Term Ecology Lab. Protocols. Available at: https://oxlel.zoo.ox.ac.uk/wp-content/uploads/2016/10/OxLEL-Fossil-pollen-extraction-protocol.pdf [Accessed 13/06/2018].

Pira, J. P., Marcos, C., & Garzona, E., 1999. Patrones de Uso del Bosque Espinoso Seco, en el Norte del Valle del Motagua. Guatemala: Asociacion de Investigacion y Estudios Sociales.

Prentice, I.C., 1985. Pollen representation, source area, and basin size: toward a unified theory of pollen analysis. *Quaternary Research*, *23*(1), pp.76-86.

R Core Team (2012). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Ramírez-Marcial, N., González-Espinosa, M. and Williams-Linera, G., 2001. Anthropogenic disturbance and tree diversity in montane rain forests in Chiapas, Mexico. *Forest ecology and management*, *154*(1-2), pp.311-326.

Ramsey, C. B. (2008). Deposition models for chronological records. *Quaternary Science Reviews*, *27*(1-2), 42-60.

Ramsey, C.B., 2009. Bayesian analysis of radiocarbon dates. *Radiocarbon*, *51*(1), pp.337-360.

Recinos, A., 1954. Monografía del departamento de Huehuetenango (Guatemala).

Redo, D., Bass, J. O., & Millington, A. C., 2009. Forest dynamics and the importance of place in western Honduras. Applied Geography, 29, 91–110.

Reimer, P.J., Bard, E., Bayliss, A., Beck, J.W., Blackwell, P.G., Ramsey, C.B., Buck, C.E., Cheng, H., Edwards, R.L., Friedrich, M. and Grootes, P.M., 2013. IntCal13 and Marine13 radiocarbon age calibration curves 0–50,000 years cal BP. *Radiocarbon*, *55*(4), pp.1869-1887.

Reyes, E. V., 1998. Poder Local y Bosques Communales en Totonicapan: Estudio de un Caso. Guatemala: Facultad Latinoamericana de Ciencias Sociales.

De Remesal, A., 1932. Historia general de las Indias Occidentales, y particular de la gobernación de Chiapa y Guatemala.. (Vol. 4). Tipografía nacional.

Roubik, D.W. and Moreno, P., 1991. Pollen and spores of Barro Colorado Island [Panama]. *Pollen and spores of Barro Colorado Island [Panama]*., *36*.

Sherman, W.L., 1979. Forced native labor in sixteenth-century Central America. University of Nebraska Press.

Stansell, N.D., Steinman, B.A., Abbott, M.B., Rubinov, M. and Roman-Lacayo, M., 2013. Lacustrine stable isotope record of precipitation changes in Nicaragua during the Little Ice Age and Medieval Climate Anomaly. *Geology*, *41*(2), pp.151-154.

Stockmarr, J. (1971) Tablets with spores used in absolute pollen analysis. *Pollen et Spores*, 8, 615–621.

Ter Braak, C.J. and Prentice, I.C., 1988. A theory of gradient analysis. In Advances in ecological research (Vol. 18, pp. 271-317). Academic Press.

Thompson, J.E.S., (ed.) 1958. *Thomas Gage's travels in the New World* (p. 191). Norman: University of Oklahoma Press.

Tucker, C. M., 2008. Changing Forests: Collective Action, Common Property, and Coffee in Honduras. New York: Springer.

Urrea, O. S., 1995. Economic and institutional analysis of agroforestry projects in Guatemala. In D. Current, E. Lutz, & S. Scherr (Eds.), Costs, benefits, and farmer adoption of agroforestry: Project experience in Central America and the Caribbean (pp. 96–113). Washington, DC: The World Bank.

Van Kempen, L., Muradian, R., Sando´val, C., & Castaneda, J. P., 2009. Too poor to be green consumers? A field experiment on revealed preferences for firewood in rural Guatemala. Ecological Economics, 68, 2160–2167.

van Wieren, S.E., 1996. Digestive strategies in ruminants and nonruminants. Van Wieren.

Van Oss, A.C., 1986. Catholic Colonialism. *A Parish History of Guatemala, 1524-1821*. Cambridge University Press.

Vasquez, F., 1994. Cronica de la provineia del Santisimo Nombre de Jesus de Guatemala. Biblioteca 'Goathemala,' 17, pp. 495

Veblen, T. T., 1974. The ecological, cultural, and historical bases of forest preservation in Totonicapan, Guatemala. Ph.D., thesis, University of California, Berkeley.

Veblen, T.T., 1976. The urgent need for forest conservation in highland Guatemala. *Biological Conservation*, *9*(2), pp.141-154.

Velez, M.I., Curtis, J.H., Brenner, M., Escobar, J., Leyden, B.W. and Popenoe de Hatch, M., 2011. Environmental and cultural changes in highland Guatemala inferred from Lake Amatitlán sediments. *Geoarchaeology*, 26(3), pp.346-364.

Wahl, D., Hansen, R.D., Byrne, R., Anderson, L. and Schreiner, T., 2016. Holocene climate variability and anthropogenic impacts from Lago Paixban, a perennial wetland in Peten, Guatemala. *Global and Planetary Change*, 138, pp.70-81.

Wallace, J., Aquilué, N., Archambault, C., Carpentier, S., Francoeur, X., Greffard, M.H., Laforest, I., Galicia, L. and Messier, C., 2015. Present forest management structures and policies in temperate forests of Mexico: Challenges and prospects for unique tree species assemblages. The Forestry Chronicle, 91(3), pp.306-317.

Walsh, M.K., Prufer, K.M., Culleton, B.J. and Kennett, D.J., 2014. A late Holocene paleoenvironmental reconstruction from Agua Caliente, southern Belize, linked to regional climate variability and cultural change at the Maya polity of Uxbenká. *Quaternary Research*, 82(1), pp.38-50.

Whitlock, C. and Larsen, C., 2002. Charcoal as a fire proxy. In *Tracking environmental change using lake sediments* (pp. 75-97). Springer, Dordrecht.

Willard, D.A., Bernhardt, C.E., Weimer, L., Cooper, S.R., Gamez, D. and Jensen, J., 2004. Atlas of pollen and spores of the Florida Everglades. *Palynology*, *28*(1), pp.175-227.

Willis, K. J., Gillson, L., & Brncic, T. M., 2004. How ‘‘virgin’’ is virgin rainforest? Science, 304, 402–403.

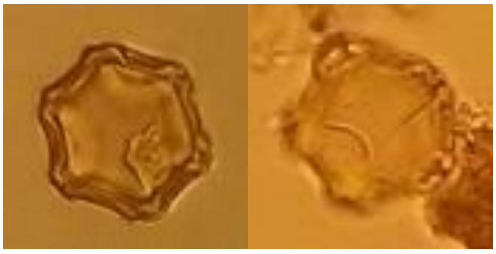
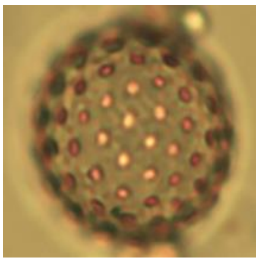
4.9 Supplementary Information

Table 4.2 Sites represented on Figure 4.1

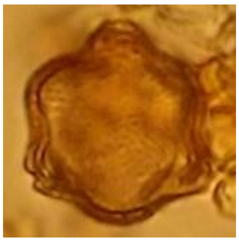
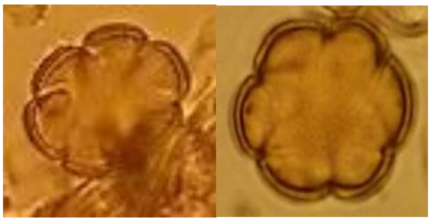
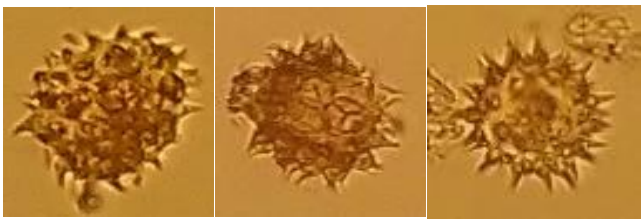
Vegetation			
Name of Site	Longitude	Latitude	References
Agua Caliente	16.16667	-89	Walsh et al. 2014
Aguada Chilonche	16.8	-90.0333	Brenner et al. 1990
Aguada Chimj	16.85	-90.1333	Brenner et al. 1990
Aguada Petapilla	14.867	-89.125	Rue et al. 2002; McNeil et al. 2010
Aguada Zacatal Nakbe	17.66907	-89.7928	Wahl et al. 2007
Biosphere Reserve of Los Petenes	20.13125	-90.4546	Gutiérrez-Ayala et al. 2012
Cenote Aktun Ha	20.27429	-87.4862	Gabriel et al. 2009
Coba	20.49151	-87.7387	Leyden et al. 1998
Cobweb Swamp	17.93772	-88.3664	Jone, 1994; Pohl et al. 1996
El Palmar	17.22809	-89.7615	Torrescano & Islebe, 2006; Luzzadder- Beach et al. 2017
La Encrucijada Biosphere Reserve	15.14967	-92.751	Joo-Chang et al. 2015
Lago Amatitlan	14.45639	-90.5661	Velez et al. 2011
Lago Naja	16.991	-91.5916	Domínguez-Vázquez & Isleb, 2008
Lago Oquevix	16.64869	-89.7502	Brenner et al. 1990
Lago Paixban	17.81556	-90.1208	Anderson & Wahl, 2016; Wahl et al. 2016
Lago Peten Itza	16.998	-89.779	Islebe et al. 1996; Curtis et al. 1998; Hillesheim et al. 2005; Mueller et al. 2009; 2010; Correa-Metrio et al. 2012
Lago Puerto Arturo	17.53333	-90.1833	Wahl et al. 2006; 2007; 2014; Anderson & Wahl, 2016
Lago Sacnab	17.06141	-89.3636	Deevey, 1979
Lago Salpeten	16.98333	-89.6667	Leyden, 1987
Lago Silvituc	18.372	-90.2948	Torrescano-Valle & Islebe, 2015
Lago Tzib	19.29693	-88.0701	Carrillo-Bastos et al. 2010
Lago Yaxha	17.06255	-89.4053	Deevey et al. 1979
Lago Yojoa	14.87372	-87.9838	Rue, 1987
Laguana las Pozas	16.2	-90.1	Johnston et al. 2001
Laguna Cuzcachapa	13.98323	-89.6713	Dull, 2007
Laguna del Espino	13.57	-89.52	Dull, 2004a
Laguna Verde	13.85417	-89.8856	Dull, 2004b
Laguna Yaloch	17.30972	-89.1747	Wahl et al. 2013
Lower Rio Naranjo	14.53871	-92.2023	Neff et al. 2006

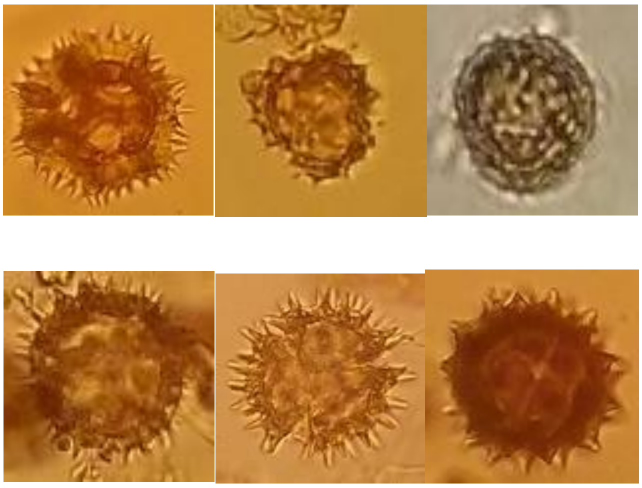
Manchon	14.51711	-92.1188	Neff et al. 2006
Miqul Meadow	15.42344	-91.4387	Caffrey et al. 2011
New River Lagoon	17.66667	-88.6667	Rushton et al. 2013
Puerto Morelos	20.84907	-86.8784	Islebe & Sánchez, 2002
Ria Lagartos Biosphere Reserve	21.57944	-88.0722	Aragón-Moreno et al. 2012
San Andres	18.14063	-93.9886	Pope et al. 2001
Sibun River	17.47205	-88.2609	Monacci et al. 2011
Sipacate	13.94102	-90.6297	Neff et al. 2006
Hydroclimate			
Aguada X'caamal	20.60167	-89.7025	Hodell et al. 2005
Cenote Aktun Ha	20.27429	-87.4862	Gabriel et al. 2009
Chen Ha Cave	17	-89	Pollock et al. 2016
Coba	20.49151	-87.7387	Whitmore et al. 1996
Hillbank	17.59937	-88.6992	Metcalfe et al. 2009
La Vaca Perdida	20.37297	-89.5692	Smyth et al. 2017
Laberinto del Fauno	20.5874	-87.134	Medina-Elizalde et al. 2016
Lago Amatitlan	14.45639	-90.5661	Velez et al. 2011
Lago Chichancanab	19.87	-88.77	Hodel et al. 1995; 2001
Lago Peten Itza	16.91667	-89.8333	Curtis et al. 1998; Hillesheim et al. 2005; Mueller et al. 2009; Pérez et al. 2010; Escobar et al. 2012
Lago Puerto Arturo	17.53333	-90.1833	Wahl et al. 2014; Anderson & Wahl, 2016
Lago Salpeten	16.98567	-89.6744	Rosenmeier et al. 2002a; 2002b
Lago Tzib	19.29693	-88.0701	Carrillo-Bastos et al. 2010
Lamanai	17.76333	-88.6519	Metcalfe et al. 2009
Macal Chasm	16.883	-89.108	Webster et al. 2007; Akers et al. 2016
Outpost	17.75195	-88.653	Metcalfe et al. 2009
Punta Laguna	20.64849	-87.6372	Curtis et al. 1996; Hodel et al. 2007
Tzabnah	20.75	-89.4667	Medina-Elizalde et al. 2010
Yok Balum	16.20833	-89.0733	Kennett et al. 2012

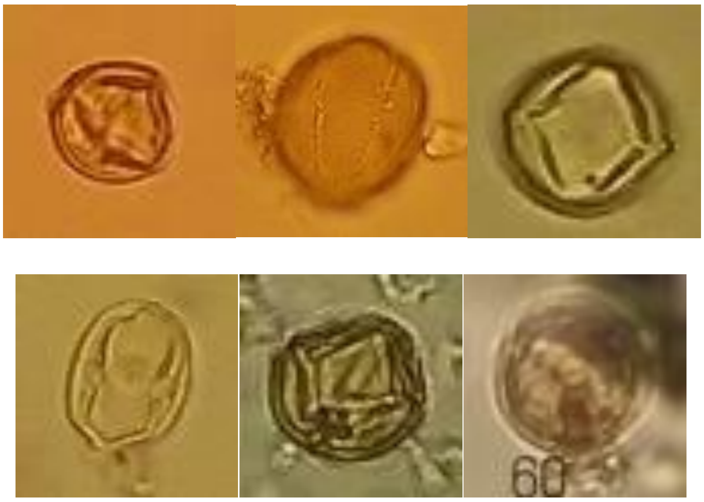
Table 4.3 Images of palynological taxa at 400x magnification identified from Cenote Kail.

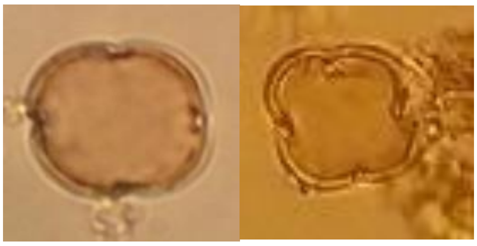
Name	**Image (not to scale)**
Abies	
Alnus	 
Amaranthaceae	 

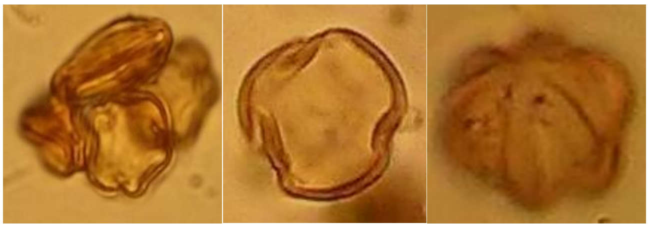
Anacardiaceae	
Aphelandra	
Apiaceae	
Brassicaceae	
Brosimum	

Bursera simaruba	
Campanulaceae	
Capsicum	
Celtis	
Cercocarpus	
Combretum	
Compositae	

	
Cyperaceae	
Ericaceae	
Euphorbiaceae	
Juniperus	

Liquidambar	
Leguminosae	
Morella cerifera	
Myrica	
Pinus oocarpa	

Poaceae	
Polygalaceae	
Pourouma	
Primulaceae	
Protium	
Quercus	

Roupala	
Rubiaceae	
Serjania	
Terminalia	
Zea mays	
Unknown	

5. The apparent resilience of the dry tropical forests of the Nicaraguan region of the Central American dry corridor to variations in climate over the last *c.* 1200 years

William J. Harvey[1], Nathan Stansell[2], Sandra Nogué[3], Katherine J. Willis[1]

[1]Long-Term Ecology Laboratory, Department of Zoology, University of Oxford, Oxford, UK

[2]Department of Geology and Environmental Geosciences, Northern Illinois University, DeKalb, IL, USA

[3]School of Geography and Environmental Sciences, University of Southampton, Highfield, Southampton, UK

Published in Quaternary

5.1 Abstract

The Central American Dry Corridor (CADC) is the most densely populated area of the Central American Isthmus and is subject to the greatest variability in precipitation between seasons. The vegetation of this region is composed of Dry Tropical Forests, (DFT) which are suggested to be highly susceptible to variations in climate and anthropogenic development. This study examines the vulnerability of past DTF surrounding the Asese Peninsula, Nicaragua to climatic and anthropogenic disturbances over the past c.1200 years. Past vegetation, climate, burning, and animal abundance were reconstructed using proxy analysis of fossil pollen, diatoms, macroscopic charcoal, and *Sporormiella*. Results from this research suggest that DTF have been highly resilient to past climatic and anthropogenic perturbations. Changes in DTF structure and composition appear to be linked to the abundance and intensity of fire. Pre-Columbian anthropogenic impacts on DTF are not detected in the record; however, DTF taxa decline slightly after European contact (1522C.E.). Overall the DTF's for the Nicaraguan region of the CADC were found to be highly resilient to both climatic and anthropogenic disturbances suggesting that this region will continue to be resilient in the face of future population expansion and climatic variation.

5.2 Introduction

Significant losses in food production across the Central American isthmus (Isthmus of Tehuantepec south to the Isthmus of Darien) resulting from a deficit in precipitation at the beginning of the harvest in 2015 rendered an estimated 2.2 million people at risk of moderate or severe food insecurity (World Food Programme, 2015). This episode is indicative of the vulnerability of the flora, fauna and human population of the Central American Dry Corridor (CADC) to seasonal patterns of rainfall, impacting agrarian practices, food and water security (Imbach et al. 2015; Durán-Quesada et al. 2017). Given these recent episodes of apparent vulnerability of the CADC to hydroclimatic changes, the aim of this research was to identify past hydroclimatic changes and assess their impacts upon the Dry Tropical Forests (DTF) for the Central Pacific lowlands of Nicaragua spanning the last c.1200 years (Figure 5.1) using proxy analysis of fossil pollen, diatoms, macroscopic charcoal, and *Sporormiella*.

Climate

Previous research examining the spatial patterns and mechanisms driving precipitation change across the Central American Isthmus over the past 2000 years have focused upon the impacts and timings of hydrological extremes including the Medieval Climate Anomaly (MCA) 950-1250C.E. and Little Ice Age (LIA) 1400-1850C.E. (Hodell et al. 1995; 2005; 2007 Curtis et al. 1996; 1998; Rosenmeier et al. 2002; Lachniet et al. 2004; Webster et al. 2007; Metcalfe et al. 2009; Carrillo-Bastos et al. 2010; Medina-Elizalde et al. 2010; Velez et al. 2011; Stansell et al. 2013; Kennett et al. 2012; Akers et al. 2016; Correa- Metrio et al. 2016; Smyth et al. 2017) and the transition between the two (e.g. Graham et al., 2007). The dates reported for the timing of the MCA and LIA are variable ranging between 800-1400C.E. for the MCA and 1400-1850C.E. for the LIA (see Metcalfe et al. 2015).

These changes in precipitation are reported to be primarily driven by the interactions of three climatic forcing's: (i) the position of the Inter Tropical Convergence Zone; (ii) the North Atlantic Oscillation; and (iii) the El Niño Southern Oscillation (ENSO) (Metcalfe et al. 2015). Warmer SSTs in the Caribbean and Gulf of Mexico are inferred for the early part of the MCA, which coincided with wetter conditions in Belize and Central Pacific Nicaragua (Kennett et al. 2012; Stansell et al. 2013). These warmer SST's are associated with a more northerly position of the ITCZ as inferred from the Cariaco Basin titanium record (Haug et al., 2001). Cooler SSTs in the Caribbean and Gulf of Mexico were associated with a southward shift in the ITCZ, weakening the summer monsoon during the LIA (Hodell et al., 2005). Precipitation at this time is reported to be spatially and temporally heterogenous with many records lacking sufficient chronological control or resolution to examine this period in detail (Metcalfe et al. 2015).

Previous work reconstructing past precipitation across the CADC during this time period has been limited with only a single terrestrial $\delta^{18}O$ record published from within this region spanning the past 1400 years (Stansell et al. 2013). This $\delta^{18}O$ record indicates comparatively wetter conditions during the Medieval Climate Anomaly (MCA) 950-1250C.E. and drier conditions during the Little Ice Age (LIA) 1400-1850C.E.).

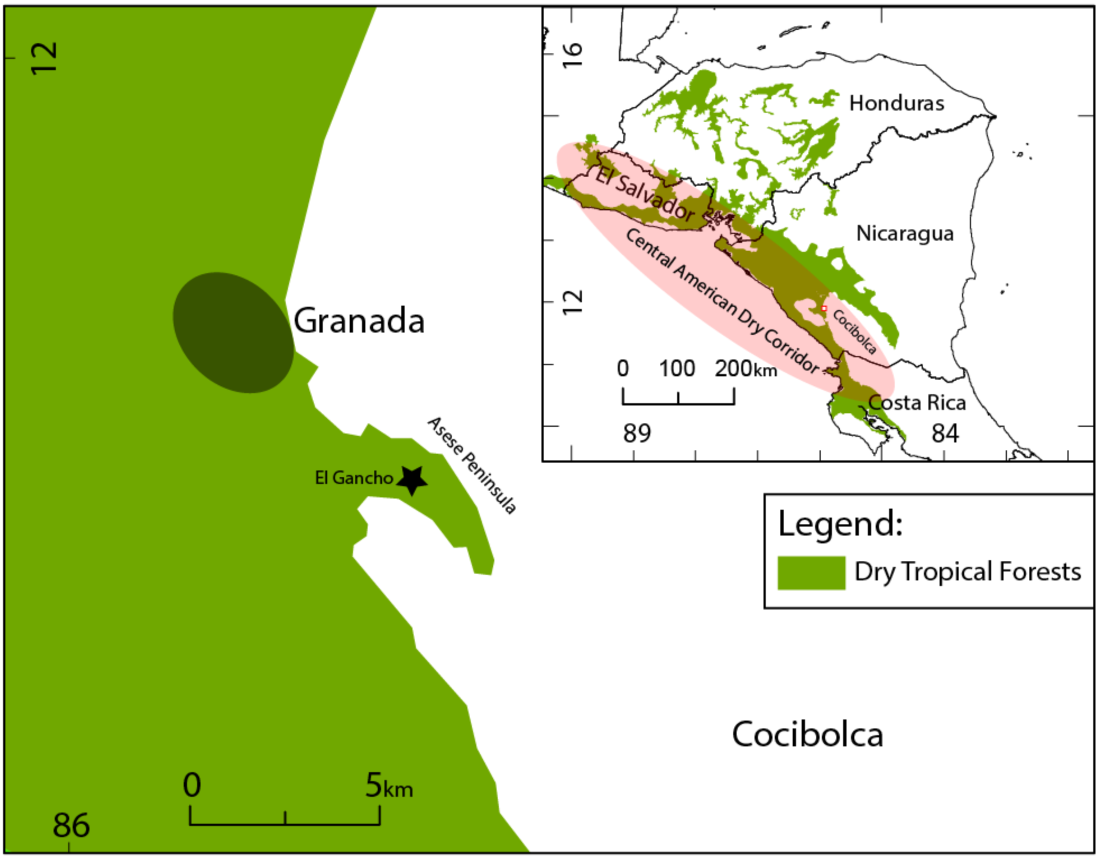


Figure 5.1 Nicaraguan region of the Central American Dry Corridor (ellipsis) and location of Granada, the Asese peninsula and El Gancho.

Vegetation

A range of vegetation types are found in the CADC which can be broadly categorised as: (i) dry tropical forests (DTF); (ii) moist tropical forests (MTF); (iii) coniferous tropical forests (CTF); and (iv) mangroves (Dinerstein et al. 2017). These formations are primarily distributed according to climate (temperature and precipitation), soil type (e.g. volcanic, alluvial), and altitude (highlands and lowlands). Past research reconstructing vegetation dynamics within the CADC has been somewhat limited, particularly for DTF for the last 1200 years (Figure 5.1). Past anthropogenic influences are typically inferred from agricultural taxa such as *Zea mays*, anthropogenic burning and evidence from nearby archaeological sites. In comparison greater forest cover, reduced burning, and an absence of agricultural taxa, appear to co-inside with intervals of evidence for reduced population (Ford & Nigh, 2009). In contrast, intervals with known archaeological evidence for more people are associated with greater forest clearance (using fire), an abundance of agricultural crops and the increase in abundance of economic or useful taxa (e.g. Dull, 2004a; 2004b; 2007).

In total three sites have been examined from the DTF to date indicating that there have been vegetation responses to known forcing over this interval in time. For example, in a study by Dull (2004a) which looked at the vegetation structure and composition of the Ahuachapan region in the CADC of El Salvador found that anthropogenic burning between c.2500-500 cal yr B.P. resulted in a more open grassland environment at the expense of woody taxa. Following this disturbance Urticales and Mimosoideae were found to have established and were attributed to the population collapse of the region. It is apparent that decreases in arboreal cover are commonly associated with anthropogenic activity, or drier conditions, and more fire; and vice versa for wetter conditions (Dull, 2004a; Velez et al. 2011).

The resilience of the DTF's to climatic and anthropogenic impacts is currently poorly understood (Willis et al. 2018). It is suggested that either the DTF's (i) will be sensitive to climatic change because they are already limited by water and are close to a habitat threshold; or (ii) they will be resilient to changes in rainfall because they are adapted to predictable seasonal drought. Similarly, DTF's will either be (i) vulnerable to anthropogenic activities, such as agrarian practices, land conversion and population density because of land use change; or (ii) they will be resilient to anthropogenic factors due to composition adaptation over time (Allen et al. 2017). Disturbance, change, and evolution through time can lead to the reorganization and renewal of the ecosystem (Carpenter et al. 2001). We define resilience by the capacity of a system (biotic or abiotic) to be perturbed while remaining in the same state.

In order to fill these knowledge gaps (detect the impacts of climate and people upon the biota residing within the CADC), this study reconstructed past precipitation, biomass burning, DTF dynamics and herbivorous mammal presence, over the last 1200 years (c.840-2004C.E). These results were then examined within the context of the archaeological record from the Central Pacific Nicaraguan region. The aim of this study was to (i) identify the past hydroclimatic changes within the Nicaraguan region of CADC; (ii) assess how the DTF responded to identified climatic shifts; and (iii) assess how anthropogenic activities have impacted the DTF of Central Pacific Nicaragua.

Study Area

The CADC is subject to severe and prolonged periods of drought. The dominant type of vegetation in the lowland (<1000m) areas are DTF (Chiabai, 2015). These occur from Chiapas (Mexico) and extend south across the central and lowland areas of Pacific Guatemala through El Salvador, Honduras, Nicaragua, and Costa Rica (Guevara-Murua et al. 2018). DTF occur: (i) in frost free environments with mean annual temperatures greater than 17ºC; (ii) mean annual rainfall of 250-2000mm; and (iii) overall greater potential evapotranspiration to precipitation (Murphy & Lugo, 1995). DTF are subject to a long dry season (5-8 months) and a shorter wet season (Imbach et al. 2015).

Most plants in the DTF cease their vegetative growth in the dry season and shed their leaves, while other produce fruits and spread their seed (González-Rivas, 2005). The most common taxa found to comprise DTF include: *Bursera simaruba*; *Caesalpinia coraria*; *Calycophyllum candidissimum; Guazuma ulmifolia; Gyrocarpus americanus; Haematoxylon brasiletto; Luehea candida; Lysiloma kellermani;* and *Phyllostylon brasiliensis* (Taylor, 1963).

These formations are typically smaller in stature, lower in biomass and less complex floristically and structurally than tropical rainforests (Murphy & Lugo, 1986). The canopy is usually closed with no substantial opening in the crown (<20%) reaching a height of approximately 15-20m (González-Rivas, 2005).

Nicaragua is covered by 2500km of DTF, which represents around 2% of the total forest cover (Harcourt & Sayer 1996). DTF once covered more than 40% of the total area of all tropical forests (Murphy & Lugo 1986). They are one of the most threatened habitats globally and are argued to deserve a high priority for conservation (Janzen, 1988; Gillespie et al. 2000; Miles et al. 2006). Prior to European contact, savannas were created within the dry tropical forests by inhabiting human populations, especially along the Pacific coast (Denevan, 1992; Cooke & Ranere, 1992). The DTF's were more intensively anthropogenically managed compared to the MTF's due to the abundance of more productive soils for crop rotation, also known as *milpa* (Murphy & Lugo, 1986; Daniels et al., 2008); however, management practices were inefficient in clearing land, allowing for immediate regeneration after several years of cultivation (Parsons et al., 2008).

The Pre-Columbian population inhabiting Nicaragua (before 1522C.E.) is unknown; however, several attempts to estimate total population have been made, with upper estimates of c.800,000 (Newson, 1987) to 1,000,000 (Denevan, 1976; Randell, 1976; Lovell & Lutz, 1991) and lower estimates of 100,000 (Kroeber, 1939). With European contact and the Spanish conquest of Nicaragua, indigenous populations were reported to have been significantly reduced from 500,000 to 200,000 by 1535C.E. (MacLeod, 1973). Latter conquests and occupation of the Mesta Central of Costa Rica (in 1570C.E.) reported further depopulation of up to 90% down to c.61,000 though warfare, slavery and introduction of epidemic diseases (Newson, 1986; 1987; & Lange & Haberland, 1992). By the end of the 16th Century there were only around 500 Spanish colonists living in Nicaragua (Healy & Pohl, 1980). Populations are suggested to have only started to increase again by *c.*1800C.E (c.83,000) (Newson, 1986) and reach upper estimates of Pre-Columbian contact levels (*c.*1,000,000) by c.1950 (Vinogradov, 2014). The current population is around six times (*c.*6,272,133) that of the maximum estimates for pre-contact levels (Worldometers, 2018).

Pasture conversion for cattle was the main cause of deforestation in Nicaragua after European contact in 1522 (Calvo-Alvarado et al., 2009), which is thought to have impacted DTF more extensively than MTF (Janzen, 1988; Toledo, 1988; Murphy & Lugo, 1995). DTF were popular settlement areas because land was easier to clear, soil fertility was higher, diseases were rare, and high-quality timbers could be found within these forests (Murphy & Lugo, 1986; Calvo-Alvarado et al., 2009).

Small-scale deforestation began in 1522C.E. with the arrival of the Spanish (Janzen, 1983; Denevan, 1992; Calvo-Alvarado et al., 2009; Griscom & Ashton, 2011). After the Central American Act of Independence in 1821C.E. landless peasants began to clear land in the DTF more permanently to raise cattle (Heckadon Moreno, 1984; Calvo-Alvarado et al., 2009). In the early 1900s' timber extraction, primarily from the DTF, increased for export (Sabogal, 1992; CalvoAlvarado et al., 2009). Targeted species included: *Swietenia humilis, Cedrela odorata, Pachira quinata, Dalbergia retusa,* and *Guaiacum sanctum* (Sabogal 1992). The major causes of DTF loss in recent years are due to agricultural expansion for coffee plantations, crop fields and further ranches (Roldan, 2001). Only fragments of dry forests remain today (Harcourt & Sayer, 1996).

El Gancho

El Gancho (11.906°N, 85.918°W, 44m above sea level) is a small, shallow (1.1m), closed basin lake, situated on top of the Asese peninsula. The Asese peninsula protrudes into the northwest quadrant of Cocibolca (Lake Nicaragua) next to the city of Granada founded in 1524C.E. (Figure 5.1). El Gancho is thought to have been formed sometime after 140-345C.E. when the Asese peninsula was created as the result of a c.57km^2 debris avalanche originating from the northeast flank of the Mombacho Volcano (van Wyk de Vries & Francis 1997; Stansell, 2013). Sedimentological analysis suggests that sediments have continuously accumulated in El Gancho since its formation (Stansell et al. 2013; Stansell, 2013). Total annual rainfall is 1298mm and mostly falls between May-October (Montenegro-Guillén, 2003).

The vegetation assemblage currently on the Asese Peninsula is comprised of taxa belonging to the DTF (Beard, 1942; 1944; Dinerstein et al. 2017). The vegetation is comprised of a higher canopy, primarily deciduous trees: e.g. *Bursera simaruba, Gliricidia sepium, Diospyros acapulcensis, Cochlospermum vitifolium,* and *Myriocarpa bifurca*; and an understory which is typically comprised of sparse and scattered evergreen or deciduous shrubs, and grass tufts e.g. *Amaranthus spinosus*, Compositae, and Poaceae (Beard, 1942; 1944; Taylor, 1963; Atwood, 1984; Bellefontaine & Petrucci, 2000; Gillespie et al. 2000). The understory is typically burnt by landowners to cleanse unwanted weeds and ticks and to prepare the land for agriculture or ranching (Atwood, 1984).

The area surrounding the Asese peninsula, was once DTF but now predominantly agricultural comprising cattle ranching and the growing of corn (*Zea mays*), beans (Leguminosae) and rice (Oryza). Most of this agriculture is grown for export (Biondi-Morra, 1993).

There are few wild animals left in this area due to extensive land management (e.g. cattle ranching and tourism); however, the mantled howler (*Alouatta palliata*), domesticated dogs (*Canis*), various species of iguana (*Iguana*) and rabbit (*Sylvilagus*) can be found on the Asese Peninsula and surrounding islands (Las Isletas). The Asese peninsula is sparsely populated with only one or two dwellings; however, the city of Granada (less than 10km away), is home to *c.*124,000 people (UNIDA, 2012).

Observations in the field between 2014-2017C.E. capture variations in lake level derived from precipitation: (i) before, (ii) during, and (iii) after a 2-year ENSO event (Figure 5.2).

Figure 5.2 El Gancho lake level and vegetation cover. (A) PreENSO: March 2014; (B) ENSO: May 2015; (C) PostENSO: March2017.

5.3 Methods

Field and sampling techniques

In June 2004 a bathymetric survey of El Gancho was conducted using a handheld sonar to identify the deepest part of the lake (1.1m) from which a 277cm composite core, with overlapping sections, was retrieved using a Livingstone piston corer (Livingstone, 1955). The upper ~168 cm of the core contains massive, very dark brown to black, organic-rich sediments with no notable changes in the stratigraphy (Stansell et al. 2013). The top 34cm of the core were extruded in the field at 0.5cm intervals to ensure sediments did not mix. Forty-two subsamples (1g wet weight) were extracted at approximately 4cm down through the sequence for proxy analysis of macro-charcoal, pollen, and dung fungal spores (*Sporormiella*), and twenty-two subsamples (0.1g wet weight) for diatom analysis at an interval of 8cm (3.5-14.5 range).

Chronology

An age-depth model was constructed using five calibrated radiocarbon dates conducted on charcoal fragments published in Stansell et al. (2013). The radiocarbon dates were (i) recalibrated against the IntCal13 radiocarbon dataset (Reimer, 2013); and (ii) converted to calendar ages and modelled using OxCal 4.3 (Table 5.1). The Bayesian model applied used a Poisson distribution and made no assumptions of the prior probability distribution to allow for posterior probability distribution to encompass the widest range of likelihoods. The Poisson parameter k_0 was taken as 1 depth^{-1}, the interpolation rate as 0.7 depth^{-1} and the $\log_{10}(k/k_0)$ as U(-2,2). The sedimentation rate per year was calculated from the results of the age depth model and used in the calculation of pollen concentrations and charcoal influx.

Table 5.1 Measured, calibrated and modelled ^{14}C ages from El Gancho.

Lab #	**Measured Age (14C BP)**		**Depth (cm)**	**2σ Calibrated Age Range (A.D.)**		**Median Calibrated Age**	**OxCal Modelled Age (A.D.)**		**Model Agreement Index**	**Median Modelled Age**
UCI-19881	630	±35	82.25	1286	1400	1343	1288	1405	99.1	1346.5
UCI-19882	860	±35	117.25	1046	1260	1153	1053	1253	105	1153
UCI-19883	1100	±30	162.25	887	1013	950	775	1012	90.7	893.5
UCI-22766	1640	±40	212.75	266	538	402	333	530	110.6	431.5
UCI-22767	1770	±30	226.25	123	345	234	186	385	103	285.5

Diatom Analysis

Fossil diatoms were used to infer past changes in lake level and area. They were cleaned and prepared using standard procedures as outlined in Berglund (1987) and followed the Oxford Long-Term Ecology Laboratory diatom protocol (OxLEL, 2014). Samples were mounted using Naphrax resin, chosen for its high refractive index, 1.73 (Fleming, 1954). A total of 300 frustules per level were counted and morphologically identified (SI) using published keys (Gasse, 1986; Round et al., 1990; Krammer & Lange-Bertalot, 1991a; 1991b; 1997; Lange-Bertalot & Krammer, 1997; & Lange-Bertalot et al. 2000). Annual diatom concentrations were calculated using the evaporative tray method and results from the age-depth model (Berglund, 1987). The diatom samples were matched to the sampling resolution of the palynological data through linear interpolation for ease of comparative analysis.

Fossil Pollen and Dung-Spore Analysis

Fossil pollen was used to reconstruct the composition of past DTF vegetation. Fossil pollen extraction and preparation followed standard palynological procedures applying the Oxford Long-Term Ecology Laboratory protocol (OxLEL, 2016). Silicone oil was used as the mounting agent to allow for rotation of grains, easing identification. Samples were spiked with known concentrations of *Lycopodium* spores (batch No. 212761 or 3862) to calculate pollen accumulation rates (e.g. Leyden, 2002). Counting and identification of pollen grains were conducted at 400x and 1000x magnification. For each level, a minimum of 300 terrestrial pollen grains were counted. Morphological identification was achieved using (i) pollen databases (Bush & Weng, 2007; APSA, 2007; Martin & Harvey, 2017); (ii) published plates: (Roubik & Moreno, 1991; Willard et al. 2004); and (iii) botanical reference materials from the OxLEL reference collections and specimens collected in the field (SI). *Amaranthus spinosus* was removed from the total palynological counts due to overrepresentation within the assemblage (e.g. Bush, 1995). Total abundance of *Amaranthus spinosus* averaged to 73% of total pollen abundance with a maximum abundance of 90%. Overrepresentation has been attributed to growth within the catchment area and also because species in the Amaranthaceae family are known for their high production of pollen and seed (Bensch et al. 2003). The abundance of coprophilous dung fungal spores (*Sporormiella*) were used to indicate herbivorous mammal abundance. *Sporormiella* spores were counted and morphologically identified (from their sigmoid aperture) on the same slides (Davis & Shafer, 2006; Baker et al. 2016).

Macroscopic Charcoal Analysis

Macroscopic fossil charcoal (>150μm) was used as a proxy to indicate past occurrence of local fires, representing burning within a 10km radius of the lake basin (e.g. Gavin et al., 2003; Lynch et al., 2004; Peters and Higuera, 2007; Higuera et al., 2007; 2011; Anderson & Wahl, 2016). Fragments were separated from the sample using a sieve (Whitlock & Anderson, 2003). All charcoal over 150μm was counted at 10x magnification. Sample weight was converted to volume using density measured from the loss on ignition (Stansell et al. 2013). Charocal Influx yr^{-1} was calculated using the sample volume, charcoal counts and age depth model.

Data Handling

Pollen and diatom counts were converted to percentages while *Sporormiella* and macroscopic charcoal were converted to influx using the exotic marker (*Lycopodium*) and the sedimentation rate (Maher 1981; Bennett 1994; Bennett & Willis, 2001; Whitlock & Larson, 2002; Baker et al. 2016). To identify discrete zones in the palynological assemblage, constrained hierarchical clustering upon the palynological data set was conducted following the broken stick model (Bennett, 1996). Before performing all ordination analyses a square-root transform was applied to the percentage data to normalise the distribution. This method of transformation was chosen because it can be applied to data sets containing zero values (Ter Braak & Prentice 1988). To check which ordination method was most appropriate for the palynological and diatom data sets, detrended correspondence analysis was conducted and the number of standard deviations away from the mean was assessed (Ter Braak & Prentice 1988). Principal component analysis (PCA) was selected and used to infer similarities between samples and taxa applying a singular value decomposition of the centered but not scaled data matrix.

Canonical correspondence analysis (CCA) conducted to quantify the relationship between environmental variables and the palynological and diatom assemblage data. $\delta^{18}O$ data from Stansell et al. (2013) was matched through interpollation to the resolution of the palynological and diatom data sets for the CCA. Ellipse's representing the discreet Zones were calculated using the parameterization (cos(theta + d/2), cos(theta - d/2)), where cos(d) is the correlation of the parameters was applied (see Murdoch & Chow, 1996). These were conducted at a confidence level of 95%. These analyses and the presentation of data was performed using R (R Core Team, 2012), applying packages Vegan (Oksanen et al. 2015) and Rioja (Juggins et al. 2009).

5.4 Results

Chronology and Resolution

Re-calibration and modelling of the five radiocarbon dates published by Stansell et al. 2013 indicated that the recovered composite core encompasses the past 1200 years in continuous sedimentation (Figure 5.3). Distance between sub samples for palynological analysis represent an average resolution of *c*.30 years. The age-depth model presents good overall agreement (Inex = 102.9) with an average age range of 190 years surrounding the median modelled age. Model agreement varied between and Index of 99.1 and 110.6 (Table 5.1).

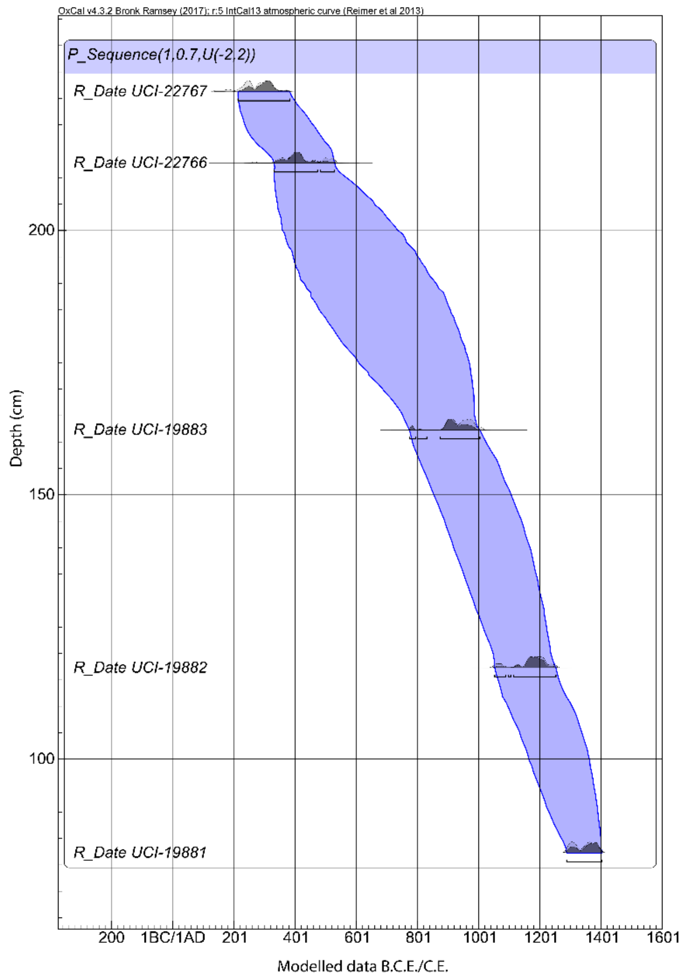


Figure 5.3 Age depth model for El Gancho.

Palaeoecological Trends: Diatoms

The diatom assemblage is well represented by a dynamic assemblage of facultatively planktonic, plantonic, benthic and epiphytic taxa (Figure 5.4). Changes within the diatom assemblage broadly reflect the palynologically defined Zones which have been superimposed.

Zone 1 (168-117cm, 5 samples, 850-1180C.E.). Benthic (32.2-60.7%) and ephyphitic (18.5-32.3%) taxa dominate this first zone (*Mastogloia smithii, Nitzschia frustulum, Navicula longicephala, Nitzschia amphibia, Encyonema silesiacum* and *Anomoeoneis vitrea*, but decrease in abundance after 1030C.E. (90.8-48.1%). *Cyclotella meneghiniana* rises from 1030-1150C.E. (6.1-20.3%) as does *Pseudostaurosira brevistriata* (2.4-23.4%). Total frustule abundance is lowest in this zone (6.6 -2.5 x10^6 frustules 1g^3 dry sediment).

Zone 2 (107.5-58cm, 10 samples, 1180-1550C.E.). Benthic and ephyphitic taxa diminish. *Pseudostaurosira brevistriata* becomes the dominant taxa between 1150-1230C.E. (23.4-59.9%). After 1340C.E. *Aulacoseira ambigua* (47.3%) succeeds *Pseudostaurosira brevistriata* (27.4%) in abundance, dominating the assemblage until the end of the zone (41.2%). *Cyclotella meneghiniana* rises between 1450-1530C.E. (12.6-32.3%). Frustule counts gradually increase (2.4-4 x10^6 frustules 1g^3 dry sediment).

Zone 3 (55.5-3.5cm, 7 samples, 1550-2004C.E.). From 1600C.E. Pse*udostaurosira brevistriata* (45.8%) succeeds *Aulacoseira ambigua* (29%). All other taxa diminish except for *Nitzschia frustulum* which increases from 1730-1970C.E. (3.1-11.8%). Cyclotella meneghiniana remains in high abundance until 1600C.E. (12.1%). Diatom frustules increase from 1570-1600C.E. (8,863,231-45,552,185 frustules 1g^3 dry sediment) and 1810-1930C.E. (37,353,262-95,983,203 frustules 1g^3 dry sediment), and decrease in number from 1700-1810C.E. (63,663,242- 37,353,262 frustules $1g^3$ dry sediment).

Ordination of the diatom assemblage data denotes clear taxonomic associations with each of the superimposed palynological Zones (Figure 5.5). The PCA explains 40.2% of the assemblage variance along Axis 1 and 23.4% along Axis 2. Zone 1 is predominantly associated with benthic and ephyphitic taxa (e.g. *Mastogloia smithii* and *Nitzschia frustulum, Navicula longicephala, Nitzschia amphibia, Encyonema silesiacum* and *Anomoeoneis vitrea*); Zone 2 is most associated with *Aulacoseira* and *Navicula* taxa; while Zone 3 defined by *Pseudostaurosira brevistriata* and *Pinnularia viridis*. Results from the CCA show a clear significant association with $\delta^{18}O$ along the first axis. More positive $\delta^{18}O$ are most associated with Zones 2 & 3.

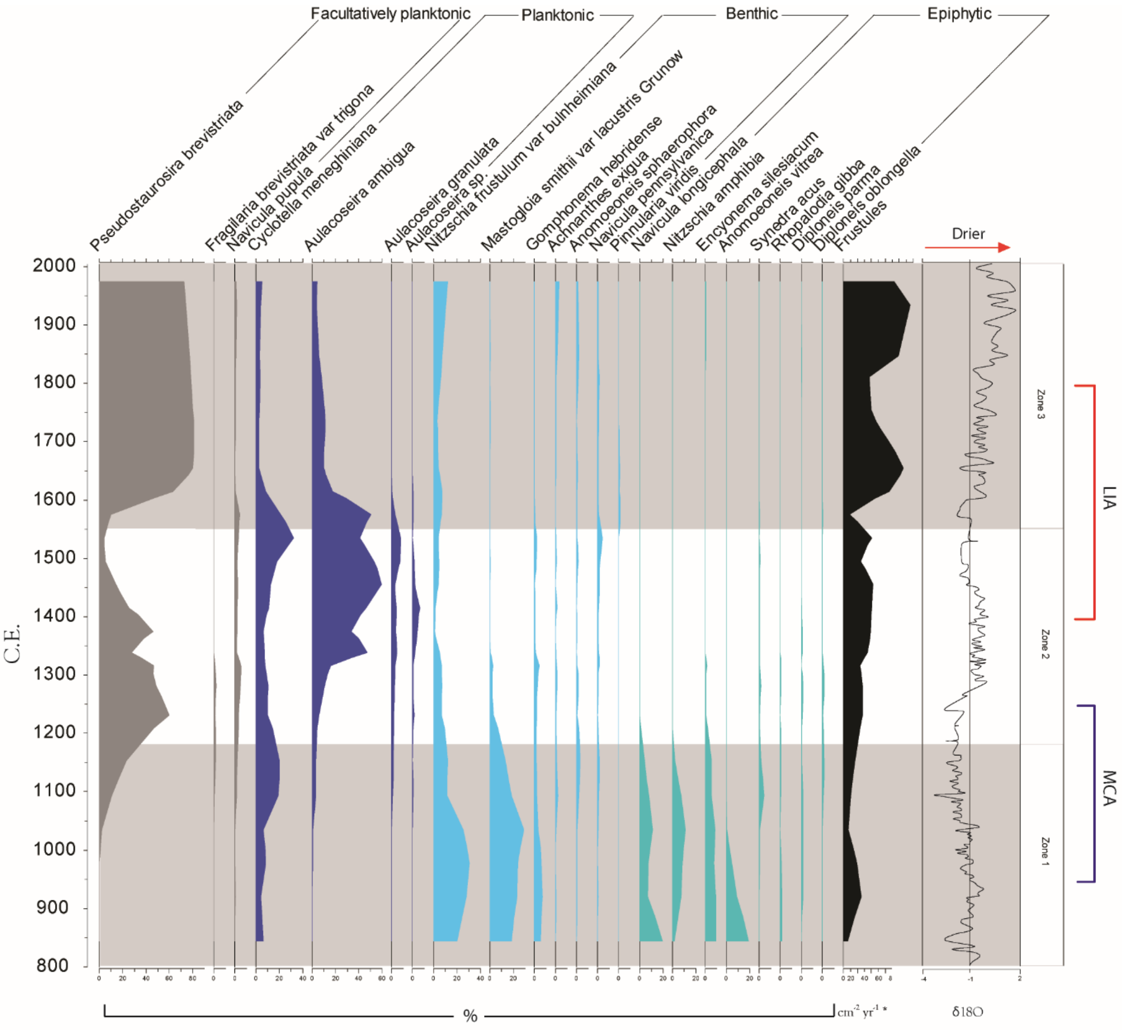


Figure 5.4 Diatom assemblage reconstructed from El Gancho with $\delta^{18}O$ data from Stansell et al. (2013).

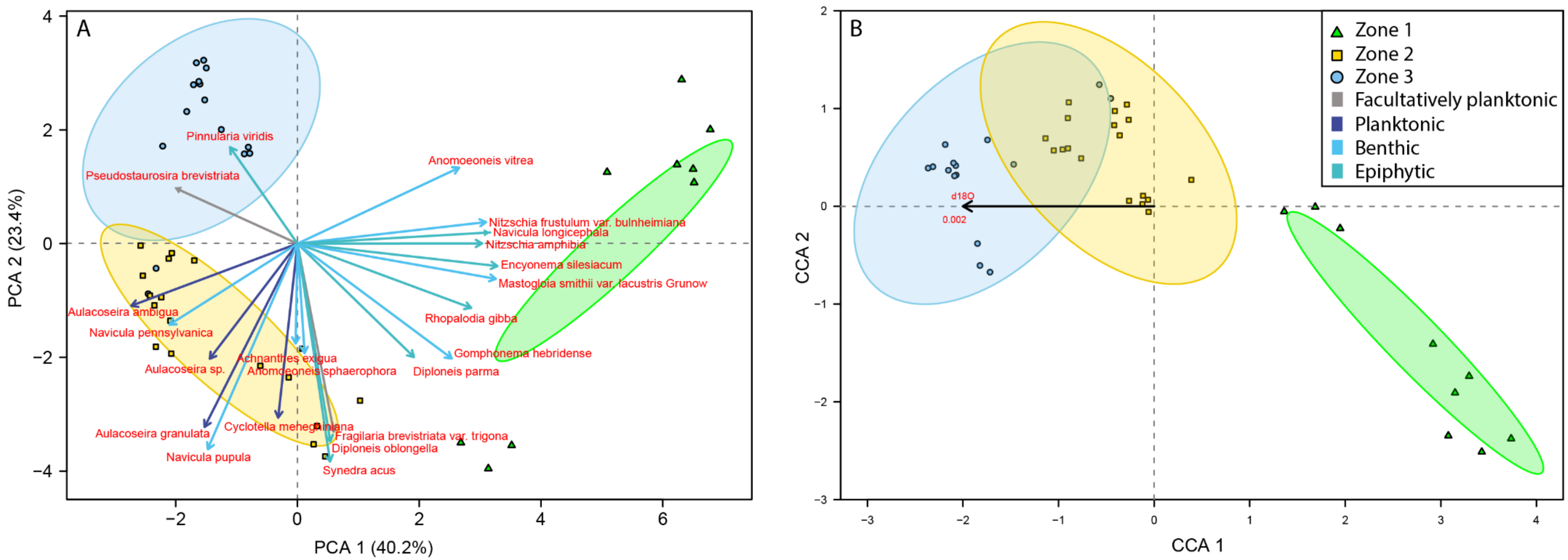


Figure 5.5 : Principal component analysis of the diatom assemblage (A). Canonical correspondence analysis of the diatom assemblage (B). Zones derived from the broken stick model conducted on the palynological assemblage represented by ellipses at a confidence of 95%. Zone 1 = green triangles; Zone 2 = yellow squares; Zone 3 = blue circles.

Palaeoecological Trends: Pollen, *Sporormiella* and Macroscopic Charcoal

Zonation of the palynological sequence indicates that three numerically derived zones can be recognised between 840-2004C.E. (Figure 5.6 & 5.7). DTF taxa (e.g. *Bursera simaruba*, *Brosimum, Protium and Terminalia*) are well represented throughout the entire 1200 years analysed, comprising 48-95% of the total palynological assemblage; however, the DTF community composition varies through time (Figure 5.6 & 5.7).

Zone 1 (168-117cm, 9 samples, 850-1180C.E.). *Bursera simaruba* (27.1-34.5%), is abundant in the first zone of this sequence, together with Leguminosae (11.5-15.5%), *Protium* (10-12.1%) and *Mimosa* (2.9-8.6%) from the DTF taxa. Taxa comprising the herbaceous understory (Poaceae, Compositeae, Cyperaceae and *Spananthe paniculata*) are abundant (33.3-17.3%) particularly at 890C.E. (36.7%), 1000C.E. (39.3%) and between 1090-1120C.E. (36.1-38.2%). Non-DTF arboreal taxa are represented in low abundance by *Pinus* (1.4-4.4%), *Alchornea* (0.1.4%) and *Roupala montana* (0-0.9%). *Sporormiella* influx is high at 980C.E. (2.6 spores cm^2yr^{-1}) between 1030-1090C.E. (4.3-3.3 spores $cm^{-2}yr^{-1}$) and at 1150C.E. (4.5 spores cm^2yr^{-1}). Macroscopic charcoal influx is high (10.3-38.1 particles $cm^{-2}yr^{-1}$), peaking between 920-980C.E. (33.2-29.8 particles $cm^{-2}yr^{-1}$) and at 1090C.E. (38.1 particles $cm^{-2}yr^{-1}$). Pollen influx is low (45,676-109,410 grains $cm^{-2}yr^{-1}$).

Zone 2 (107.5-58cm, 18 samples, 1180-1550C.E.). DTF taxa increase from 1180-1370C.E. (75-95.3%) and persistently dominate the assemblage in abundances greater than 70% through to the end of this zone. High abundance DTF taxa include *Bursera simaruba* (6.5-45.6%), *Brosimum* (0-38.7%), *Terminalia* (4.1-16.4%), *Protium* (0-13%) and *Celtis* (0-16.7%). *Celtis* peaks at 1230C.E. (16.7%). Coussapoa is persistent in low abundances between 1230-1530C.E (2.4-4.4%), at which point Anacardiaceae (3.3%) and *Mimosa* (3.3%) supersede. Herbaceous taxa decline and remain in low abundance until after 1440C.E. (20.8-3.6%). From 1480C.E., herbaceous taxa begin to increase through to the end of this zone (5.3-24.4%). *Capparis* (Caper) appears for the first time at c.1500C.E. accompanied by an increase in Poaceae. (2.6-6.7%). The abundance of non-DTF arboreal taxa remain in low abundance with the exception of a short-lived peak from *Roupala montana* at 1320C.E. (23.7%). *Sporormiella* influx decreases from the beginning of this Zone (2.7 spores $cm^{-2}yr^{-1}$) and remains in low abundance between 1230-1480C.E (0-0.7 spores $cm^{-2}yr^{-1}$). After 1480C.E. *Sporormiella* influx increases substantially (0.7-2.7 spores $cm^{-2}yr^{-1}$). Macroscopic charcoal influx remains high until 1300C.E. (30.6 particles $cm^{-2}yr^{-1}$) where it transitions down to a lower influx by 1400C.E. (5.1 particles $cm^{-2}yr^{-1}$). Between 1400-1530C.E. macroscopic charcoal influx remains comparatively low (0.1-7.9 particles $cm^{-2}yr^{-1}$). Pollen influx increases particularly after 1300C.E. (266,775 grains $cm^{-2}yr^{-1}$) and is particularly high between 1440-1480C.E. (1,413,110-1,333,889 grains $cm^{-2}yr^{-1}$).

Zone 3 (55.5-3.5cm, 15 samples, 1550-2004C.E.). DTF taxa decrease from 1560-1640C.E. (83.6-48.4%) and increase from 1640-1750C.E. (48.4-80%). The DTF assemblage is predominantly comprised of *Bursera simaruba* (6.4-36.7%), *Brosimum* (4.4-33.3%), *Protium* (0-9.6%), Leguminosae (2.2-7.1%), Anacardiaceae (1.4-10.1%), and *Rhus* (0-5.9%). Poaceae and Cyperaceae increase in abundance permanently after 1530C.E. and 1600C.E. Cyperaceae peaks at 1600C.E. (15.8%) and 1640C.E. (25.8%). DTF taxa decrease in abundance between 1750-1850C.E. reflected in the reduction of *Bursera simaruba* (36.7-19.5%), *Brosimum* (10-2.4%), and *Mimosa* (13.3-0%). Herbaceous taxa increase from 1750-1850C.E. (16.7-46.3%). DTF abundance increases again from after 1850C.E. (48.8%) through to 1970C.E. (79.1%) with the increased abundance of *Bursera simaruba* (19.5-29.8%), *Protium* (4.9-10.5%), Leguminosae (2.4-11.9%), *Rhus* (2.4-10.5%), and *Terminalia* (0-6%). *Sporormiella* influx remains high between 1550-1570C.E. (2-2.8 spores $cm^{-2}yr^{-1}$) and is high in 1650C.E. (3.4 spores $cm^{-2}yr^{-1}$). After 1650C.E. *Sporormiella* influx delcines (3.4-0.8 spores $cm^{-2}yr^{-1}$). The abundance of macroscopic charcoal decreases towards the present from 1560-1970C.E (3-0.03 particles $cm^{-2}yr^{-1}$). Pollen influx reduces overall (682,686 - 145,700 grains $cm^{-2}yr^{-1}$) but peaks at 1650C.E. and (1,773,492 grains $cm^{-2}yr^{-1}$) and 1850C.E. (1,391,104 grains $cm^{-2}yr^{1}$).

PCA of the pollen assemblage displays taxa most associated with each Zone and explains 16.4% of variance on Axis 1 and 12.6% of variance on Axis 2 (Figure 5.7a). Zone 1 is most associated with *Protium*, Leguminosae, Compositeae and *Spananthe paniculate*; Zone 2 with *Bursera simaruba, Brosimum, Terminalia, Coussapoa* and *Celtis*; and Zone 3 with *Rhus, Trema, Cordia, Capparis, Curtella americana* and *Mimosa*.

CCA of the palynological assemblage delineates that macroscopic charcoal, *Sporormiella* and $\delta^{18}O$ are all statistically significant drivers of variation within the palynological assemblage. Macroscopic charcoal is most associated with Zones 1 & 2 along the first axis, orthogonally placed to $\delta^{18}O$ which is most associated with Zone 3 (Figure 5.7b). *Sporormiella* is associated in part with all Zones along the second axis.

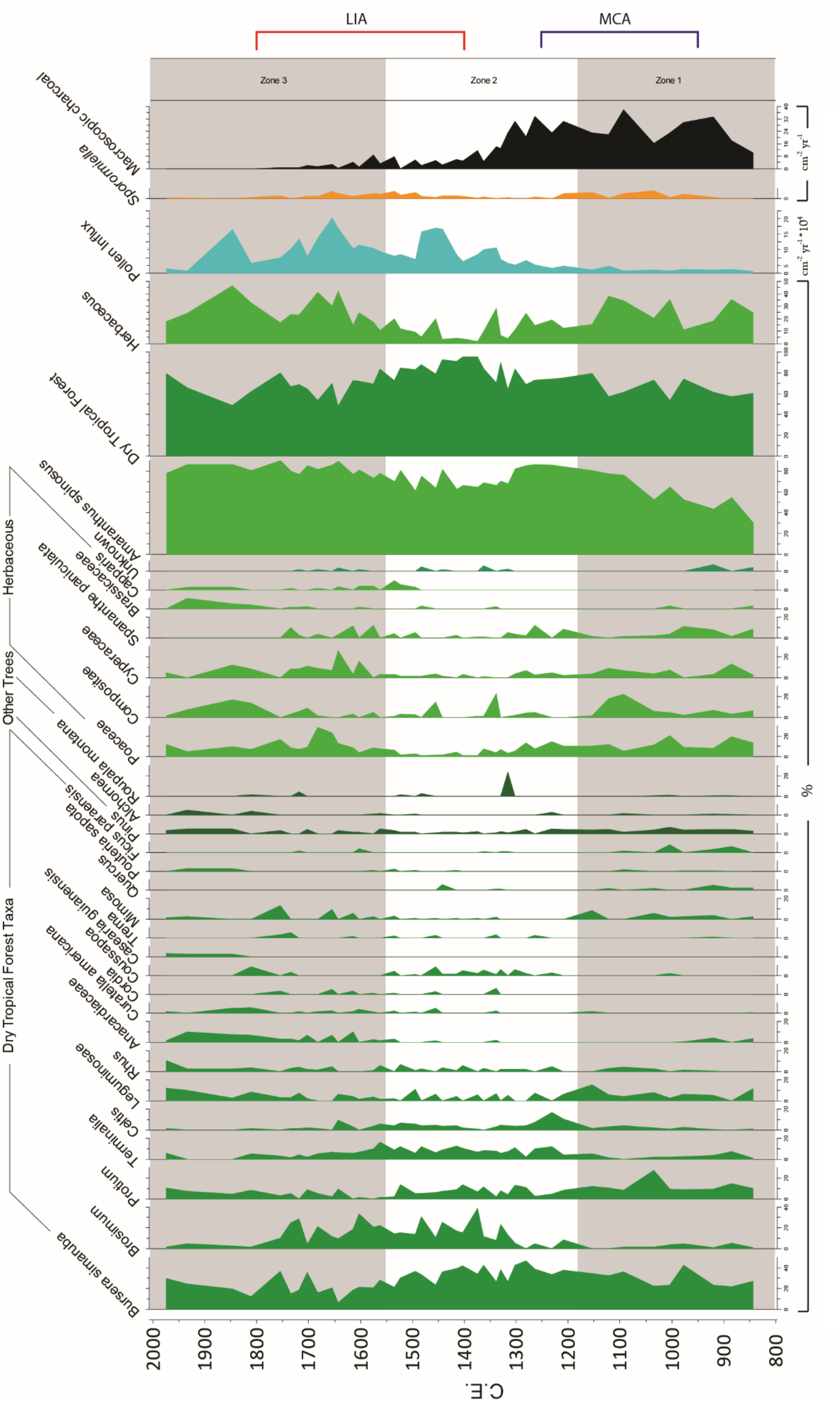


Figure 5.6 Palynological assemblage, *Sporormiella*, and macroscopic charcoal reconstructed from El Gancho, Nicaragua

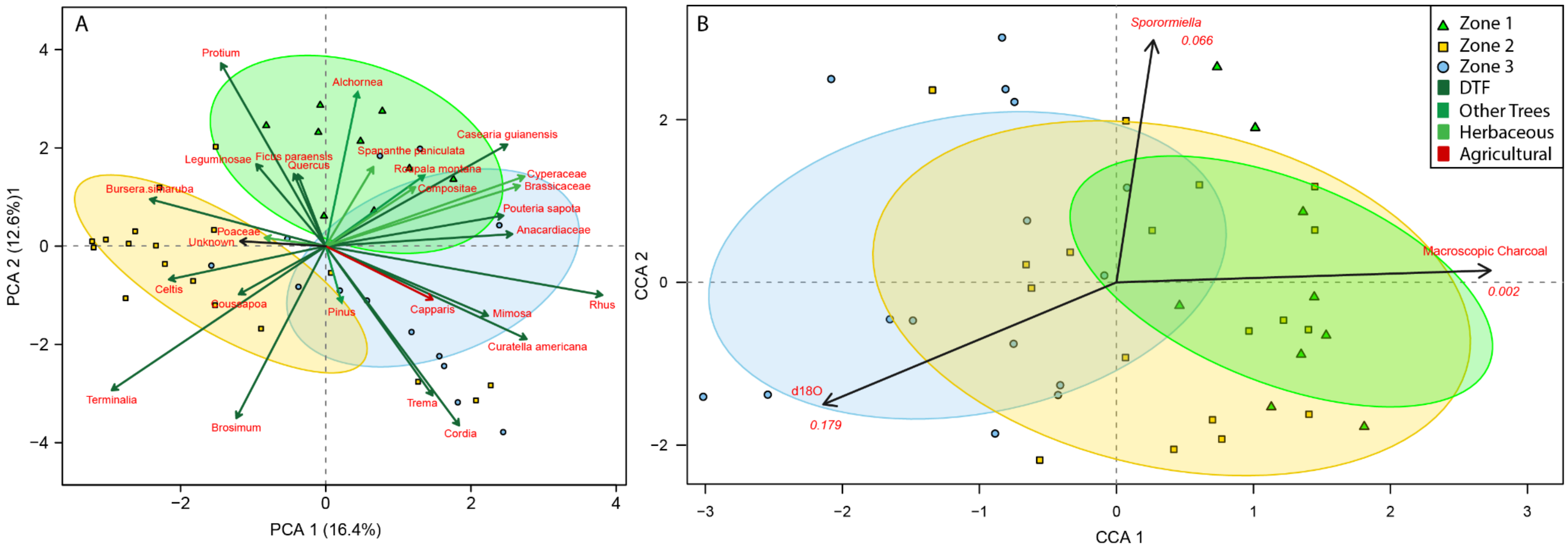


Figure 5.7 : Principal component analysis of the palynological assemblage (A). Canonical correspondence analysis of the palynological assemblage (B). Zones derived from the broken stick model represented by ellipses at a confidence of 95%. Zone 1 = green triangles; Zone 2 = yellow squares; Zone 3 = blue circles.

5.5 Discussion

Precipitation changes in the Nicaraguan region of the Central American Dry Corridor during the Medieval Climate Anomaly and Little Ice Age

Interpretation of the diatom assemblage indicates that the Nicaraguan region of the CADC was wettest during the MCA (950-1250C.E.) and drier during the transition to the LIA (1250-1400C.E.) and throughout the LIA (1400-1800C.E.). The transition between the MCA and LIA surrounding El Gancho is marked by a shift from wetter to drier conditions around 1300C.E.

The high abundance of benthic and epiphytic diatom taxa between 840-1180C.E. (Zone 1) indicates that wetter conditions were apparent in the region in the earliest part of this record during the MCA. The shallow basin that El Gancho currently occupies is poorly constrained and is surrounded by low lying topography (Figure 5.2). Subject to wetter conditions El Gancho's basin is suggested to have expanded laterally, increasing in area but not necessarily depth. El Gancho is assumed to have been at its maximum expanse and depth during this period time. The high abundance of benthic and epiphytic diatom taxa, as well as Cyperaceae from the palynological assemblage, therefore, probably reflect the permanent inundation of water for a larger area by occupying the available habitat niche (e.g. Cyperaceae and *Potamogeton*: Dull, 2004a; 2004b; 2007).

The time surrounding the transition between the MCA and LIA (c.1200-1400C.E.) leading into the first half of the LIA (1400-1600C.E.) is defined by the replacement of benthic and epiphytic diatoms by the increasing abundance of diatom taxa indicative of changing conditions (e.g. *Pseudostaurosira brevistriata* and *Aulacoseira ambigua*) inferred to indicate a trend towards drier conditions (Figures 5.4 & 5.5). While the entire lake habitat is suitable for benthic and epiphytic diatoms to thrive, we suggest that these taxa were outcompeted by *Pseudostaurosira brevistriata and Aulacoseira* spp.

The rapid expansion and retraction of this water body between the wet season and the dry season is thought to have facilitated continuous biannual disturbance promoting a habitat more conducive for these two taxa to dominate the assemblage. This evidence further suggests that El Gancho retreated in area abandoning the large shallow expanse surrounding the central depocenter. After *c.*1200C.E. diatoms *Aulacoseira* spp. and *Pseudostaurosira brevistriata* comprise between 50-90% of the diatom assemblage. The succession of *Aulacoseira ambigua* at 1340-1600C.E. is suggested to represent a rapid reduction in lake area, whereby the water occupying El Gancho retreated to the deepest part of its basin, abandoning the expansive shallow periphery. The succession back to facultatively planktonic taxa (*Pseudostaurosira brevistriata*) after 1600C.E. is inferred to indicate that El Gancho continued to reduce in size, losing depth and available habitat for the planktonic diatom taxa to thrive (Figure 5.4). *Pseudostaurosira brevistriata* is a facultatively planktonic taxa and therefore we suggest that the available habitat niche provided conditions amiable to this taxa's success over the other taxa present, such as *Aulacoseira ambigua*, in effect diluting the abundance of the other taxa. We previously explored the salinity and nutrient groupings for all diatom taxa and did not find conclusive trends associated with the most likely scenario presented in my results and interpretation.

The interpretation of the diatom record supports the $\delta^{18}O$ precipitation reconstruction presented by Stansell et al. (2013) which also indicates wetter conditions for the MCA, particularly between *c.*950-1300C.E. and drier conditions thereafter. The response of the diatom assemblage to drier conditions during the transition between the MCA and LIA appears to lag behind the $\delta^{18}O$ presented in Stansell et al. (2013) by *c.*50 years, this could represent a biological lag response to hydroclimatic changes (Figure 5.4).

How did the Dry Tropical Forest's respond to these wet-dry climatic shifts?

Three stages can be discerned from the last 1200 years of vegetation change in the DTF occupying the Asese Peninsula (Figure 5.6). The first zone corresponds with wetter conditions from c.800-1200C.E., while the second (c.1200-1550C.E.) and third Zones (c.1550-2004C.E.) with relatively drier conditions (Figure 5.6).

The wettest period of the last 1200 years (c.800-1250C.E.) is primarily comprised of DTF taxa. The dominance of these taxa in the pollen diagram are taken to indicate a relatively closed canopy. Perhaps unusually with this forest type, there is evidence for intervals of greater burning. We suggest that this is in response to the wetter conditions from *c*.800-1250C.E. facilitating greater accumulation of vegetative biomass. This would have enabled larger fuel loads to develop and burn between seasons (e.g. Lynch et al. 2004; Anderson & Wahl, 2016). Fire in the CADC generally occurs in the transitions between the dry season and wet season as biomass dries out (Giglio et al. 2006). Evidence from this record also suggested that the burning facilitated some openings in the canopy as indicated by the abundance of Poaceae, Compositeae, Cyperaceae and *Spananthe paniculate* during the MCA (Brown & Hebda, 2003; Bush, 2004; Figueroa-Rangel et al. 2011). Deciduous vegetation and grasses are more susceptible to burning due to their smaller water holding capacity (Budowski, 1966). The increased burning during the MCA was undoubtably facilitated by this more open environment providing a positive feedback between burning and vegetation, as driven by hydroclimate.

At the transition into relatively drier conditions (1250-1400C.E.) there is a change in the composition of DTF taxa including the succession of *Brosimum, Terminalia and Celtis* (Figure 5.6). The highest abundance of these DTF taxa occurs under these drier conditions. In conjunction with this change in composition, reduced burning during this time occurred, probably associated with lower fuel loads. This reduction in burning (c.1300C.E.) appears to have resulted in an increasingly closed canopy, blocking light to the understory and the reduction in the presence of open ground taxa. Evidence of this closed canopy is also presented in the increase in the abundance of diatom flora *Aulacoseira spp.* which is suggested to be responsive to low-light levels, thriving in a well-developed forest with closed canopies (Wang et al. 2008).

Anthropogenic Activity in the Dry Tropical Forests: Population and Land Management

Pre-Columbian human occupation of the Asese Peninsula has been documented from at least c.600C.E. through to 1250C.E. with a hiatus during the Late Sapoa period c.1100-1150C.E. (McCafferty & McCafferty, 2011). The nearby occupation of two municipalities within the Masaya region, as well as the occupation of Ometepe, was continuous from c.200B.C.E. through to the present day (Healy & Pohl, 1980; Lange & Haberland, 1992; Román-Lacayo, 2013).

Despite this continuous Pre-Columbian occupation, there is no evidence of substantial deforestation in the pollen record of the Asese Peninsula during this interval in time (c.850-1522C.E.). However, after the arrival of the Spanish in 1522C.E. some is evident from other records. Deforestation on Ometepe Island, for example, from 775C.E indicates that areas of Nicaragua were undergoing deforestation during Pre-Columbian times (Avnery et al. 2011); however, this is not evident from the palynological record presented from El Gancho. While I found no palynological evidence of Pre-Columbian agriculture (e.g. *Zea mays*), the abundance of fruiting trees and edible herbs are likely to have been utilised by local people for materials and sustenance. *Amaranthus spinosus*, Anacardiaceae, *Bursera simaruba*, *Brosimum*, *Capparis*, *Celtis*, Leguminosae and *Protium* are all examples of edible flora found in El Gancho and were also eaten as part of the Pre-Columbian diet (White, 1999). *Amaranthus spinosus* is a pioneering herbaceous plant with a similar nutritional value to that of spinach and dominates the palynological record throughout (Schnetzler et al. 2018).

The introduction of *Capparis* in the palynological record from c.1500C.E. possibly provides evidence for European contact. *Capparis* (commonly known as a caper) places its origins surrounding the Mediterranean in Europe, this taxon is not native to the Americas and would only have arrived with the Spanish conquistadors (Rivera et al. 2002). In addition, the reduction of select arboreal taxa e.g. *Bursera simaruba*, and *Protium*, could reflect deforestation for building materials and the creation of pastures; however, this is also within the range of natural variability (Kaimowitz, 1997; McNeil, 2012).

Evidence of herbivorous mammalian presence from *c*.950 – 1250C.E. aligns with the inferred wetter conditions brought about during the MCA. There is no current evidence for pre-Columbian domestication of the native fauna, and therefore we suggest that greater vegetative growth during this period of time provided an increased food source for native herbivourous mammals including deer, peccary, and tapir allowing for their numbers to swell. Reductions in dung fungal spore abundance after the shift towards drier conditions, between the MCA and LIA, suggests that herbivorous mammals were largely absent from the Asese peninsula after 1250C.E. until the arrival of the Spanish. Dung fungal spore evidence indicates that animal abundance on the Asese peninsula increased after the arrival of the Spanish through until 1650C.E. This possibly represents the import of cattle brought into Granada (established 1524C.E.) from Europe. These cattle would possibly have been kept on the Asese peninsula, a natural pen, until they could be sold at market (Burns, 1991). The rise in population and clearance of land for agrarian practices leading up to 1800C.E. may well therefore account for the apparent reduction of DTF taxa in and around the Asese peninsula from c.1700-1850C.E. During this time the abundance of DTF taxa reduce and economically important taxa such as Anacardiaceae increase.

Resilience of the dry tropical forests surrounding the Asese Peninsula

The reconstruction of the DTF surrounding the Asese peninsula, over the past 1200 years, show little evidence of vulnerability to climatic and anthropogenic impacts. While the composition of taxa comprising the DTF assemblage changes in response to the identified hydroclimatic and anthropogenic perturbations, the ecological structure of the DTF has remained remarkably resilient. High seasonal variation within the CADC has exposed the residing DTF to biannual disturbance since the modern configuration of the North American Monsoon c.4000B.C.E. (Metcalfe et al. 2015). Cole et al. (2014) identifies high frequency disturbance as the most significant factor in determining resilience in tropical forests, which is clear from the reconstructions of DTF around the Asese Peninsula. Biannual disturbance caused by seasonal variation over the last four millennia is the likely reason why these DTF are so resilient, allowing these DTF to adapt and increase their resilience over time (Li et al. 2018).

Studies of satellite data (Seddon et al. 2016) and meta-analyses (Allen et al. 2017) examining resilience of vegetation in this region in recent decades to climatic perturbations suggest that DTF are sensitive to changes in precipitation/drought intensity, frequency, and/or timing; however, the results presented from El Gancho suggest that the DTF around the Asese peninsula are not particularly sensitive to climatic and anthropogenic fluctuations, at least not over the past 1200 years. While I do see some evidence for the reorganisation of taxa between the palynological Zones, likely responding to more frequent or severe drought or variability in rainfall (see Chadwick et al. 2015, Feng et al. 2013, Greve et al. 2014), the palynological abundance of DTF taxa in the record from El Gancho never fall below 50% and exceeds 90% from c.1350-1420C.E., when fire reduces and climate switches to overall drier conditions (Figure 5.6). I can use these finding to suggest that the vegetation surrounding the Asese peninsula has not been subject to a tipping point leading to a switch to a different stable state and vegetation type during the time frame studied (Willis et al. 2018).

Specific DTF taxa such as *Bursera simaruba* and *Brosimum,* which are prominent in the palynological record from El Gancho, are known to have a high wood density comprised of greater cell wall material and narrow vessels, which limit their hydraulic efficiency but increase their resistance to drought-induced water scarcity (Brodribb et al. 2002; Scholz et al. 2007). High wood density has previously been demonstrated to be an important factor in enabling persistence of woody taxa during intervals of drought (Willis et al. 2018). These species may also resist extended periods of drought by tapping into subsoil water reserves with their deep roots (Borchert 1994; Allen et al. 2017).

5.6 Conclusions

The results from this research suggest that DTF have been highly resilient to past climatic and anthropogenic perturbations over the past 1200 years (Table 5.2). Interpretations of changes in climate between the MCA and LIA support wetter conditions during the MCA (950-1250C.E.) and drier conditions in the transition between the MCA and LIA (1250-1400C.E.) and the LIA (1400-1850C.E.). The proxy analysis of the diatom record independently supports this interpretation of the $\delta^{18}O$ first presented by Stansell et al. (2013).

Changes in DTF composition appear to be linked to the abundance and intensity of fire with a high amount of burning during the MCA and low burning thereafter c.1300C.E. Pre-Columbian anthropogenic impacts on DTF are not detected in the palynological record; however, DTF taxa are noted to decline slightly after European contact (1522C.E.).

After European contact, and through until c.1650C.E., there is an increase in dung fungal spore abundance which possibly represents the increased import of cattle brought into the city of Granada.

It is apparent that over the past 1200 years there have been significant fluctuations in climatic and anthropogenic impacts; however, evidence from El Gancho suggests that changes in the structure of DTF surrounding the Asese Peninsula have responded with little consequence. Drought resilient traits of the dominant DTF taxa (e.g. *Bursera simaruba* and *Brosimum*) including high wood density and long roots may have helped this community resist climatic and anthropogenic impacts over the past 1200 years.

Rapid agricultural growth from c.1800C.E. has allowed for larger populations to be supported; however, it has also increased the reliance on agriculture. Areas that were once covered by DTF’s that have since been converted to pastures and plantations do appear to be highly threatened by seasonal hydrological fluctuations.

Table 5.2 Chronology of palynological zones, archaeological periods (Healy & Pohl & Pohl, 1980; Lange & Haberland, 1992; Roman-Lacayo, 2013), local populations (Kroeber, 1939; Newson, 1987; Denevan, 1976; Randell, 1976; Lovell & Lutz, 1991; McCafferty & McCafferty, 2011; Roman-Lacayo, 2013) and climatic shifts (Stansell et al. 2013).

Age (C.E.)	Zone	Archaeological Period			Population			Hydroclimate			DTF	Fire
		Ometepe	Rivas	Masaya	Nicaragua	Masaya	El Rayo	Diatom	δ18O	Regional		
2000					6,000,000							
1900					1,000,000							
1800	3	Post-Conquest	Post-Conquest	Post-Conquest	81,000							
1700												Low
1600					61,000			Drier	Drier	LIA		
1500												
1400	2	Santa Ana	Alta Gracia	Ometepe		3630						
1300		San Lazaro	Las Lajas							Transition		
1200												
1100		La Paloma	La Virgen		100,000-1,000,000					MCA		High
1000	1			Sapoa		4070	Occupied	Wetter	Wetter			
900		Gato	Apompua									
800												

5.7 Acknowledgements

I would like to give thanks to Julio, Veronica and Julio Jr. Gomez, and Maurice Hodgson for their support while conducting field work in Nicaragua, and Gillian Petrokofsky, Peter Long and Carol Adolf from the Oxford Long-Term Ecology Lab., and Ian Matthews from Royal Holloway. This research was funded by the Natural Environment Research Council of the United Kingdom NE/L002612/1, US National Science Foundation EAR-1502989, the Geological Society of America and St Edmund Hall, University of Oxford.

5.8 References

Allen, K., Dupuy, J.M., Gei, M.G., Hulshof, C., Medvigy, D., Pizano, C., Salgado-Negret, B., Smith, C.M., Trierweiler, A., Van Bloem, S.J. and Waring, B.G., 2017. Will seasonally dry tropical forests be sensitive or resistant to future changes in rainfall regimes?. *Environmental Research Letters*, 12(2), p.023001.

Akers, P.D., Brook, G.A., Railsback, L.B., Liang, F., Iannone, G., Webster, J.W., Reeder, P.P., Cheng, H. and Edwards, R.L., 2016. An extended and higher-resolution record of climate and land use from stalagmite MC01 from Macal Chasm, Belize, revealing connections between major dry events, overall climate variability, and Maya sociopolitical changes. *Palaeogeography, palaeoclimatology, palaeoecology*, 459, pp.268-288.

Anderson, L. & Wahl, D., 2016. Two Holocene paleofire records from Peten, Guatemala: Implications for natural fire regime and prehispanic Maya land use. *Global and Planetary Change*, 138, pp.82-92.

APSA, 2007. The Australasian Pollen and Spore Atlas V1.0. Australian National University, Canberra. Available at: http://apsa.anu.edu.au/ [Accessed 13/06/2018].

Atwood, J.T., 1984. A floristic study of volcán Mombacho department of Granada, Nicaragua. Annals of the Missouri Botanical Garden, pp.191-209.

Avnery, S., Dull, R.A. and Keitt, T.H., 2011. Human versus climatic influences on late-Holocene fire regimes in southwestern Nicaragua. *The Holocene*, 21(4), pp.699-706.

Baker, A.G., Cornelissen, P., Bhagwat, S.A., Vera, F.W. and Willis, K.J., 2016. Quantification of population sizes of large herbivores and their long- term functional role in ecosystems using dung fungal spores. *Methods in Ecology and Evolution*, 7(11), pp.1273-1281.

Beard, J.S., 1942. Montane vegetation in the Antilles. *Caribbean Forest*, 3, pp.61-74.

Beard, J.S., 1944. Climax vegetation in tropical America. *Ecology*, 25, pp. 127-158.

Bellefontaine, R. & Petrucci, Y. 2000. Management of natural forests of dry tropical zones. FAO Conservation Guide 32.

Bensch, C.N., Horak, M.J. and Peterson, D., 2003. Interference of redroot pigweed (Amaranthus retroflexus L.), Palmer amaranth (A. palmeri), and common waterhemp (A. rudis) in soybean. *Weed Science*, 51(1), pp.37-43.

Bennett, J.P., 1974. Concepts of mathematical modeling of sediment yield. *Water Resources Research*, 10(3), pp.485-492.

Bennett, K.D., 1996. Determination of the number of zones in a biostratigraphical sequence. *New Phytologist*, 132(1), pp.155-170.

Bennett, K.D. and Willis, K.J., 2001. Pollen. Tracking Environmental Change Using Lake Sediments. Volume 3: Terrestrial, Algal, and Siliceous Indicators.

Berglund, B.E., 1987. Handbook of Holocene palaeoecology and palaeohydrology.

Biondi-Morra, B.N., 1993. Hungry dreams: the failure of food policy in revolutionary Nicaragua, 1979-1990. Cornell University Press.

Borchert, R., 1994. Soil and stem water storage determine phenology and distribution of tropical dry forest trees. Ecology, 75(5), pp.1437-1449.

Brodribb, T.J., Holbrook, N.M. and Gutierrez, M.V., 2002. Hydraulic and photosynthetic co- ordination in seasonally dry tropical forest trees. *Plant, Cell & Environment*, *25*(11), pp.1435-1444.

Brown KJ and Hebda RJ (2003) Coastal rainforest connections disclosed through a Late Quaternary vegetation, climate, and fire history investigation from the Mountain Hemlock Zone on southern Vancouver Island, British Colombia, Canada. *Review of Palaeobotany and Palynology* 123: 247–269.

Budowski, G., 1966, March. Fire in tropical American lowland areas. In Proceedings of the fifth annual Tall Timbers Fire Ecology Conference (pp. 24-25).

Burns, E.B., 1991. Patriarch and folk: the emergence of Nicaragua, 1798-1858. Harvard University Press.

Bush, M.B., Piperno, D.R., Colinvaux, P.A., De Oliveira, P.E., Krissek, L.A., Miller, M.C. and Rowe, W.E., 1992. A 14 300- yr paleoecological profile of a lowland tropical lake in Panama. *Ecological Monographs*, 62(2), pp.251-275.

Bush, M.B., 1995. Neotropical plant reproductive strategies and fossil pollen representation. *The American Naturalist*, 145(4), pp.594-609.

Bush, M.B., 2002. On the interpretation of fossil Poaceae pollen in the lowland humid neotropics. *Palaeogeography, palaeoclimatology, palaeoecology*, 177(1-2), pp.5-17.

Bush M.B., De Oliveira P.E., Colinvaux P.A., Miller M.C. & Moreno J.E. 2004. Amazonian paleoecological histories: One hill, three watersheds. *Palaeogeography Palaeoclimatology Palaeoecology*, 214, pp.359–393.

Bush, M.B. and Weng, C., 2007. Introducing a new (freeware) tool for palynology. *Journal of Biogeography*, 34(3), pp.377-380.

Calvo-Alvarado, A., McLennan, B., Sanchez-Azofeifa, A., Garvin, T., 2009. Deforestation and forest restoration in Guanacaste, Costa Rica: putting conservation policies in context. *Journal of Forest Ecology and Management* 258, 931–940.

Carpenter, S., Walker, B., Anderies, J. M., Abel, N. (2001). From Metaphor to Measurement: Resilience of What to What? Ecosystems. 4 (8), 765-781.

Carrillo-Bastos, A., Islebe, G.A., Torrescano-Valle, N. and González, N.E., 2010. Holocene vegetation and climate history of central Quintana Roo, Yucatán Península, Mexico. *Review of Palaeobotany and Palynology*, 160(3-4), pp.189-196.

Chadwick R., Good P., Martin G and Rowell D.P., 2015 Large rainfall changes consistently projected over substantial areas of tropical land. *Nature Climate Change*, 6, 177–81.

Chiabai, A. ed., 2015. Climate change impacts on tropical forests in Central America: an ecosystem service perspective. Routledge.

Chivas A. R., De Deckker P., Wang S. X. and Cali J. A., 2002. Oxygen-isotope systematics of the nektic ostracod Australocypris robusta. In The Ostracoda: Applications in Quaternary Research. Geophysical Monograph 131 (eds. J. A. Holmes and A. R. Chivas). American Geophysical Union, Washington, DC, pp. 301–313.

Cole, L.E., Bhagwat, S.A. and Willis, K.J., 2014. Recovery and resilience of tropical forests after disturbance. *Nature communications*, 5, p.3906.

Cooke, R., Ranere, A.J., 1992. Prehistoric human adaptations to the seasonally dry forests of Panama. *World Archaeology*, 24, 114–133.

Correa- Metrio, A., Vélez, M.I., Escobar, J., St- Jacques, J.M., López- Pérez, M., Curtis, J. and Cosford, J., 2016. Mid- elevation ecosystems of Panama: future uncertainties in light of past global climatic variability. *Journal of Quaternary Science*, 31(7), pp.731-740.

Curtis, J.H., Hodell, D.A. and Brenner, M., 1996. Climate variability on the Yucatan Peninsula (Mexico) during the past 3500 years, and implications for Maya cultural evolution. *Quaternary Research*, 46(1), pp.37-47.

Curtis, J.H., Brenner, M., Hodell, D.A., Balser, R.A., Islebe, G.A. and Hooghiemstra, H., 1998. A multi-proxy study of Holocene environmental change in the Maya lowlands of Peten, Guatemala. *Journal of paleolimnology*, 19(2), pp.139-159.

Daniels, A.E., Painter, K., Southworth, J., 2008. Milpa imprint on the tropical dry forest landscape in Yucatan, Mexico: remote sensing and field measurement of edge vegetation. *Agriculture, Ecosystems, and Environment*, 123, 293–304.

Davis, O.K. and Shafer, D.S., 2006. *Sporormiella* fungal spores, a palynological means of detecting herbivore density. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 237(1), pp.40-50.

Decrouy L. and Vennemann T., 2013. Potential influence of the chemical composition of water on the stable oxygen isotope composition of continental ostracods. *Journal of Paleolimnology*, 50, 577– 582.

Denevan, William M. 1976. The native population of the Americas in 1492. Madison: University of Wisconsin Press.

Denevan, W.M., 1992. The pristine myth: the landscape of the Americas in 1492. *Annuals of the Association of American Geographers*, 82, 369–385.

Devriendt, L.S., McGregor, H.V. and Chivas, A.R., 2017. Ostracod calcite records the 18O/16O ratio of the bicarbonate and carbonate ions in water. *Geochimica et Cosmochimica Acta*, 214, pp.30-50.

Dinerstein, E., Olson, D., Joshi, A., Vynne, C., Burgess, N.D., Wikramanayake, E., Hahn, N., Palminteri, S., Hedao, P., Noss, R. and Hansen, M., 2017. An ecoregion-based approach to protecting half the terrestrial realm. *BioScience*, 67(6), pp.534-545.

Dull, R.A., 2004a. An 8000-year record of vegetation, climate, and human disturbance from the Sierra de Apaneca, El Salvador. *Quaternary Research*, 61(2), pp.159-167.

Dull, R.A., 2004b. A Holocene record of Neotropical savanna dynamics from El Salvador. *Journal of Paleolimnology*, 32(3), pp.219-231.

Dull, R.A., 2007. Evidence for Forest Clearance, Agriculture, and Human- Induced Erosion in Precolumbian El Salvador. *Annals of the Association of American Geographers*, 97(1), pp.127-141.

Durán-Quesada, A.M., Gimeno, L. and Amador, J., 2017. Role of moisture transport for Central American precipitation. *Earth System Dynamics*, 8(1), p.147.

Fleming, W.D., 1954. Naphrax: a synthetic mounting medium of high refractive Index new and improved methods of preparation. *Journal of the royal microscopical Society*, 74(1), pp.42-44.

Feng, X., Porporato, A. and Rodriguez-Iturbe, I., 2013. Changes in rainfall seasonality in the tropics. *Nature Climate Change, 3*(9), p.811.

Figueroa-Rangel, B.L., Willis, K.J. and Olvera-Vargas, M., 2012. Late-Holocene successional dynamics in a transitional forest of west-central Mexico. *The Holocene*, 22(2), pp.143-153.

Ford, A. & Nigh, R., 2009. Origins of the Maya forest garden: Maya resource management. *Journal of Ethnobiology*, 29(2), pp.213-236.

Gasse, F. (1986). East African Diatoms: Taxonomy, Ecological Distribution (Vol. 11). Berlin: Cramer.

Gavin, D.G., Brubaker, L.B. and Lertzman, K.P., 2003. An 1800-year record of the spatial and temporal distribution of fire from the west coast of Vancouver Island, Canada. *Canadian Journal of Forest Research*, 33(4), pp.573-586.

Giglio, L., Csiszar, I. and Justice, C.O., 2006. Global distribution and seasonality of active fires as observed with the Terra and Aqua Moderate Resolution Imaging Spectroradiometer (MODIS) sensors. *Journal of Geophysical Research: Biogeosciences*, 111(G2).

Gillespie, T.W., Grijalva, A. & Farris, C.N. 2000. Diversity, composition, and structure of tropical dry forests in Central America. *Plant Ecology*, 147, 37-47.

González, R.B. 2005. Tree species diversity and regeneration of tropical dry forest in Nicaragua. Doctoral Thesis. Umea. Sweden.

Graham, N.E., Hughes, M.K., Ammann, C.M., Cobb, K.M., Hoerling, M.P., Kennett, D.J., Kennett, J.P., Rein, B., Stott, L., Wigand, P.E. and Xu, T., 2007. Tropical Pacific–mid-latitude teleconnections in medieval times. *Climatic Change*, 83(1-2), pp.241-285.

Greve, P., Orlowsky, B., Mueller, B., Sheffield, J., Reichstein, M. and Seneviratne, S.I., 2014. Global assessment of trends in wetting and drying over land. *Nature geoscience*, *7*(10), p.716.

Griscom, H.P. & Ashton, M.S., 2011. Restoration of dry tropical forests in Central America: a review of pattern and process. *Forest Ecology and Management*, 261(10), pp.1564-1579.

Guevara-Murua, A., Williams, C.A., Hendy, E.J. and Imbach, P., 2018. 300 years of hydrological records and societal responses to droughts and floods on the Pacific coast of Central America. *Climate of the Past*, 14(2), pp.175-191.

Haug, G.H., Hughen, K.A., Sigman, D.M., Peterson, L.C. and Röhl, U., 2001. Southward migration of the intertropical convergence zone through the Holocene. *Science*, 293(5533), pp.1304-1308.

Healy & Pohl, P. and Pohl, M., 1980. Archaeology of the Rivas Region, Nicaragua. Wilfrid Laurier Univ. Press.

Harcourt, C.S. & Sayer, J.A. 1996. The Conservation atlas of tropical forest. The Americas. Simon & Schuster, pp.206-211.

Heckadon Moreno, S., 1984. Panama's expanding cattle front: the Santeno Campesinos and the colonization of the forests. Doctoral Thesis. University of Essex.

Higuera, P.E., Peters, M.E., Brubaker, L.B. and Gavin, D.G., 2007. Understanding the origin and analysis of sediment-charcoal records with a simulation model. *Quaternary Science Reviews*, 26(13-14), pp.1790-1809.

Higuera, P.E., Gavin, D.G., Bartlein, P.J. and Hallett, D.J., 2011. Peak detection in sediment–charcoal records: impacts of alternative data analysis methods on fire-history interpretations. *International Journal of Wildland Fire*, 19(8), pp.996-1014.

Hodell, D.A., Curtis, J.H. and Brenner, M., 1995. Possible role of climate in the collapse of Classic Maya civilization. *Nature*, 375(6530), pp.391.

Hodell, D.A., Brenner, M. and Curtis, J.H., 2005. Terminal Classic drought in the northern Maya lowlands inferred from multiple sediment cores in Lake Chichancanab (Mexico). *Quaternary Science Reviews*, 24(12), pp.1413-1427.

Hodell, D.A., Brenner, M. and Curtis, J.H., 2007. Climate and cultural history of the northeastern Yucatan Peninsula, Quintana Roo, Mexico. *Climatic Change,* 83(1), pp.215-240.

Imbach, P., Locatelli, B., Zamora, J.C., Fung, E., Calderer, L., Molina, L. and Ciais, P., 2015. Impacts of climate change on ecosystem hydrological services of Central America: water availability. In Climate Change Impacts on Tropical Forests in Central America (pp. 81-106). Routledge.

Janzen, D.H., 1967. Synchronization of sexual reproduction of trees within the dry season in Central America. *Evolution,* 21(3), pp.620-637.

Janzen, D., 1983. Costa Rican Natural History. The University of Chicago Press, Chicago.

Janzen, D. 1988. Management of habitat fragments in a tropical dry forest: growth. *Annals of the Missouri Botanical Garden,* 75, pp.105-116.

Juggins, S., 2015. rioja: Analysis of Quaternary science data. R package version (0.9-5), The Comprehensive R Archive Network.

Kaimowitz, D., 1997. Policies affecting deforestation for cattle in Central America. In Sustainable agriculture in Central America (pp. 51-66). Palgrave Macmillan, London.

Kennett, D.J., Breitenbach, S.F., Aquino, V.V., Asmerom, Y., Awe, J., Baldini, J.U., Bartlein, P., Culleton, B.J., Ebert, C., Jazwa, C. and Macri, M.J., 2012. Development and disintegration of Maya political systems in response to climate change. Science, 338(6108), pp.788-791.

Krammer, K., & Lange-Bertalot, H., 1991a. Bacillariophyceae: Teil 3: Centrales, Fragilariaceae, Eunotiaceae (Suesswasserflora von Mitteleuropa). Berlin: Spektrum Akademischer Verlag.

Krammer, K., & Lange-Bertalot, H., 1991b. Bacillariophyceae: Teil 4: Achnanthaceae, Kritische Erganzungen Zu Achnanthes S.L., Navicula S.Str., Gomphonema (Suesswasserflora Von Mitteleuropa). Berlin: Spektrum Akademischer Verlag.

Krammer, K., & Lange-Bertalot, H., 1997. Bacillariophyceae: 2. Teil: Bacillariaceae, Epithemiaceae, Surirellaceae (Suesswasserflora von Mitteleuropa). Berlin: Spektrum Akademischer Verlag.

Krammer, K. and Lange-Bertalot, H., 2000. Bacillariophyceae: English and French translation of the keys (Vol. 5). Spektrum Akademischer Verlag Gmbh.

Kroeber, A.L. 1939. Cultural and natural areas of native North America. University of California Publications in American Archaeology and Ethnology, Vol. 38. Berkeley: University of California Press, 1-242.

Lange-Bertalot, H., & Krammer, K. (1997). Süßwasserflora von Mitteleuropa, Bd. 02/1: Bacillariophyceae, 1. Teil: Naviculaceae, A: Text; B: Tafeln. Berlin: Spektrum Akademischer Verlag.

Lange-Bertalot, H., Krammer, K., & Bate, N. (2000). Süßwasserflora Von Mitteleuropa, Bd. 02/5: Bacillariophyceae: Teil 5: English And French Translation Of The Keys. Berlin: Spektrum Akademischer Verlag.

Lachniet, M.S., Burns, S.J., Piperno, D.R., Asmerom, Y., Polyak, V.J., Moy, C.M. and Christenson, K., 2004. A 1500- year El Niño/Southern Oscillation and rainfall history for the Isthmus of Panama from speleothem calcite. *Journal of Geophysical Research: Atmospheres*, 109(D20).

Lange, F.W. & Haberland, W., 1992. The Archaeology of Pacific Nicaragua. University of New Mexico Press.

Leyden, B.W., 2002. Pollen evidence for climatic variability and cultural disturbance in the Maya lowlands. *Ancient Mesoamerica*, 13(1), pp.85-101.

Li, X. and Liu, W., 2010. Oxygen isotope fractionation in the ostracod Eucypris mareotica: results from a culture experiment and implications for paleoclimate reconstruction. *Journal of Paleolimnology*, 43(1), p.111.

Li, D., Wu, S., Liu, L., Zhang, Y. and Li, S., 2018. Vulnerability of the global terrestrial ecosystems to climate change. *Global change biology*, 24(9), pp. 4095-4106.

Livingstone, D.A., 1955. A lightweight piston sampler for lake deposits. *Ecology*, 36(1), pp.137-139.

Lovell, W.G. & Lutz, C.H., 1991. The Historical Demography of Colonial Central America. In Yearbook. Conference of Latin Americanist Geographers (pp. 127-138). Conference of Latin Americanist Geographers.

Lynch, J.A., Clark, J.S. and Stocks, B.J., 2004. Charcoal production, dispersal, and deposition from the Fort Providence experimental fire: interpreting fire regimes from charcoal records in boreal forests. *Canadian Journal of Forest Research*, 34(8), pp.1642-1656.

Maher, L.J., 1981. Statistics for microfossil concentration measurements employing samples spiked with marker grains. *Review of Palaeobotany and Palynology*, 32(2-3), pp.153-191.

MacLeod, M.J. 1973. Spanish Central America: A socioeconomic history, 1520-1720. Berkeley: University of California Press.

Martin, A.C. and Harvey, W.J., 2017. The Global Pollen Project: a new tool for pollen identification and the dissemination of physical reference collections. *Methods in Ecology and Evolution*, 8(7), pp.892-897.

McCafferty, G.G. and McCafferty, S.D., 2011. Bling things: Ornamentation and identity in Pacific Nicaragua. Identity Crisis: Archaeological Perspectives on Social Identity, pp.243-252.

McNeil, C.L., 2012. Deforestation, agroforestry, and sustainable land management practices among the Classic period Maya. *Quaternary International*, 249, pp.19-30.

Medina-Elizalde, M., Burns, S.J., Lea, D.W., Asmerom, Y., von Gunten, L., Polyak, V., Vuille, M. and Karmalkar, A., 2010. High resolution stalagmite climate record from the Yucatán Peninsula spanning the Maya terminal classic period. *Earth and Planetary Science Letters*, 298(1-2), pp.255-262.

Metcalfe, S., Breen, A., Murray, M., Furley, P., Fallick, A. and McKenzie, A., 2009. Environmental change in northern Belize since the latest Pleistocene. *Journal of Quaternary Science*, 24(6), pp.627-641.

Metcalfe, S.E., Barron, J.A. and Davies, S.J., 2015. The Holocene history of the North American Monsoon:'known knowns' and 'known unknowns' in understanding its spatial and temporal complexity. *Quaternary Science Reviews*, 120, pp.1-27.

Miles, L., Newton, A.C., DeFries, R.S., Ravilious, C., May, I., Blyth, S., Kapos, V. and Gordon, J.E., 2006. A global overview of the conservation status of tropical dry forests. *Journal of Biogeography*, 33(3), pp.491-505.

Miranda, M.C., 1997. The last glacial maximum in the basin of Mexico: the diatom record between 34,000 and 15,000 years BP from Lake Chalco. *Quaternary International*, 43, pp.125-136.

Montenegro-Guillén, S., 2003. Lake Cocibolca/Nicaragua. Lake Basin Management Initiative Experience and Lessons Learned Brief USAID. World Bank, Washington, 12.

Murdoch, D.J. and Chow, E.D., 1996. A graphical display of large correlation matrices. The American Statistician, 50(2), pp.178-180.

Murphy, P. G. & Lugo, A.E. 1986. Ecology of tropical dry forest. Annual. *Review of Ecology and Systematics*. 17, 67-88.

Murphy, P.G. & Lugo, A.E., 1995. Dry forests of Central America and the Caribbean. *Seasonally dry tropical forests*, pp.9-34.

Newson, L. A. 1986. The cost of conquest: Indian decline in Honduras under Spanish rule. Dellplain Latin American Studies, No. 20. Boulder, CO: Westview Press.

Newson, L.A. 1987. Indian survival in colonial Nicaragua. Norman: University of Oklahoma Press.

Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Wagner, H. and Oksanen, M.J., 2015. Package 'vegan'

OxLEL, 2014. Diatom Preparation Procedure. Oxford Long-Term Ecology Lab. Protocols. Available at: https://oxlel.zoo.ox.ac.uk/wp-content/uploads/2014/04/OxLEL-diatom-protocol.pdf [Accessed 13/06/2018].

OxLEL, 2016. Pollen Preparation Procedure. Oxford Long-Term Ecology Lab. Protocols. Available at: https://oxlel.zoo.ox.ac.uk/wp-content/uploads/2016/10/OxLEL-Fossil-pollen-extraction-protocol.pdf [Accessed 13/06/2018].

Peters, M.E. & Higuera, P.E., 2007. Quantifying the source area of macroscopic charcoal with a particle dispersal model. *Quaternary Research*, 67(2), pp.304-310.

R Core Team (2012). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Ramsey, C.B., 2009. Bayesian analysis of radiocarbon dates. *Radiocarbon*, 51(1), pp.337-360.

Reimer, P.J., Bard, E., Bayliss, A., Beck, J.W., Blackwell, P.G., Ramsey, C.B., Brown, D.M., Buck, C.E., Edwards, R.L., Friedrich, M. and Grootes, P.M., 2013. Selection and treatment of data for radiocarbon calibration: an update to the International Calibration (IntCal) criteria. *Radiocarbon*, 55(4), pp.1923-1945.

Rivera, D., Inocencio, C., Obon, C., Carreno, E., Reales, A. and Alcaraz, F., 2002. Archaeobotany of capers (Capparis)(Capparaceae). *Vegetation History and Archaeobotany*, 11(4), pp.295-314.

Roldan, H. 2001. Recursos forestales y cambio en el uso de la tierra, Republica de Nicaragua. Santiago, Chile. pp.73.

Roman-Lacayo, M., 2013. Social and Environmental Risk and the Development of Social Complexity in Precolumbian Masaya, Nicaragua (Doctoral dissertation, University of Pittsburgh).

Rosenmeier, M.F., Hodell, D.A., Brenner, M., Curtis, J.H., Martin, J.B., Anselmetti, F.S., Ariztegui, D. and Guilderson, T.P., 2002. Influence of vegetation change on watershed hydrology: implications for paleoclimatic interpretation of lacustrine δ18O records. *Journal of Paleolimnology*, 27(1), pp.117-131.

Roubik, D.W. and Moreno, P., 1991. Pollen and spores of Barro Colorado Island [Panama]. *Pollen and spores of Barro Colorado Island [Panama]*., 36.

Round, F.E., Crawford, R.M. and Mann, D.G., 1990. Diatoms: biology and morphology of the genera. Cambridge University Press.

Sabogal, C., 1992. Regeneration of tropical dry forests in Central America, with examples from Nicaragua. *Journal of Vegetative Science*, 3, pp.407–414.

Schnetzler, K.A., 2018. Food uses and amaranth product research: a comprehensive review. In Amaranth Biology, Chemistry, and Technology (pp. 155-184). CRC Press.

Scholz, G., Liebner, F., Koch, G., Bues, C.T., Günther, B. and Bäucker, E., 2007. Chemical, anatomical and technological properties of Snakewood [Brosimum guianense (Aubl.) Huber]. Wood science and technology, 41(8), p.673.

Seddon, A.W., Macias-Fauria, M., Long, P.R., Benz, D. and Willis, K.J., 2016. Sensitivity of global terrestrial ecosystems to climate variability. *Nature*, 531(7593), p.229.

Smyth, M.P., Dunning, N.P., Weaver, E.M., van Beynen, P. and Zapata, D.O., 2017. The perfect storm: climate change and ancient Maya response in the Puuc Hills region of Yucatán. *Antiquity*, 91(356), pp.490-509.

Stansell, N.D., Steinman, B.A., Abbott, M.B., Rubinov, M. and Roman-Lacayo, M., 2013. Lacustrine stable isotope record of precipitation changes in Nicaragua during the Little Ice Age and Medieval Climate Anomaly. *Geology*, 41(2), pp.151-154.

Stansell, N.D. (2013). Radiocarbon ages for the timing of debris avalanches at Mombacho Volcano, Nicaragua. Bulletin of Volcanology 75(1), pp. 1-4

Taylor, B.W., 1963. An outline of the vegetation of Nicaragua. *The Journal of Ecology*, pp.27-54.

Ter Braak, C.J. and Prentice, I.C., 1988. A theory of gradient analysis. In Advances in ecological research (Vol. 18, pp. 271-317). Academic Press.

Toledo, V.M., 1988. La diversidad biológica de México. Ciencia y Desarrollo 8, 7–16.

UNIDA. 2012. Población Total, estimada al 30 de Junio del año 2012. Available at: http://www.inide.gob.ni/estadisticas/Cifras%20municipales%20a%C3%B1o%202012%20INIDE.pdf. [Accessed 22/08/2018].

van Wyk de Vries B, Francis PW (1997) Catastrophic collapse at stratovolcanoes induced by gradual volcano spreading. *Nature,* 387:387–390.

Velez, M.I., Curtis, J.H., Brenner, M., Escobar, J., Leyden, B.W. and Popenoe de Hatch, M., 2011. Environmental and cultural changes in highland Guatemala inferred from Lake Amatitlán sediments. *Geoarchaeology,* 26(3), pp.346-364.

Vinogradov, A., 2014. Demography: The population of the countries of the world from most ancient times to the present dayr (Statistical Tables) (Volume 1) (Russian Edition). CreateSpace Independent Publishing Platform.

Wang, L., Lu, H., Liu, J., Gu, Z., Mingram, J., Chu, G., Li, J., Rioual, P., Negendank, J.F., Han, J. and Liu, T., 2008. Diatom‐ based inference of variations in the strength of Asian winter monsoon winds between 17,500 and 6000 calendar years BP. *Journal of Geophysical Research: Atmospheres*, 113(D21).

Webster, J.W., Brook, G.A., Railsback, L.B., Cheng, H., Edwards, R.L., Alexander, C. and Reeder, P.P., 2007. Stalagmite evidence from Belize indicating significant droughts at the time of Preclassic Abandonment, the Maya Hiatus, and the Classic Maya collapse. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 250(1-4), pp.1-17.

White, C.D., 1999. Reconstructing Ancient Maya Diet. University of Utah Press.

Whitlock, C. and Larsen, C., 2002. Charcoal as a fire proxy. In Tracking environmental change using lake sediments (pp. 75-97). Springer, Dordrecht.

Whitlock, C. and Anderson, R.S., 2003. Fire history reconstructions based on sediment records from lakes and wetlands. In Fire and climatic change in temperate ecosystems of the western Americas (pp. 3-31). Springer, New York, NY.

Willard, D.A., Bernhardt, C.E., Weimer, L., Cooper, S.R., Gamez, D. and Jensen, J., 2004. Atlas of pollen and spores of the Florida Everglades. *Palynology*, 28(1), pp.175-227.

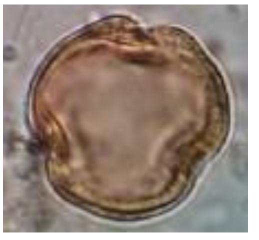
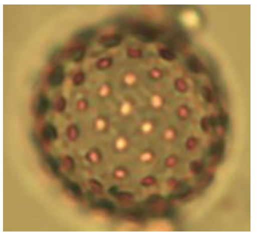
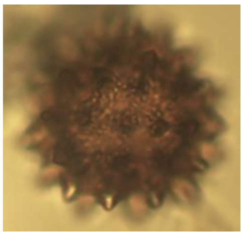
Willis, K.J., Jeffers, E.S. and Tovar, C., 2018. What makes a terrestrial ecosystem resilient?. *Science*, 359(6379), pp.988-989.

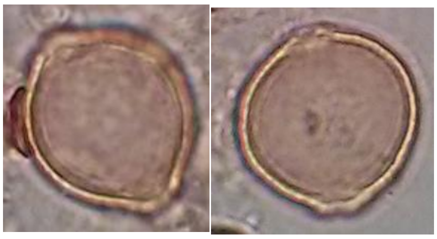
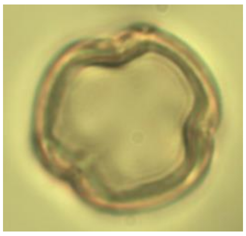
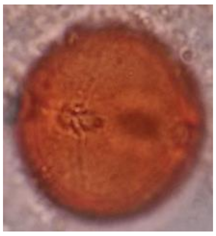
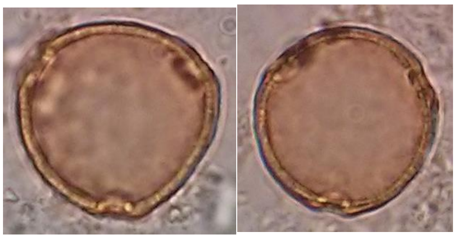
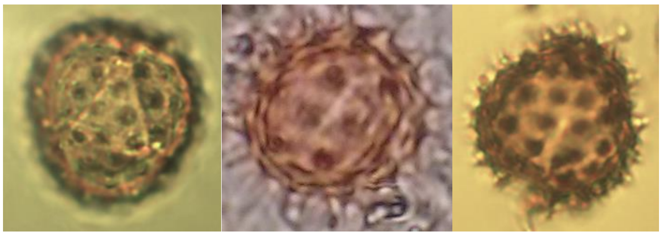
Wold Food Programme, 2015. Analysis of the Impact of the drought on food security in Guatemala, El Salvador, and Honduras. World Food Programme – Latin America and the Caribbean.

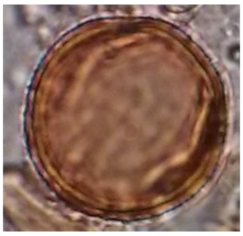
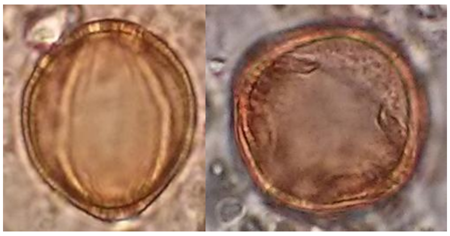
Worldometers, 2018. Nicaragua Population. Available at: http://www.worldometers.info/world-population/nicaragua-population/ [Accessed: 25/04/2018].

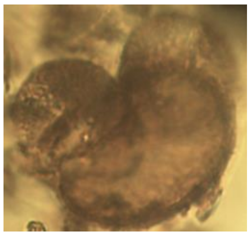
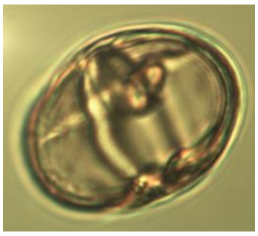
5.9 Supplementary Information

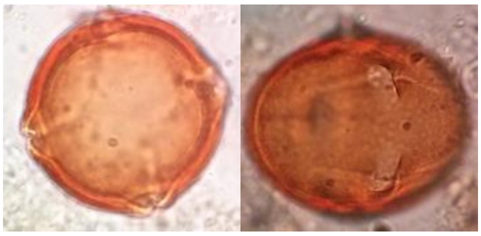
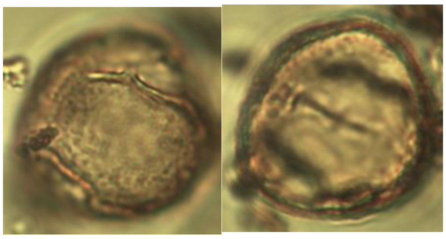
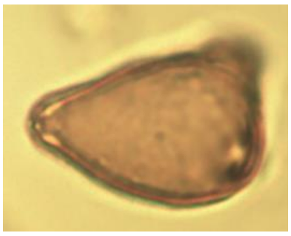
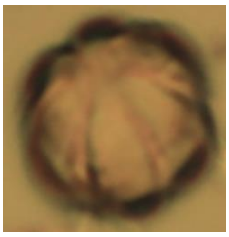
Table 5.3 Images of palynological taxa at 400x magnification identified from El Gancho.

Name	**Image (not to scale)**
Alchornea	
Amaranthus spinosus	
Anacardiaceae	
Bidens laevis	
Brassicaceae	

Brosimum	
Bursera simaruba	
Capparis	
Casearia guianensis	
Celtis	
Compositae	

Cordia	
Coussapoa	
Curatella americana	
Cyperaceae	
Ficus paraensis	

Leguminosae	
Mimosa	
Pinus	
Poaceae	
Pouteria sapota	

Protium	
Quercus	
Rhus	
Roupala	
Spananthe paniculata	
Terminalia	

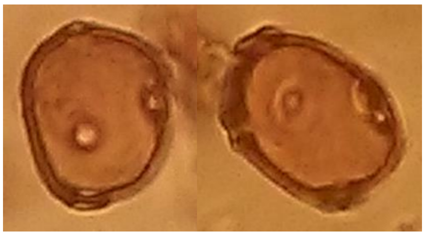
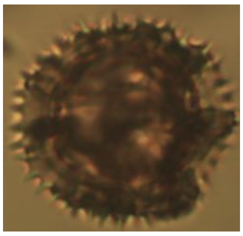
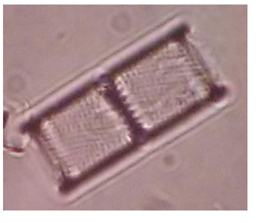
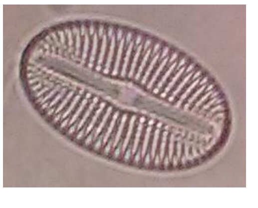
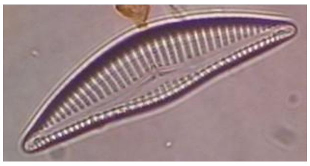
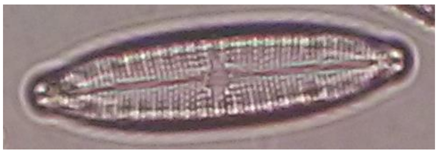
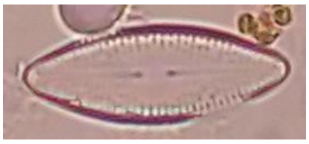
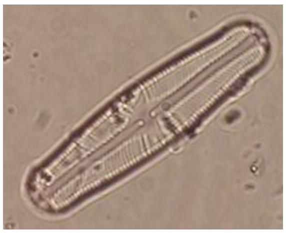
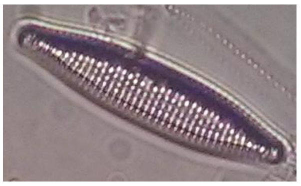
Trema	
Unknown	
Youngia japonica	

Figure 5.8 *Amaranthus spinosus* field specimen. Collected May 20th 2015 from 11°54'22.4"N 85°55'08.4"W.

Table 5.4 Images of diatom taxa at 400x magnification identified from El Gancho.

Name	**Image (not to scale)**
Achnanthes exigua	
Anomoeoneis sphaerophora	
Anomoeoneis vitrea	
Aulacoseira ambigua	
Aulacoseira granulata	
Aulacoseira sp.	
Cyclotella meneghiniana	
Diploneis oblongella	

Diploneis parma	
Encyonema silesiacum	
Fragilaria brevistriata var. trigona	
Gomphonema hebridense	
Mastogloia smithii var. lacustris Grunow	
Navicula longicephala	
Navicula pennsylvanica	
Navicula pupula	

Nitzschia amphibia	
Nitzschia frustulum var. bulnheimiana	
Pinnularia viridis	
Pseudostaurosira brevistriata	
Rhopalodia gibba	
Synedra acus	

6. GENERAL DISCUSSION

6.1 Main Findings

Knowledge of the responses of the ecological dynamics of the Central American Isthmus to climatic and anthropogenic forcing throughout the Holocene, and the associated drivers, is important for predicting and managing current and future impacts of changes to these systems. This thesis aimed to advance the current knowledge and understanding of the drivers of vegetation change for the mixed coniferous pine-oak forests of uplands of Guatemala and the dry tropical forests of lowlands of Nicaragua spanning the Middle-Late Holocene. This was achieved through the synthesis of previously published terrestrial palaeoenvironmental data sets presenting reconstructions of past climate, vegetation, fire, and herbivorous mammal presence for the Central American Isthmus spanning the Holocene (Chapter 2), combined with the collection and analysis of a wide range palaeoecological proxies from lake sediment cores extracted from (i) the uplands of Guatemala spanning the Middle-Late Holocene 4000B.C.E. – 1500C.E. (Cenote Kail: Chapter 3) and the Historical Period 1500-2015C.E. (Cenote Kail: Chapters 4); and (ii) the lowlands of Central Pacific Nicaragua spanning the Late-Holocene 800-2004C.E. (El Gancho: Chapter 5).

From the analysis of these palaeoenvironmental proxies past vegetation dynamics (pollen), fire regimes (charcoal), herbivorous mammal presence (dung fungal spores: *Sporormiella*) and precipitation dynamics (diatoms) were reconstructed to address the four central questions as follows:

1. **"What is the current, published, scientific evidence-based knowledge of vegetation dynamics and drivers of change across the Central American Isthmus?" (Chapter 2)**
2. **"What have been the dominant drivers of change in the vegetation dynamics of the mixed coniferous forests of Central America during the Pre-Columbian Era?" (Chapter**
3. **"How has Colonial and Post-Colonial land-use change influenced the current landscape, and what implications does this have for the future?" (Chapter 4).**
4. **"How resilient are the dry tropical forests of Central America to climatic and anthropogenic perturbations?" (Chapter 5)**

Key findings are discussed below in relation to each of these four research questions.

I. What is the current, published, scientific evidence-based knowledge of vegetation dynamics and drivers of change across the Central American Isthmus? (Chapter 2)

As of July 2017C.E. there were: (i) 64 publications which present 56 study sites and 80 palynological records reconstructing vegetation dynamics across the Central American Isthmus covering all or part of the Holocene. Precipitation, burning and agrarian practices were identified and explored as the dominant drivers of past vegetation change.

To examine the current published scientific evidence-base for vegetation dynamics and drivers of change across the Central American Isthmus I took a systematic approach to mapping all terrestrial palaeoenvironmental proxies and then synthesised all palynological records (representing changes in vegetation dynamics) and drivers of vegetation dynamics including precipitation ($\delta^{18}O$ data sets), burning (charcoal records) and herbivory (*Sporormiella*).

The majority of terrestrial palynological data sets were found to have been produced from the lowlands of Mexico and Guatemala, primarily within the the extent of the Mayan empire. These records best represent the Late-Holocene 4000 – 0 cal yrs B.P. Relatively few records have been produced from upland sites and/or from El Salvador, Honduras and Nicaragua, indicating that these areas have been comparatively understudied and require further research.

Changes in precipitation are reported to have driven changes in vegetation structure, composition and type across the Central American Isthmus throughout the Holocene relating to changes in the timing and amount of precipitation driving change in vegetation dynamics through (i) water availability and (ii) the impact to natural ignitions and fuel loads.

An increase in precipitation during the Early Holocene *c.*12000 – 8000 cal yrs B.P. is unilaterally reported for existing records which are suggested to have facilitated the expansion of mesic forest across the Isthmus; however, these records are limited in spatial coverage, restricted to the lowlands of Guatemala and Panama. After this initial homogenous climatically-driven shift, vegetation is reported to have responded heterogeneously to a combination of climatic and anthropogenic forcing.

Burning associated with anthropogenic activities is reported as a prominent driver of vegetation change from *c.*5000 cal yrs B.P. Land clearance for agriculture was found to be the most widely reported driver of vegetation changes across the Central American Isthmus after *c.*4000 cal yrs B.P. The first palynological evidence for agriculture is reported from San Andres, Tabasco, Mexico, *c.*7050 cal yrs B.P. followed by the spread of agriculture across Guatemala and its adjacent territories between *c.*5500-4500 cal yrs B.P.

This study pioneers the use of systematic mapping in the field of palaeoecology rigorously identifying all literature pertaining to the dynamics and drivers of vegetation dynamics covering the Central American Isthmus spanning the Holocene. The results from this study reveal that after the initial expansion of mesic forests during the Early Holocene, the most widely reported driver of vegetation dynamics was agrarian practices, particularly those involving *swidden* for practicing *milpa*, from *c.*4000 cal yrs B.P.

II. *What have been the dominant drivers of change in the vegetation dynamics of the mixed coniferous forests of Central America during the Pre-Columbian Era? (Chapter 3)*

The pine-oak forests within the Southern Maya area were transformed by Pre-Columbian human populations through practices of agriculture and burning for quicklime production over thousands of years, extending back into the Archaic Period.

To determine the Pre-Columbian drivers of forest dynamics in the mixed coniferous forests of Central America I generated a new high-resolution multiproxy palaeoecological record using pollen, macroscopic charcoal, microscopic charcoal and *Sporormiella* in the uplands of Guatemala, which covers 4000B.C.E. – 1500C.E.

The results indicate that the Mid-Late Holocene vegetation baseline for this region is best described as mixed coniferous pine-oak forests. Palynological evidence from this record indicates that people were manipulating these forests and practicing agriculture from as early as 3850B.C.E. These practices were found to have driven changes in forest composition from oak dominated deciduous coniferous mosaics to pine dominated stands during the Archaic Period between 3850 - 3300B.C.E. I found that after cultivation ceased 3300B.C.E. the original mixed pine-oak forests were able to re-establish within 100 years. This follows the expected recovery time of c.80 years for typical pine-oak forests after a disturbance event (Kappelle, 2006; Figueroa-Rangel et al. 2008). My record further suggests that these forests remained stable between 3200 – 1150C.E. until *swidden*, and *milpa* agriculture was practiced from 970 - 100B.C.E. This initiated a further shift from mixed pine-oak forests to pine dominated forests between 970 – 870B.C.E.

As burning became increasingly prevalent 650 - 50B.C.E. the mixed pine-oak forests dramatically shifted to pine dominated forests until the end of the Pre-Columbian Era

1522C.E. Recovery of these forests coincided with reduced burning and the staged collapse of the Maya Empire 800-1522C.E. Burning between 650B.C.E. – 800C.E. is linked to the anthropogenic production of quicklime through burning, which required substantial fuel. This type of burning accords with what Anderson & Wahl (2016) propose for the Central Lowlands of Guatemala.

Fire has been identified as the dominant driver of structural and successive turnover within pine-oak forest systems, however, the drivers of fire (climatic/anthropogenic) are still highly debated (Islebe & Hooghiemstra, 1997; Domínguez-Vázquez & Islebe, 2008; Figueroa-Rangel et al. 2008; 2010; 2012; Velez et al. 2011). Terrestrial hydroclimatic reconstructions from the pine-oak forests of uplands of Guatemala suggest that only modest changes in precipitation amounts occurred over the last several millennia, suggesting relatively drier conditions between 250B.C.E. – 125C.E. and 875 – 1375C.E. (Velez et al. 2011). This is also suggested to be true in the neighbouring highlands of Chiapas, Mexico (Franco-Gaviria et al. 2018). I therefore conclude that although climate may have contributed to forest dynamics, anthropogenic activities were the primary driver of pine-oak forest turnover during the Pre-Columbian Era.

The importance of this study is twofold. Firstly, it shows that agrarian practices and burning were the dominant drivers of succession in the mixed pine-oak forests of upland Guatemala, and secondly provides the earliest evidence for agriculture in the Southern Maya Area, predating lowland agriculture by *c.*350 years.

III. How has Colonial and Post-Colonial land-use change influenced the current landscape, and what implications does this have for the future? (Chapter 4)

After European contact and the Spanish conquest anthropogenic use of land was drastically altered to facilitate agriculture, the rearing of livestock, large scale timber extraction and new settlements.

To investigate the impacts of Colonial and Post-Colonial land-use change the influence upon the current landscape I produced a new high-resolution palaeoenvironmental reconstruction using pollen, macroscopic charcoal, microscopic charcoal and *Sporormiella* from the uplands of Guatemala spanning 1550 – 2015C.E. and combined this analysis with historical documentation and earth observation satellite data.

Results from this research indicate that land clearance for the establishment of new settlements around the Cuchumatanes highlands began from at least 400 cal yrs B.P. (1550C.E.) as indicated by the decline of hard wood tree taxa evidenced in my palynological record. This is supported by Parish records from across the Cuchumatanes highlands that report land clearance for new settlements from 1537C.E. under a scheme called 'congregación' or 'reducción' involving the forced removal of indigenous peoples from their villages into colonial settlements (Van Oss, 1986). The impact of land clearance upon the composition of the pine-oak forests for this area are distinctly evident from 1700C.E. when pine forests become dominant and hard wood tree taxa permanently diminish. These forests are indicated to have been forced into this new stable state by sustained logging and sustained intensive pastoral activities from 1700 – 1800C.E. The high influx of dung fungal spores suggests that the herbivorous mammal abundance was high during this time reflecting domestic bovids brought over during the Spanish Conquest. Cattle and sheep are known to damage the reproductive success of taxasuch as *Quercus*, by ingesting and digesting their seeds (acorns) hindering their recovery within these forests (van Wieren, 1996; Kappelle, 2006). During the early 17th century Spanish settlers began to expand into the countryside (MacLeod, 1973), and by the end of the century the damage caused to the forests is evident from excessive forest clearing and extensive grazing. This has also been reported across other palynological reconstructions for this time in the uplands of Guatemala (Velez et al. 2011) and El Salvador (Dull, 2004a).

The high sedimentation rate and precise ^{210}Pb dating of Cenote Kail has enabled a rare validation of the palaeolimnological catchment area through cross comparisons of satellite data with the charcoal proxy data. This approach has enabled a calibration of the charcoal data sets to allow for a quantitative analysis of burning, comparable to modern day observations. Burning, locally and regionally, is limited and in line with the modern regime, which suggests that fire has been managed and controlled since European contact. Extensive ranching may have helped supress natural burning regimes through fuel load management and/or land use change from the previous anthropogenic practices including *milpa*, or quicklime production. The conservation of the deciduous hard wood taxa may be achieved by continuing to limit the presence of fire in these forests, and by controlling or removing domestic bovids. This would allow for hard wood taxa such as oak (*Quercus*) and sweetgum (*Liquidambar*) to re-establish over the course of 80-200 years (Kappelle, 2006).

There are few palaeoecological studies that have attempted to discuss changes in vegetation dynamics during the Historic Period 1500C.E.; this is probably because many of these records have low temporal resolution - greater than 200 years between samples (e.g. Deevey et al. 1979; Curtis et al. 1998; Mueller et al. 2009) and/or are missing sediment from the last c.500 years (e.g. Neff et al. 2006; Caffrey et al. 2011).). Of the records that do exist, authors report evidence for widespread forest recovery after the initial arrival of the Spanish 1500-1600C.E. across lowland Guatemala (Brenner et al. 1990; Wahl, 2016; Anderson & Wahl, 2016), Mexico (Leyden, 1987) and El Salvador

(Dull, 2004a; 2007). My palaeoecological reconstruction of the Cuchumatanes highlands is the highest resolution reconstruction of vegetation dynamics during the Colonial and Post-Colonial period for the Central American Isthmus to date. This research provides an intimate and robust integration of the palaeoecological data with historical records and satellite data, bridging the gap between modern ecological measurements and long-term ecology.

This is the first sub-decadal palaeoenvironmental study from across the Central American Isthmus and is also the first palaeoenvironmental study that attempts to quantitatively validate a palaeoenvironmental charcoal proxy record with earth observation satellite data from this region. This resolution and precise dating have allowed for detailed changes in anthropogenic land-use to be discerned, linking colonial settlements and pastoral activities with the decline and suppression of the hard wood taxa oak and sweetgum from 1700C.E. to present.

IV. *How resilient are the dry tropical forests of Central America to climatic and anthropogenic perturbations? (Chapter 5)*

The dry tropical forests of Central Pacific Nicaragua have been found to be highly resilient to climatic and anthropogenic impacts during the last 1200 years.

To assess the resilience of the dry tropical forests of Central Pacific Nicaragua I have produced the first palynological reconstruction for this region spanning the past 1200 years. I have also independently reconstructed precipitation, burning and herbivory using diatoms, macroscopic charcoal and dung fungal spores respectively to infer drivers of disturbance to these forests.

The reconstruction of the dry tropical forests surrounding the Asese peninsula, over the past 1200 years, presents little evidence for vulnerability to climatic and anthropogenic impacts. While the composition of taxa comprising these dry tropical forests subtly changes in response to the hydroclimatic shifts between the Medieval Climate Anomaly (MCA) 900 – 1250C.E. and Little Ice Age (LIA) 1400 – 1850C.E. as well as anthropogenic perturbations, such as European contact, the ecological structure of the dry tropical forests has remained remarkably resilient. Cole et al. (2014) identifies high frequency disturbance as the most significant factor in determining resilience in tropical forests. Biannual disturbance caused by seasonal variation over the last four millennia is the likely reason why these dry tropical forests have remained so resilient, allowing them to adapt and increase their resilience over time (Li et al. 2018).

Wetter conditions during the MCA facilitated increased vegetative growth and accumulation of vegetative biomass, which in turn led to greater burning. Higher intensity burning was found to drive larger openings in the canopy suppressing some of the dry tropical forest taxa. Similarly, some dry tropical forest taxa were found to reduce after European contact associated with deforestation for building materials and the creation of pastures. However, the palynological abundance of dry tropical forest taxa never falls below 50% and exceeds 90% from 1350 – 1420C.E. This indicates that DTF have persisted in relatively high abundance and maintained an established canopy, with some larger gaps at times, throughout the past 1200 years.

There have been significant fluctuations in climatic and anthropogenic impacts over the past 1200 years for Central Pacific Nicaragua; however, evidence from my research suggests that changes in the structure of dry tropical forests surrounding the Asese Peninsula have responded with little consequence. Drought resilient traits of the dominant dry tropical forest taxa (e.g. *Bursera simaruba* and *Brosimum*) including high wood density and long roots may have helped this community resist climatic and anthropogenic perturbations in the past.

This research is the first palynological reconstruction for dry tropical forests across the Central American Isthmus and shows high resilience to climatic and anthropogenic disturbances through time. This biome was previously reported to be highly threatened as a result of increasing human settlement and extensive agrarian practices and to have been reduced to less than 1% of its original area (Janzen, 1988). Results from my research suggest that these dry tropical forests, at least those surrounding the Asese peninsula, have not been vulnerable in the past and therefore should continue to be resilient going forward into the future.

6.2 Concluding remarks

This thesis has found that: (i) past palaeoenvironmental research has focused upon the lowland Maya Area, covering the Late Holocene, leaving large research gaps across the rest of the Central American Isthmus; (ii) mechanisms driving changes in precipitation are not well understood and nor are their spatial impacts. Further work is required along the Pacific coast and across higher elevations to understand how precipitation has changed across space and through time; (iii) fire has been an important component of ecosystem forest dynamics since the early Holocene; driven by climate from c.12000-6000B.P., (10000 – 4000B.C.E.) and a combination of climate and people from 6000 – -55B.P (4000B.C.E. – 2015C.E.); (iv) widespread changes in vegetation structure and composition are primarily driven by anthropogenic agrarian practices from c.6000 cal yrs B.P. (4000B.C.E.); (v) the mixed-coniferous pine-oak forests in the Southern Maya Area were transformed by anthropogenic activities during the Middle-Late Holocene c.6000 – 450B.P. (4000B.C.E. – 1500C.E.) and again during the historic period c.450 – 55B.P. (1500 – 2015C.E.); (iv) the dry tropical forests of Central Pacific Nicaragua are highly resilient to climatic and anthropogenic impacts during the Late Holocene c.1150 – 0B.P. (800 – 1950C.E.); and (vii) high resolution charcoal data from lake sediment records (sub decadal) can be successfully compared and calibrated against satellite data to inform upon a catchment area when high sedimentation cores are extracted and precisely dated.

While the research presented in this thesis significantly contributes towards our improved understanding of the relationships between vegetation, climate, fire, herbivory and anthropogenic forcing across the Central American Isthmus, a great deal of further research is required to fully understand and quantify these dynamics for different regions and vegetation types across space and through time.

6.3 References

Caffrey, M.A., Taylor, M.J. and Sullivan, D.G., 2011. A 12,000-year Record of Vegetation and Climate Change from the Sierra de Los Cuchumatanes, Guatemala. *Journal of Latin American Geography*, 10(2), pp.129-151.

Cole, L.E., Bhagwat, S.A. and Willis, K.J., 2014. Recovery and resilience of tropical forests after disturbance. *Nature communications*, 5, p.3906.

Curtis, J.H., Brenner, M., Hodell, D.A., Balser, R.A., Islebe, G.A. and Hooghiemstra, H., 1998. A multi-proxy study of Holocene environmental change in the Maya lowlands of Peten, Guatemala. *Journal of paleolimnology*, 19(2), pp.139-159.

Deevey, E., Rice, D.S., Rice, P.M., Vaughan, H.H., Brenner, M. and Flannery, M.S., 1979. Mayan urbanism: impact on a tropical karst environment. *Science*, 206(4416), pp.298-306.

Domínguez-Vázquez, G. and Islebe, G.A., 2008. Protracted drought during the late Holocene in the Lacandon rain forest, Mexico. Vegetation History and Archaeobotany, 17(3), pp.327-333.

Dull, R.A., 2004a. An 8000-year record of vegetation, climate, and human disturbance from the Sierra de Apaneca, El Salvador. *Quaternary Research, 61*(2), pp.159-167.

Dull, R.A., 2004b. A Holocene record of Neotropical savanna dynamics from El Salvador. Journal of Paleolimnology, 32(3), pp.219-231.

Dull, R.A., 2007. Evidence for Forest Clearance, Agriculture, and Human- Induced Erosion in Precolumbian El Salvador. Annals of the Association of American Geographers, 97(1), pp.127-141.

Figueroa-Rangel, B.L., Willis, K.J. and Olvera-Vargas, M., 2008. 4200 years of pine-dominated upland forest dynamics in west- central Mexico: human or natural legacy. *Ecology*, *89*(7), pp.1893-1907.

Figueroa-Rangel, B.L., Willis, K.J. and Olvera-Vargas, M., 2010. Cloud forest dynamics in the Mexican neotropics during the last 1300 years. *Global Change Biology*, *16*(6), pp.1689-1704.

Figueroa-Rangel, B.L., Willis, K.J. and Olvera-Vargas, M., 2012. Late-Holocene successional dynamics in a transitional forest of west-central Mexico. *The Holocene*, *22*(2), pp.143-153.

Islebe, G.A. and Hooghiemstra, H., 1997. Vegetation and climate history of montane Costa Rica since the last glacial. *Quaternary Science Reviews*, *16*(6), pp.589-604.

Janzen, D. 1988. Management of habitat fragments in a tropical dry forest: growth. *Annals of the Missouri Botanical Garden,* 75, pp.105-116.

Kappelle, M., 2006. Neotropical montane oak forests: overview and outlook. In *Ecology and conservation of neotropical montane oak forests*. Springer, Berlin, Heidelberg.

Leyden, B.W., 1987. Man and climate in the Maya lowlands. *Quaternary Research*, 28(3), pp.407-414

Li, D., Wu, S., Liu, L., Zhang, Y. and Li, S., 2018. Vulnerability of the global terrestrial ecosystems to climate change. *Global change biology*, 24(9), pp. 4095-4106.

Mueller, A.D., Islebe, G.A., Hillesheim, M.B., Grzesik, D.A., Anselmetti, F.S., Ariztegui, D., Brenner, M., Curtis, J.H., Hodell, D.A. and Venz, K.A., 2009. Climate drying and associated forest decline in the lowlands of northern Guatemala during the late Holocene. *Quaternary Research*, 71(2), pp.133-141.

Neff, H., Pearsall, D.M., Jones, J.G., Arroyo, B., Collins, S.K. and Freidel, D.E., 2006. Early Maya adaptive patterns: Mid-late Holocene paleoenvironmental evidence from Pacific Guatemala. *Latin American Antiquity*, 17(3), pp.287-315.

Van Oss, A.C., 1986. Catholic Colonialism. *A Parish History of Guatemala, 1524-1821*. Cambridge University Press.

van Wieren, S.E., 1996. Digestive strategies in ruminants and nonruminants. Van Wieren.

Velez, M.I., Curtis, J.H., Brenner, M., Escobar, J., Leyden, B.W. and Popenoe de Hatch, M., 2011. Environmental and cultural changes in highland Guatemala inferred from Lake Amatitlán sediments. Geoarchaeology, 26(3), pp.346-364.