Holocene environmental change inferred from fossil pollen and microcharcoal at Cenote Jennifer, Cayo Coco, Cuba

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Abstract

The Holocene vegetation history of Cayo Coco, Cuba, was examined using a 300 cm-long sediment core collected from Cenote Jennifer, a 13 m-deep flooded sinkhole (cenote). The core age model was developed with 15 Accelerator Mass Spectrometry radiocarbon dates and lead-210. Fossil pollen and spores, microscopic charcoal, and dinoflagellate cysts were used to identify past changes in local and regional vegetation and aqueous conditions.

The results show that sedimentation began approximately 9000 cal yr ago when local sea level began to rise causing the basin to fill with water. The palynological evidence indicates a shift from an arid environment with taxa such as Poaceae and Swartzia spp., to one dominated by Typha sp. until ~7600 cal yr BP, and then thorny coastal scrubland dominated by Buxus glomerata. From ~6500 to ~2500 cal yr BP, dry evergreen forest taxa dominate the palynological record. By ~2400 cal yr BP, mangroves dominated the coast in the vicinity of the sinkhole. An analysis of regional sea level and paleoclimatic records indicates that a rise in sea level, and subsequently the groundwater table, was the primary driver of changes in vegetation from ~9000 to 5000 cal yr BP. The palynological and sedimentological evidence suggests a catastrophic rise event occurred around ~7600 cal yr BP, supporting the interpretation of rapid sea level rise identified at other sites in the northern Caribbean.

Local scale climate change was detected in the palynomorph and charcoal record during the Little Ice Age when Cenote Jennifer recorded moist conditions, unlike the signals of drought common in palynological studies elsewhere in the insular Caribbean. This suggests complex local responses to regional climate signals at Cenote Jennifer. However, the appearance of microscopic charcoal around ~5000 cal yr BP is consistent with microcharcoal records from Lake Miragoâne, Haiti, and Laguna Saladilla, Dominican Republic, and may reflect a trend of increasing winter insolation during the Holocene that led to drier conditions and hence more fire activity. The microcharcoal record also shows evidence of modern day burning for charcoal production from 1850-1970 CE. Two possible prehistoric human occupation periods were identified (~850 to 50 BCE and ~450 to 1350 CE) based on the presence of disturbance taxa, microcharcoal, and possibly Ipomoea batatas (sweet potato) pollen, a common cultivar of that time, although this latter finding still needs to be confirmed.

The findings indicate that the vegetation around Cenote Jennifer has been less affected by climate and more by sea level change and human impact, at least at the centennial to millennial
timescale. This is likely due to its coastal setting and karst topography, both increasing its sensitivity to sea level change. This work indicates how sensitive coastal environments underlain by karst are to sea level, climate change, and human impacts, and that it can be expected that such tropical coastal environments will undergo profound changes over the next few centuries given the combined effects of natural and anthropogenic impacts.
Résumé

L'histoire de la végétation de l'Holocène est examinée utilisant une carotte de sédiments de 300 cm de long prélevés du Cenote Jennifer, une doline (cenote) inondée de 13 m de profondeur sur Cayo Coco, Cuba. Le modèle d'âge-profondeur a été établi avec 15 datation au radiocarbone utilisant la spectrométrie de masse par accélérateur et le plomb-210. Le pollen fossilié et les spores végétales, le charbon de bois microscopique, et les kystes de dinoflagellés ont été utilisés pour identifier les changements passés de la végétation aux niveaux locale et régionale et les conditions des eaux.

Les résultats montrent que la sédimentation a commencé il y a environ 9000 années auparavant quand le bassin se rempli d'eau suite au niveau de la mer locale qui augmente. L'enregistrement palynologique indique un changement d'un environnement aride avec quelques taxons tels Poaceae et Swartzia spp, à un dominé par Typha sp. jusqu'à ~ 7600 cal ans BP, puis une brousse côtière épineuse dominée par Buxus glomerata. De ~6500 à ~2500 cal ans BP, une forêt sèches dominent le profil palynologique. À partir de ~ 2400 cal ans BP, les mangroves ont dominé la côte dans les environs de Cenote Jennifer. Une analyse du niveau de la mer régionale et des enregistrements paléoclimatiques indique que la hausse du niveau de la mer était le principal moteur de changements dans la végétation de ~ 9000 à 5000 cal ans BP. En particulier, l’enregistrement palynologique et sédimentologique suggère un événement de hausse catastrophique est enregistré à ~ 7600 cal ans BP. Ceci soutien l’interprétation de hausse rapide du niveau de la mer identifié à d'autres sites dans le nord des Caraïbes.

Le changement climatique à l'échelle local a été détecté dans les palynomorphes et le microcharbon pendant le petit âge glaciaire, où il est possible que Cenote Jennifer a enregistré des conditions humides, contrairement aux signaux de sécheresse qui sont communs dans les études palynologiques ailleurs dans les Caraïbes insulaires. Cela suggère des réponses locales complexes aux signaux climatiques régionaux à Cenote Jennifer. Cependant, l'apparition de charbon microscopique à ~ 5000 cal ans BP est en accord avec les enregistrements de microcharbon du Lac Miragoâne, Haïti et Laguna Saladilla, République Dominicaine, et peut refléter une tendance d'insolation croissante d'hiver aux cours de l'Holocène qui a conduit à des conditions plus sèches et par conséquent plus d'activité de feu. L’enregistrement de microcharbon de Cenote Jennifer montre également la preuve contemporaine de production de charbon de bois de 1850 à 1970 EC. Deux périodes possibles d’occupation humaine
préhistorique ont également été identifiés (~ 850-50 AEC et ~ 450-1350 EC) basé sur la présence de taxon correspondant à la perturbation, le microcharbon, et l'apparition possible du pollen de *Ipomoea batatas* (patate douce), une variété cultivée commune de ce temps, bien que ce dernier résultat do

Globalement, les résultats indiquent que la végétation autour de Cenote Jennifer a été moins affectée par le climat et plus par le changement du niveau de la mer et de l'impact humain, au moins à l’occasion séculaires et millénaires. Cela est probablement dû à sa position dans un environnement côtier et la topographie karstique, qui à la fois augmente sa sensibilité aux changements de niveau de la mer. Ce travail indique la sensibilité à la hausse du niveau de la mer des milieux côtiers reposant sur le karst, le changement climatique et les impacts humains. Il peut être prévu que ces milieux côtiers tropicaux vont subir de profonds changements au cours des prochains siècles, étant donné les effets combinés naturel et anthropique.
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1.1 Introduction

Coastal zones include complex and dynamic systems that provide a perspective into climatic changes and anthropogenic impacts operating at a range of timescales (Peros et al. 2007a; Peros et al. 2015). In the tropics, coastal zones comprise a range of marine and terrestrial biomes which include forests (evergreen and deciduous), scrublands and savannas, mangroves, saltmarshes, estuaries, coral reefs, seagrasses, and coastal shelf communities (Martínez et al. 2007). Approximately 60% of the world’s population lives in coastal environments, making them particularly vulnerable to human impacts and thus a focal point for scientific research (Martínez et al. 2007).

The coastlines of the Caribbean have a particularly high level of vulnerability to multiple climate stressors. The Intergovernmental Panel on Climate Change 5th Assessment Report reports that future climate stressors include sea level rise, increased tropical and extratropical cyclones, increasing air and sea surface temperatures, and changing rainfall patterns (Nurse et al. 2014). However, data gaps for the Caribbean region, particularly over long time scales, hinder adaptation planning and implementation. Paleoenvironmental records can help fill gaps in baseline environmental data making them critical to addressing gaps identified in the 5th Assessment Report for small islands. These research and data gaps are: (1) the need to detect and attribute past climate impacts and drivers on small islands to specific climate change processes; (2) a need for site-specific data and long-term quality-controlled data, particularly for individual islands; (3) recognition that the diversity of one island region to another and between countries translates to variable climate change risk profiles with different responses to impacts, vulnerabilities, and adaptation; and (4) the need to increase in-country specific climate data to develop a better profile of each country’s heterogeneity and complexity (Nurse et al. 2014).

Sea level rise (SLR), specifically, poses one of the most recognized and severe threats to low-lying coastal areas and islands. On small islands, the majority of human communities, infrastructure, and tourism facilities are located in coastal zones, and on-island relocation opportunities are limited making them vulnerable to extreme tides, surge events, and SLR (Nurse et al. 2014). Sea level rise inundates coastal aquifers and wetlands, destroying sensitive ecosystems that are essential for human water use and consumption. Accelerating SLR superimposed on increasing extreme oceanic events (e.g., storm surges, El Niño-Southern
Oscillation) increases the risk of sea floods, coastal erosion, degradation of groundwater resources, and coral reef degradation (Nurse et al. 2014). Coastal squeeze, caused by the construction of sea walls to protect human interests, interferes with the landward migration of salt marshes and mangrove forests and is also a major concern on Caribbean islands (Mycoo 2011).

All the islands of the Caribbean are expected to be profoundly affected by rising sea levels and increasing human populations, therefore, understanding how low-elevation coastal systems in this region respond to SLR and human impacts is important for future planning and mitigation efforts. Investigations into past ecosystem changes provide a foundation to better understand the complexities of coastal environments. Changes in sea level, climate, and anthropogenic impacts operate on multiple timescales, often exceeding those of the instrumental record, particularly in the Caribbean (Hillman and D'Agostino 2009). Since direct measurements of long-term climate and sea level variability are unavailable, it is necessary to use indirect proxy indicators to reconstruct earlier changes. Paleoenvironmental research can provide a greater understanding of how coastal systems will respond to future environmental variability (Parr et al. 2003; Willard and Cronin 2007; Rick and Lockwood 2013). Additionally, in the interest of understanding the causes of global-scale environmental change, further research and data are needed for the tropics, an area for which few paleoenvironmental studies exist (Peros et al. 2007a; Peros et al. 2015).

Sediments from lacustrine and marine basins are a common source of paleoenvironmental evidence since they act as natural sediment traps and preserve various proxies of past environmental changes (Haug et al. 2001; Hodell et al. 1991; Higuera-Gundy et al. 1999; Lane et al. 2009). However, the scarcity of lakes in the Caribbean region makes undertaking paleoenvironmental research in this region difficult, but basins developed from long-term karst processes referred to as sinkholes (cenotes), blueholes, and other cave systems, accumulate sediment sequences similarly to lakes (van Hengstum et al. 2011). Coastal sinkholes are unique environments that have not been studied extensively and whose paleoenvironmental potential is underutilized. Coastal sinkholes are common in the Caribbean, and investigations have shown that they can provide records of Holocene sea level change (Gabriel et al. 2009; van Hengstum et al. 2011), vegetation changes (Kjellmark 1996), storm impacts, climate change, and prehistoric activities (Schmitter-Soto et al. 2002, Alvarez-Zarikian et al. 2005, Florea et al. 2007).
For example, Gabriel et.al (2009) highlighted the importance of sinkhole sediments as paleoenvironmental archives by showing that they provide valuable information on past vegetation and hydrological conditions, as well as having great potential for testing and refining sea level curves within the Caribbean Basin.

1.2 Objectives
This thesis will utilize a coastal sinkhole (hereafter referred to as a cenote) to develop a continuous, ~9000 year-long fossil pollen record from Cayo Coco, northern Cuba, and in doing so contribute to our understanding of the factors causing coastal vegetation change on low-elevation, tropical, carbonate environments over long-timescales. The specific questions that this thesis will address are:

1. How has the vegetation on Cayo Coco changed over the course of the Holocene?
2. Is there any evidence for human activity in the sedimentary/pollen record?
3. What have been the main processes (i.e., sea level change, climate change, human impacts) that have caused changes in vegetation on Cayo Coco, and how has the relative importance of each changed with time?
4. How does the Cayo Coco record compare to other Caribbean paleoecological records?

I will attempt to answer these questions by analyzing fossil pollen, microcharcoal, and dinoflagellate cysts from a sediment core extracted from Cenote Jennifer. To answer research questions 1 and 2, fossil pollen and microcharcoal data will be used to reconstruct past vegetation communities. These indicators have been shown to reflect local- to regional-scale vegetation and fire, the latter of which can be attributed to human activity, such as land clearance and settlement (Kennedy et al. 2006; Lane et al. 2009; Caffrey et al. 2015). To answer research questions 3 and 4, I will then compare my results to other paleoenvironmental and archaeological data from Cuba and elsewhere in the Caribbean. The identification of similarities between the Cenote Jennifer results and other studies regarding the direction of changes, as well as their timing, will help me identify the main processes controlling vegetation change as well as their relative importance.
My thesis will contribute to a better understanding of the long-term patterns of and factors causing environmental change in coastal tropical environments. It will also complement the paleoecological research of Peros et al. (2007a, b; 2015) and Gregory et al. (2015) which was undertaken on coastal lagoons in Cuba. In addition, my research will contribute to a greater understanding of the utility of cenotes as a paleoenvironmental data source (van Hengstum et al. 2011; Kovacs et al. 2013), the implications for which are significant since this would open new avenues for paleoenvironmental data acquisition on islands in the Caribbean that were previously thought to have limited potential for paleoenvironmental research.

1.3 Palynology and its use in the Caribbean
One of the most common proxies used in environmental reconstructions is fossil pollen (Birks and Birks 1980; Bennett and Willis 2001; Ellison 2008), which has been shown to have great utility at reconstructing past vegetation communities. Consequently, past vegetation community changes can then be used to study the mechanisms which drive vegetation change, including climate and sea level variability, human activities, and other factors. However, the interpretation of pollen records can be complex. For example, on a continental scale vegetation is determined primarily by climate boundaries, yet on a regional to local scale, vegetation distribution is largely controlled by hydrologic and edaphic factors. Coastal sites are also affected by changes in sea level (Peros et al. 2007a; Ellison 2008).

The main principles of palynology are: (1) pollen grains are extremely resistant and are found in many different types of deposits; (2) pollen grains are produced in large abundance; (3) pollen grains are more widely and evenly distributed than other fossils; and (4), pollen grains can be retrieved in large quantities with little difficulty (Faegri and Iversen 1989). The main assumption of palynology is that a vegetation community in the past will produce a similar pollen assemblage as its modern analog (Flenley 1973; Williams and Jackson 2007). A pitfall of this assumption is that fossil vegetation communities may have no modern analogues, due to the presence of non-analogue climates, plant dispersal mechanisms, and even predation by now-extinct megafauna (Williams and Jackson 2007). However, various statistical approaches and frameworks have been successful in identifying non-analogues in order to reliably interpret fossil pollen assemblages (Gavin et al. 2003; Williams and Jackson 2007).
When conducting palynological research in the Neotropics, there are other issues to consider. First, a large number of plants are entomophilous or zoophilous (insect or animal pollinated) and do not produce a great deal of pollen (Faegri and van der Pijl 1979; Colinvaux et al. 2000). Despite assumptions that Neotropical fossil pollen assemblages would have little value, Bush (1995) and Colinvaux et al. (2000) have shown that the pollen of both entomophilous and anemophilous (wind-pollinated) plants are well represented in Neotropical sediments. Second, plant diversity is high. The Neotropics include some of the most substantial biodiversity hotspots in the world, with over 10,000 species of vascular plants, one-third of which are endemic (Hedges 2001; Graham 2003). With so many species, pollen types are not well documented, and few pollen keys have been published for the region. Exceptions are those by Palacios Chávez et al. (1991) and Roubik and Moreno (1991) for Central America, and Colinvaux et al. (1999) for South America. The only key currently available for the insular Caribbean is the online *Key to the Pollen of The Bahamas* by Snyder et al. (2007).

### 1.4 Literature Review

#### 1.4.1 Holocene paleoenvironmental research in the Caribbean and Cuba

Sedimentary-based paleoenvironmental research in the Neotropics has traditionally focused on Central and South America (Hillyer et al. 2009; Raczka et al. 2013; Correa-Metrio et al. 2013; Bush et al. 2015a; Bush et al. 2015b), while there has been only limited research on the hundreds of islands which make up the insular Caribbean (Fritz et al. 2011; Caffrey et al. 2015; Peros et al. 2015). For the most part, the lack of interest in the Caribbean was due to the scarcity of lakes, which are conventional sources of long sedimentary records. Moreover, it was also believed that temperature-based seasonality in the Caribbean had not changed enough—even over glacial-interglacial cycles—to be detectable in the paleoenvironmental record compared to temperate or boreal regions (Bennett and Willis 2001; Metcalfe and Nash 2012). However, over the last several decades, the idea of low seasonality has been refuted and an increase in the number of paleoenvironmental studies based on sediment cores from lakes and lagoons in the Caribbean has contributed to our understanding of Holocene climatic changes in this region (Hodell et al. 1991; Higuera-Gundy et al. 1999; Lane et al. 2008; Caffrey et al. 2015; Peros et al. 2015). In the case of Cuba, research has also relied on high-resolution speleothems, in addition to sediment core-based paleoecological investigations (Pajon et al. 2001; Fensterer et al. 2012; Fensterer et al.
2013; Peros et al. 2007a, b; Peros et al. 2015; Gregory et al. 2015) to add to our knowledge of Holocene paleoclimatology in the region. The following sections highlight some of the key findings of studies from the Caribbean and Cuba to enable the results from Cenote Jennifer to be placed into a broader context (see Appendix A for comparison chart of Northern Hemisphere and Caribbean paleoenvironmental events).

1.4.2 Paleoenvironmental studies in the Caribbean

Early Holocene (~11700 to 8200 cal yr BP)

Few records are available for the early Holocene (see Walker et al. 2012 for formal Holocene subdivision explanations). One of the longest paleoenvironmental records from the Caribbean comes from a sediment core extracted from Lake Miragoâne, Haiti, a large natural freshwater lake (Brenner and Binford 1988; Higuera-Gundy et al. 1999). The Lake Miragoâne record spans 10300 ^14^C yr BP (11960 cal yr BP) to the present, and three studies using pollen, charcoal, and $\delta^{18}O$ isotopes from ostracodes (Candona sp.) were published from the same 7.67-meter core (see Brenner and Binford 1988; Hodell et al. 1991; Higuera-Gundy et al. 1999). A hard-water lake error (HWLE) affected the radiocarbon dating of the core and resulted in an error of ~1025 yr due to the contribution of ‘old’ carbon (Hodell et al. 1991; Higuera-Gundy et al. 1999). To apply a HWLE correction, a paired wood and ostracod sample was measured from the same depth and the age difference of ~1000 yrs was subtracted from ostracod dates to obtain corrected ages (Higuera-Gundy et al. 1999). Because of this dating uncertainty, the chronology for this core was considered provisional, and as such, the dates were not calibrated and were reported as radiocarbon years BP by Higuera-Gundy et al. (1999). The dating issues associated with this core produced an unreliable chronology which makes it difficult to compare directly to other Caribbean records. In order to compare the Lake Miragoâne record to other calibrated records from the Caribbean, the ages are calibrated here by applying the 1025 yr HWLE correction using the CALIB 7.0.4 program. Only the calibrated dates are reported below.

From 11960-9500 cal yr BP, the pollen record is dominated by shrub and tree pollen, mainly species from montane hardwood forests that today are common above 800 meters above sea level (Higuera-Gundy et al. 1999). An abundance of Podocarpus pollen, an evergreen tree common to montane forests, and an abundance of highland taxa suggest that montane hardwood forest descended to low elevations under cooler conditions. The charcoal record at this time is
low, and it is possible that cooler climate led to infrequent fires which allowed dry-adapted montane taxa to colonize (Higuera-Gundy et al. 1999). Moist forest indicators are low, but increase around 9500 cal yr BP, suggesting initially that stands of moist forest developed further from the lake. High Palmae pollen percentages, several species of which grow in dry habitats, suggest a dry open forest was present (Higuera-Gundy et al. 1999). A warmer and wetter period is indicated after 9300 cal yr BP, inferred from the δ¹⁸O record, which suggests an increase in moisture availability and an increase in lake levels (Hodell et al. 1991; Higuera-Gundy et al. 1999).

From 9500-6500 cal yr BP, there is an increase in Amaranthaceae pollen and a decline in shrub pollen, suggesting an open landscape, and low charcoal counts indicate that forest fires were still rare (Higuera-Gundy et al. 1999). The arboreal pollen is mainly from dry forest taxa (but quite low < 6%), and Amaranthaceae and other herbs dominate (reaching >40%) the non-arboreal pollen assemblage. The δ¹⁸O record shows increasing moisture availability until 8500 cal yr BP, however, pollen from moist forest remains relatively low (Higuera-Gundy et al. 1999). The presence of dry forest taxa, with a high percentage of Curatella pollen (a drought tolerant tree present today in savannas), suggests an open grassy savanna-like landscape with dry forest interspersed within it (Higuera-Gundy et al. 1999).

Middle Holocene (~8200 to 4200 cal yr BP)

The middle Holocene has more proxy records available from the Caribbean. In the Lake Miragoâne record, lake levels were at their highest between 8200 and 6400 cal yr BP, and the establishment of forests was inferred from an increase in tree pollen percentages (Higuera-Gundy et al. 1999).

Sedimentary records from Trinidad and Belize show lower sea levels were recorded at about 7000 cal yr BP (Ramcharan 2004; Ramcharan and McAndrews 2006; Monacci et al. 2009), as indicated by the establishment of mangroves (mainly Rhizophora mangle, red mangrove) which form at or near mean sea level (Tomlinson 1986). The presence of Rhizophora pollen coupled with mangrove peat can indicate changes in relative sea levels since Rhizophora occupies the upper half of the intertidal zone (Ramcharan 2004; Ramcharan and McAndrews 2006). A sedimentary record from Barbados suggests that mangrove formation began around ~6000 cal yr BP when the rate of post-glacial SLR slowed (Ramcharan 2005). Rhizophora pollen
was also identified in a core from Laguna Saladilla in the Dominican Republic around ~8030 cal yr BP, although it is unclear whether the mangrove was growing near the site or elsewhere in the region (Caffrey et al. 2015). However, marine mollusks and manganese fragments from the core support the interpretation of a marine phase at Laguna Saladilla from 8030-5550 cal yr BP (Caffrey et al. 2015). It is possible that this marine phase was due in part to the catastrophic SLR event of 7600 cal yr BP (when sea level rose by several meters in a span of a few years) identified by Blanchon and Shaw (1995), which would have created an open water estuary extending to the position of modern-day Laguna Saladilla (Caffrey et al. 2015).

From 6500 to 4250 cal yr BP, tree pollen from Trema and Cecropia dominate at Lake Miragoâne. Both species are common in upland and lowland moist forests (Higuera-Gundy et al. 1999). Dry forest is still present in the record, including the fire resistant and drought tolerant Curatella. Higuera-Gundy et al. (1999) suggest this zone denotes generally moister conditions. However, charcoal increases in this zone and Ambrosia and Pinus are present. These species are indicators of increased fire activity, and today Pinus is known to quickly invade burnt sites (Higuera-Gundy et al. 1999). The greater frequency of fires recorded in the middle Holocene, under what would have been wet conditions, can be explained climatically. Seasonality in the northern tropics can be discerned in the early Holocene when dry winters favored lightning induced ignition (Higuera-Gundy et al. 1999). However, fires may have been limited by fuel production in shrub-dominated landscapes. As the forest expanded, more fuel was available for natural combustion (Higuera-Gundy et al. 1999). Conversely, the presence of charcoal from 6500 to 4250 cal yr BP could also be a signal of early human disturbance as was argued in a study from a site in Puerto Rico by Burney et al. (1994).

Charcoal analysis was also undertaken on a sediment core from Laguna Tortuguero in Puerto Rico (Burney et al. 1994). The charcoal record starts at 7000 cal yr BP, although from 7000-5300 cal yr BP, very low charcoal counts are recorded, suggesting wildfires were not common. The small size of the particles detected, compared to the rest of the core, also imply long-distance transport from other islands or the continental mainland (Burney et al. 1994). Around ~5300 cal yr BP, a major shift in the Holocene fire history of the island occurred, when a sudden spike in charcoal is recorded. Burney et al. (1994) argue that this increase above background levels was due to anthropogenic burning. However, other charcoal records in the Caribbean show marked increases around 5000 cal yr BP that are thought to be related to
changes in winter insolation (Caffrey and Horn 2014; Caffrey et al. 2015). Caffrey and Horn (2014) examined microscopic charcoal records from three lakes covering the last ~7000 years (including the Lake Miragoâne record and the Laguna Tortuguero record) and concluded that a shift beginning ca. 6000-5000 cal yr BP in all records was due to increasing winter insolation which drove shifts in winter drying and may have led to more frequent and intense natural fires.

Late Holocene (~4200 cal yr BP to Present)

The late Holocene sub-epoch has the highest number of proxy records available for interpretation. From 4250 to 3050 cal yr BP a wet period is identified at Lake Miragoâne in Haiti, supported by high percentages of Moraceae and other moist forest taxa as well as lower δ¹⁸O values (Higuera-Gundy et al. 1999). Drying commenced around ~3500 cal yr BP, according to the δ¹⁸O record, but a temporary return to moister conditions is present from ~1600 cal yr BP to ~750 cal yr BP. By 750 cal yr BP, drier conditions returned, and early agriculturists had colonized the area. In the northern Caribbean, a dry period is also recorded from 3200 to 1500 cal yr BP at Church’s Blue Hole on Andros Island in The Bahamas (Kjellmark 1996). The dry climate at Church’s Blue hole was evidenced by the presence of Dodonaea, Piscidia, and Xylosma pollen, all from shrubs tolerant to dry conditions (Kjellmark 1996).

Contradictorily, Laguna Saladilla did not record a dry period but rather a freshening of the lake around ~3680-2500 cal yr BP inferred from increases in Typha and Cyperaceae pollen (Caffrey et al. 2015). Caffrey et al. (2015) suggest that this lack of a drying trend could be due to shifts in the position of the Intertropical Convergence Zone (ITCZ). As the ITCZ moved south in the late Holocene, precipitation at Lake Miragoâne would have been reduced while Laguna Saladilla, on the north coast of Hispaniola, received increased winter rainfall (Caffrey et al. 2015). However, it is also possible that the freshening of the lake is due to changes in geomorphology, which would have shifted the location of a nearby river to have it discharge into the lake, thus freshening it (Caffrey et al. 2015). From 2500 cal yr BP to present, diatom and mollusk proxies indicate the lake was freshwater, and an increase in Amaranthaceae and a decline in Typha and arboreal pollen indicate a drier climate, consistent with other Caribbean sites (Caffrey et al. 2015).

In The Bahamas, a moist mesic climate is identified from ~1500-740 cal yr BP (Kjellmark 1996). Hardwood thickets, represented by higher pollen percentage values of Palmae,
Metopium toxiferum, and Salvia bahamensis, become dominant. A significant increase in the percentage of Pinus caribaea pollen at about 900 cal yr BP indicates that the hardwood thicket was later partly displaced by the current pinewood vegetation, dominated by Pinus caribaea, the pine typical of this region (Kjellmark 1996). This change in vegetation is corroborated by another study in The Bahamas, on Abaco Island, where a shift to a pine-dominated landscape is recorded around ~1000 cal yr BP, suggesting a regionally dry climate (Slayton 2010). Hardwood thickets can still be found interspersed within the pinewoods in The Bahamas today (Kjellmark 1996; Slayton, 2010). Changes from a hardwood thicket-dominated community to a pinewoods community coincided with an increase in charcoal at 740 cal yr BP, suggesting a change in fire regime (Kjellmark 1996). Other records from The Bahamas show some similarities. Steadman et al. (2007) found plant macrofossils and pollen supporting the interpretation of a grassland or grassy woodland with a more open canopy, which was likewise interpreted by Slayton (2010).

A study by Lane et al. (2009) on two lakes on the Cordillera Central, Dominican Republic, produced additional evidence of a dry period which could be due to a shift in the position of the ITCZ, resulting in decreased moisture to the region. A drought is recorded around ~1210 cal yr BP, inferred from a decline in pollen from arboreal taxa and an increase in herbaceous pollen, indicating a period of aridity (Lane et al. 2009). A steady increase in $\delta^{13}C_{TOC}$ at the same time indicates a local increase in drought tolerant C$_4$ plants and a peak in charcoal suggest a shorter fire return interval (Lane et al. 2009). Lane et al. (2009) suggest that this dry period coincides with a series of droughts linked to the demise of the Mayan civilization in Central America (Haug et al. 2003; Lane et al. 2009).

Studies of other sites in the region, however, do not provide evidence of a dry period during this time. Jessen et al. (2008) analyzed a core extracted from a lagoon in St. Croix, US Virgin Islands, and found an increase in mangrove pollen, indicating the development of mangrove swamps at 2500 cal yr BP. Likewise, in north-central Cuba, an expansion of mangroves is recorded around ~1700 cal yr BP (Peros et al. 2007a), which is not seen in other mangrove records from Trinidad and Spanish Lookout Cay, Belize (Ramcharan and McAndrews 2006; Monacci et al. 2009).

Paleoenvironmental records from several Caribbean sites reveal changes during the Medieval Warm Period (MWP) (950 to 1200 CE) and the Little Ice Age (LIA) (1550 to 1850 CE) that contrast with records found elsewhere. Lane et al. (2009) suggested that the MWP was
relatively wet in the Caribbean, based on a decrease in the $\delta^{18}$O in ostracods and charophytes from Laguna Castilla and Laguna de Salvador, Dominican Republic. Gischler et al. (2008) interpreted low temperatures from $\delta^{18}$O of calcareous skeletons of marine organisms (including mollusks, foraminifera, calcareous algae, and corals) during the MWP from a core extracted from the Great Blue Hole off the coast of Belize. Regarding the LIA, Lane et al. (2009) note that this may have been one of the most arid periods in the Caribbean of the last 2000 years, and provide $\delta^{18}$O evidence from ostracods and charophytes to support this view. Likewise, Gischler et al. (2008) interpreted high temperatures coinciding with the LIA, which due to high evapotranspiration would have led to aridity in the region. Other paleoecological records in the region have also shown a dry LIA (Saenger et al. 2009; Lane et al. 2011). However, the data is not consistent at all sites. For example, González et al. (2010) developed a palynological record from San Andres Island, Colombia, in the southwest Caribbean Sea, which indicates that the latest part of the LIA may have been more humid due to hydroclimatological changes brought on by an increase in hurricanes and storms between 1770 and 1800 CE.

From 1350 to 1700 CE, dry forest tree species dominated around Lake Miragoâne, and an increase in Poaceae pollen may be from human impact. An increase in Cladium and Typha suggest marsh expansion around Lake Miragoâne, supported by $\delta^{18}$O data which indicates declining lake levels over the last 3000 years (Higuera-Gundy et al. 1999). From 1700 CE to present, the pollen record indicates that deforestation occurred, represented by an increase in pioneers and successional taxa (Celtis, Cecropia) and dry-adapted Bursera and Sapindus trees (Higuera-Gundy et al. 1999). The decline in forest pollen around 1700 CE is indicative of land clearance. At this time, watershed soil erosion was interpreted from a decline in organic matter coupled with an increase in carbonates. However, pollen concentration and organic matter increased between 1850 and 1950 CE, which may reflect forest recovery as large plantations would have been divided into smaller subsistence plots following Haiti’s independence from France in 1804 CE (Higuera-Gundy et al. 1999).

**Human Impact**

The Greater Antilles were first settled around 6000 cal yr BP by small populations of hunter-gatherers (Cooper and Peros 2010). It is not clear if these people impacted vegetation to a degree that would be detectable in the pollen record. However, later migrations of people, especially
those who were horticulturalists, appear to have had an impact on vegetation that is detectable in the paleoecological record (Siegel et al. 2015).

One line of evidence for the detection of prehistoric people is the presence of maize (*Zea mays*) pollen, which is an indicator of settlement and agriculture (Higuera-Gundy et al. 1999; Lane et al. 2008; Lane et al. 2010). Maize pollen is very useful in this regard because of its distinctiveness and size, making it easily identifiable taxonomically, and because the grain itself does not travel very far from its source (Lane et al. 2010). For example, from 1350-1700 CE, *Zea mays* pollen is present at Lake Miragoâne, which is indicative of the presence of Taino agriculture in the area (Higuera-Gundy et al. 1999). Likewise, Lane et al. (2008) report the earliest evidence of maize pollen on Hispaniola at 1060 CE, also from Taino agriculture.

Microcharcoal has also been used to indicate prehistoric settlement as it is produced by the burning of vegetation, although, as discussed previously, its interpretation can be difficult. For instance, around 950 CE, records start to show an increase in fire activity on several islands (Higuera-Gundy et al. 1999; Beets et al. 2006; Kennedy et al. 2006; Lane et al. 2008; Slayton 2010). In The Bahamas, an increase in fire activity after 922 CE may coincide with the arrival of humans (Slayton 2010), however, Kjellmark (1996) points out that it is difficult to separate the human and natural fire regimes, and cautions that climate-driven changes cannot be ruled out. Furthermore, from 1150-1350 CE increased charcoal and pine pollen is interpreted by Slayton (2010) to represent the arrival and settlement of the Lucayan Tainos on Abaco Island, also in The Bahamas.

Other investigators have used signals of land clearance and deforestation to infer human settlement and human impacts, often evidenced by a decrease in tree pollen and an increase in invasive species or herbaceous species, such as *Ambrosia* (Brenner and Binford 1988; Kjellmark 1996; Higuera-Gundy et al. 1999; Lane et al. 2009; Slayton 2010). Some examples are the San Andres Island (Colombia) palynological record, which shows a marked decrease in mangrove pollen around the time of the establishment of large coconut plantations on the island (González et al. 2010). At Lake Miragoâne in Haiti, low pollen concentrations and carbonate-rich sediments since 1950 CE document severe deforestation from agriculture (Higuera-Gundy et al. 1999).
1.4.3 Cuban paleoenvironmental research
Early Holocene (~11700 to 8200 cal yr BP)

Pajón et al. (2001), using a speleothem collected in the Dos Anas cave system in the Province of Pinar del Rio, western Cuba, recorded abrupt climate warming at the end of the Pleistocene (~12500 cal yr BP) based on the δ¹⁸O composition of a stalagmite. This abrupt warming may be an unusual response associated with the Younger Dryas (YD) climate event (Pajón et al. 2001). Fensterer et al. (2013) collected two speleothems from the same cave system which provided a nearly continuous, high-resolution record of past precipitation changes during the last 12.5 thousand years. The δ¹⁸O record from these speleothems included major climatic events, such as the YD (from 12900 to 11700 cal yr BP) and the 8200 cal yr BP (8.2 ka) cooling events (Fensterer et al. 2013). These events are assumed to relate to the weakening of the thermohaline circulation and a southward shift of the ITCZ (Fensterer et al. 2013). The initiation of the YD is not represented as the chronology is poorly constrained prior to 12500 cal yr BP. However, around ~12000 cal yr BP the increase in δ¹⁸O likely indicates a drier climate in the northern Caribbean at this time. The 8.2 ka event was identified by an increase in δ¹⁸O around 8300 cal yr BP which may reflect drier conditions (Fensterer et al. 2013).

The speleothem record produced by Fensterer et al. (2013) suggests a general relationship between North Atlantic climate and precipitation in the northern Caribbean during the Holocene. This relationship was determined by the detection of Bond events in the speleothem record. Bond events are periods of decreased sea surface temperatures that occurred in the North Atlantic approximately every 1500 years (Bond et al. 2001). The record produced by Fensterer et al. (2013) reveals increased δ¹⁸O suggesting drier conditions at 11.3, 10.3, 9.7, 5.2, 4.6, and 1.5 ka. The correspondence of the δ¹⁸O record to the timing of Bond events 8, 7, 6, 4, 3, and 1 suggests that drier conditions in the Caribbean corresponded with cooler phases in the North Atlantic (Fensterer et al. 2013). However, Bond event 5 is not visible, possibly due to a large change in δ¹⁸O values between 10 and 6 ka, and a hiatus between 2.5 and 3.3 ka may reflect dry climate conditions during Bond event 2.

Middle Holocene (~8200 to 4200 cal yr BP)

The period starting just before 8200 cal yr BP to 6000 cal yr BP is represented in the speleothem record by a shift from drier to wetter conditions (Fensterer et al. 2013), and is comparable to the
δ¹⁸O record from Lake Miragoâne, Haiti which shows a similar shift at this time (Hodell et al. 1991). Fensterer et al. (2013) argue that this change to a wetter climate regime in western Cuba may have been insolation driven as higher insolation values resulted in an enhanced hydrological cycle in the northern Caribbean.

The longest sediment-based paleoenvironmental dataset for Cuba comes from 10 sediment cores extracted from in and around Laguna de la Leche, a shallow coastal lagoon in northern Cuba, by Peros et al. (2007a). A multiproxy analysis of paleosalinity was further undertaken at the same locale by Peros et al. (2007b).

Intense evaporation was recorded in Laguna de la Leche from 6800 to 4800 cal yr BP, as denoted by high δ¹⁸O values suggesting a drier period (Peros et al. 2007b). During this time, Laguna de la Leche was a partially closed, shallow oligohaline lake (Peros et al. 2007b). At 6200 cal yr BP, an abrupt increase in ostracods, gastropods, and charophytes indicates the formation of a shallow brackish lake (Peros et al. 2007a, b). Palynological evidence from Laguna de la Leche indicates a dry period prior to ~6500 until ~4800 cal yr BP, characterized by high Amaranthaceae, Asteraceae, and Typha domingensis pollen (Peros et al. 2007a). The presence of Acrostichum aureum spores suggests that it was still a shallow brackish lake since this fern needs freshwater to germinate but lives in brackish environments once established.

From ~4800 to 4200 cal yr BP, δ¹⁸O are fairly low at Laguna de la Leche, recording wetter conditions due to increased relative sea level and potentially deeper, fresher water, due to an influx of isotopically-depleted rain or hurricane water (Peros et al. 2007b). Water levels continued to increase after 4200 cal yr BP, as indicated by a shift from local (non-arboreal) to mostly regional (arboreal) pollen rain and a decrease in pollen influx (Peros et al. 2007a). The appearance of foraminifera (typical of marine environments) indicated that rising sea levels breached a shallow ridge.

Late Holocene (~4200 cal yr BP to Present)
Laguna de la Leche was a shallow lagoon from ~4200 cal yr BP to 2000 cal yr BP, perhaps with a permanent connection to the sea, triggering an increase of the mangroves Rhizophora mangle, Avicennia germinans (black mangrove) and the mangrove associate Conocarpus erectus (buttonwood) (mangrove associates are plants that occasionally occur in intertidal sediments but are also found in terrestrial environments) (Peros et al. 2007a). The early stage of lagoon
development (4000 – 2800 cal yr BP) at site SC01 in southeastern Cuba was a shallow polyhaline to euryhaline system inferred by high abundances of four *Quinqueloculina* species, a foraminifera common in high salinity environments (Peros et al. 2015). The presence of high percentages of black mangrove pollen reinforces the foraminiferal data that suggest high salinity levels occurred since black mangroves prefer salinities exceeding 15 ppt (Peros et al. 2015).

Sediment records from two lagoons on the southwest coast of Cuba, Punta de Cartas (PC) and Playa Bailen (PB), began at 4000 cal yr BP, corresponding to the inception of the lagoon at site SC01 (Gregory et al. 2015). The *Ammonia–Quinqueloculina* foraminifera assemblage between 4000 and 3000 cal yr BP at site PB indicates salinities ranging from polyhaline (18–30‰) to euhaline (30–35‰) conditions (Gregory et al. 2015), comparable to the salinities found at site SC01 (Peros et al. 2015). There are no foraminifera present from ~3000 yr BP to ~2300 yr BP at site PB and from ~3500 yr BP to ~2500 yr BP at site PC, suggesting a harsher anoxic environment with low salinities (Gregory et al. 2015).

At site SC01, the period from 2800 to 2000 cal yr BP is initially characterized by salinities ranging from oligohaline to normal marine salinities (Peros et al. 2015); at Playa Bailen and Punta de Cartas, foraminifera assemblages indicate a shift to a more marine polyhaline environment from ~2300 yr BP to ~1400 yr BP and from ~2500 to 1500 yr BP, respectively (Gregory et al. 2015). At 1400 yr BP, a higher diversity of foraminifera at site PB indicates a shift to marine salinities (euhaline to metahaline range, 30–40‰) which persisted to the present day (Gregory et al. 2015).

Mangrove deposits had surrounded Laguna de la Leche and separated it from the ocean by ~1700 cal yr BP (Peros et al. 2007a). Extensive mangrove development characterizes the period from 1700 cal yr BP to the present, and an increase in δ¹⁸O values suggests greater evaporation, and thus a drier environment (Peros et al. 2007a, b). Conversely, site SC01 was likely fresher than present from ~1000 to ~700 cal yr BP as indicated by a decrease in *Quinqueloculina* (tolerant to high salinities) and an increase in *Ammonia tepida* (tolerant to lower salinities) species (Peros et al. 2015), unlike at sites PB and PC which recorded less input of freshwater (Gregory et al. 2015).

Finally, Gregory et al. (2015) used XRF data as a proxy for rainfall in the PB and PC records. Sediment titanium (Ti) concentrations, used to infer the amount of terrigenous input into an aquatic system, are high at 4000 yr BP and progressively decrease, with a distinctive decline
recorded at both sites from 1200–1100 yr BP, indicating drier conditions and less freshwater entering the lagoons at this point (Gregory et al. 2015). Similarly, a speleothem studied by Fensterer et al. (2012), from the Dos Anas cave system, presents high-resolution $\delta^{18}$O values over the last 1300 years. The speleothem record was strongly correlated to the Atlantic Multidecadal Oscillation for the last 1300 yr BP and recorded dry conditions during cold phases in the North Atlantic (such as the LIA), suggesting teleconnections between the northern Caribbean and the North Atlantic climate during the late Holocene (Fensterer et al. 2012).

### 1.4.4 Summary

The paleoenvironmental records from Cuba generally reflect a shift to drier conditions from the middle to late Holocene. Variations in oxygen isotopes, foraminifera assemblages, and Ti from three different locales support this trend. A southward shift of the ITCZ could be part of the explanation for reduced late Holocene precipitation in Cuba since it is one of the main drivers of precipitation on the island.

The few published pollen records for Cuba are restricted to mainly the middle and late Holocene, have low temporal and taxonomic resolution and may have dating problems. Additionally, no charcoal records have been developed for Cuba. Thus, additional records are needed that cover the early (as well as middle and late) Holocene, have high temporal and taxonomic resolution, and better age-depth models. Analysis of the sediments from Cenote Jennifer will help fill these gaps.
Chapter 2: Study Area and Methodology

2.1 Study area

2.1.1 Geology

Cuba is the largest and most geologically complex island in the Caribbean (Figure 1a). The Sabana-Camagüey Archipelago spans much of the north coast of the Cuban mainland. It spans 465 km and is comprised of cays which developed on coral and limestone during the early Quaternary (Alcolado et al. 1998; Alcolado et al. 2007). The Sabana-Camagüey Archipelago sustains marine and terrestrial habitats which include flora and fauna with a high level of endemism (Alcolado et al. 2007). The mean elevation of the Archipelago is approximately 5 m above sea level (Alcolado et al. 2003). To the north of the cays is the Old Bahamas Channel, to the south the archipelago is separated from the mainland by a longitudinal tectonic depression which presently supports a network of shallow hypersaline lagoons (Alcolado et al. 1998; Alcolado et al. 2007). Fore-reefs, a type of reef which is closest to the open ocean, fringe the Archipelago to the north (Alcolado et al. 2003).

Cayo Coco is the second largest cay within the Archipelago with an area of 370 km² (Alcolado et al. 1998). It is subdivided into its own carbonate shelf facies belonging to the Bahamas Platform represented by Aptian (125-113 Ma) through Turonian (94-90 Ma) deep-water limestone (Iturralde-Vinent 1994). Cayo Coco has been tectonically stable throughout the Holocene (Iturralde-Vinent 1994). The most recent important tectonic change associated with Cuba is the displacement occurring along the Swan and Oriente strike-slip fault systems on the south-eastern portion of the island of Cuba, at the northern boundary of the Caribbean plate, however, this movement has had no effect on the tectonic position of Cayo Coco (Iturralde-Vinent 1994; Calais et al. 1998). Most of the soils of Cayo Coco are shallow and poorly developed, having formed on limestone (Borhidi 1996; Alcolado et al. 2007). The study site, Cenote Jennifer, is located in exposed limestone on the northeast of Cayo Coco (Figure 1b, c).

2.1.2 Description of Cenote Jennifer

Cenote Jennifer (22° 31’ 50.40” N, 78° 22’ 57.40” W) is a dissolution cenote situated 2 km inland from the Old Bahamas Channel. The surface of the surrounding limestone is on average 7 m above sea level. Its formation likely occurred when relative sea level was lower during Pleistocene glacial periods and acidic rainwater infiltrated crevices and fractures in the
The rock surface surrounding Cenote Jennifer dips from the southwest to the northeast by approximately 8°, resulting in a difference of elevation of the basin edge of approximately 4 m along a southwest to northeast gradient (Figure 2). Cenote Jennifer has a surface area of approximately 400 m² with a total depth of 17 m from the highest point of the surrounding rock surface to the sediment-water interface. The water depth ranges between 9 m near the edge of the cenote to 15 m at its centre.

The vegetation directly surrounding the cenote is characterized as a thorny limestone shrubwood, consisting of *Picrodendron baccatum* (Jamaican walnut), and *Bursera simaruba* (gumbo-limbo) trees and a shrub layer of *Buxus spp.*, *Randia spp.* and *Croton spp.*, while approximately 50 m to the north is a shallow hypersaline lagoon fringed by *Avicennia germinans* and *Conocarpus erectus* (see Appendix D for list of common names of species discussed).

Water chemistry measurements made with a Hanna multiparameter meter in June 2014 show that the Cenote Jennifer water column is highly stratified. Salinity varies from mesohaline conditions (~12 ppt or ~21600 µS cm⁻¹) at the water surface to polyhaline conditions (~18.3 ppt or ~30000 µS cm⁻¹) near the base of the cenote (Figure 3). The dissolved oxygen concentration indicates that DO is ~3 ppm in the upper 6 m and abruptly drops to almost 0 ppm from 6 – 10 below the water surface. Thus, Cenote Jennifer has an anoxic bottom from a depth of approximately 8 m downward (Table 1, Figure 3), suggesting that the potential for bioturbation is limited. In June 2014, the temperature of the water column ranged from ~ 30.5°C at the surface to ~ 14°C at the bottom, and the pH averaged 6.9 throughout the column, being more alkaline at the top (7.3) and more acid at the bottom (~6.4) (Table 1).

### 2.1.3 Climate of Cuba and Cayo Coco

Under the Köppen climate classification system, Cuba has a tropical wet and dry climate (Aw). The climate of the Caribbean is highly influenced by the El Niño-Southern Oscillation (ENSO), and the positions of the Intertropical Convergence Zone (ITCZ), and the Azores-Bermuda (A-B) subtropical high-pressure system. During ENSO years, Cuba experiences an increase in sea level of 0.20-0.29 cm yr⁻¹, an average sea surface temperature increase of 0.13°C, and associated seawater warming (Alcolado et al. 2003). Long-term variations in moisture availability are tied to the intensity and position of the ITCZ (Hodell et al. 2005; Taylor et al. 2012; Fensterer et al.
2013). The shift in the position of the ITCZ is caused by changes in solar radiation as well as sea surface temperature gradients (Saenger et al. 2009; Fritz et al. 2011). In July to August the ITCZ is positioned at approximately 15°N, bringing increased rainfall and strengthened winds in the northern Caribbean. As it shifts southward to approximately 15°S from December to January, precipitation decreases and winds weaken (Fritz et al. 2011; Taylor et al. 2012). The A-B subtropical high-pressure system controls the intensity of the trade winds (Alcolado et al. 2007) and determines the direction of hurricane tracks, with a more northerly A-B subtropical high directing hurricanes over the northern Caribbean (including Cuba), and a more southerly position directing hurricanes toward Central America and the Gulf of Mexico (Liu and Fearn 2000). Given that the intensity of the hurricane season strongly affects the amount of precipitation received in Cuba (Ricklefs and Bermingham 2008) the position of the A-B subtropical high plays a large role in influencing inter-decadal climate variability in the region.

The average monthly temperature of Cayo Coco varies from 23.3°C in January to 28.7°C in July. Mean annual precipitation is 1076 mm based on a record from 1985 to 1990 (Alcolado et al. 1998). The rainy season is from May to October, with the highest rainfall occurring in September and October and the dry season is from November to April (Alcolado et al. 1998). Due to its location off the north coast of Cuba, westerly winds predominate on Cayo Coco, while ocean currents are easterly (Alcolado et al. 2007). The tides on the ocean side of Cayo Coco are semidiurnal with a maximum range of 1.2 m (Alcolado et al. 1998). Hurricanes affect Cayo Coco approximately once every 6.6 years, usually from August to October. The last high-intensity hurricane to cross Cayo Coco was in 1932 (Alcolado et al. 2007). The 1932 Cuba hurricane, also called the Santa Cruz del Sur Hurricane, made landfall November 9th in the south of the province of Camagüey as a category 5 on the Saffir–Simpson hurricane scale. Sustained winds were 135 knots (kt) (or ~250 km hour⁻¹), 140 kt at landfall and gusts of 180 kt with winds extending as far as 65 km from the centre (Pielke et al. 2003). Most damages reported were from cities on the mainland of central Cuba and were associated with high winds. There is no data to indicate what impacts the hurricane had on the island of Cayo Coco.

2.1.4 Vegetation of Cuba and Cayo Coco
Cuba has high plant diversity and is home to more than half of the Caribbean’s endemic plants (Borhidi 1996; Alcolado et al. 2007). Borhidi (1996) divided Cuba into six ecoregions: (1) Dry
forest, including evergreen forest, semi-deciduous forest, mixed semi-deciduous (known locally as mogote), wet sclerophyllous low forest (known as charrascal), dry thorny limestone shrubwood (known as manigua), and dry sclerophyllous low forest (known as cuabal); (2) Moist forest, including true rain forest, mountain rainforest, mountain rainforest in laterite soils, and cloud forest; (3) Wetlands, including grass and tree dominated; (4) Mangrove, consisting of various assemblages of mangrove species, wetland forest, marsh, peatland, sedge marsh, riparian swale, riparian forest, aquatic vegetation, coastal dune, as well as marine environments such as seagrass beds and coral reef; (5) Cactus scrub including coastal scrubland, sub-coastal scrubland, coastal thorny semi-desert, coastal sclerophyllous scrubland, and rocky coastal scrubland; and (6) Pine forest, the only ecoregion in which the upper story is dominated by one species, the Caribbean pine tree (Pinus caribaea), with various other species controlled by soil type found in the brushy understory (Borhidi 1996).

Two main vegetation types are present on Cayo Coco. The first is a dry evergreen forest type mainly consisting of dry thorny limestone shrubwood known as manigua, a local term often used for secondary shrubwood developed after logging (Borhidi 1996; Alcolado et al. 2007). The characteristic tree species include Picrodendron baccatum, Bursera simaruba, Lysiloma bahamense, Thrinax radiate, Cordia leucosedestena, and Thounia pseudopunctata (Borhidi 1996). The shrub layer contains Croton lucidus, Jacquinia berteroi, Randia spinifex, and Savia species, among many others. Some common succulents are Agave underwoodii, Melocactus harlowii, and Harrisia fernowii. There are also herbs and drought-tolerant epiphytes and lianas: Tillandsia circinnata, Tillandsia balbisiana, Mesechites rosea, Passiflora santiaganaa, Jacquementia jamaicensis and Morida royoc (Borhidi 1996). The second vegetation type is mangrove forest vegetation. In the intertidal zone, Rhizophora mangle forms a belt between low and mean tide levels (Borhidi 1996). Avicennia germinans is usually dominant between mean and high tide levels, however, some stands are intermixed with Laguncularia racemosa (white mangrove). Avicennia is often accompanied by other species, such as Acrostichum aureum. In the uppermost intertidal zone pure stands of the extremely salt resistant Conocarpus erectus can often be found (Borhidi 1996).
2.2 Methods

2.2.1 Field methods

A 2.6 m long sediment core (core CJ01) was recovered from Cenote Jennifer in December 2011 by SCUBA divers in 5 sections using a Russian Peat Corer. The watery uppermost sediments containing the mud-water interface were collected in two push cores of 24 cm (core CJ01 D0) and 26 cm (core CJ02 D0) length. The mud-water interface cores were then extracted on site in 1-cm intervals, and each sample was placed in a ziplock plastic bag for return to Bishop’s University. The CJ01 core was used for exploratory analysis of the cenote sediments and both cores CJ01 and CJ02 were used for lead-210 dating. In June 2014, a 3.3 m long core (core CJ03) was retrieved from Cenote Jennifer using a Livingston piston corer (Livingstone 1955) from a floating platform positioned in the centre of the cenote and anchored with rope to trees on the bank at water level (Figure 4). The core was recovered in 4 successive drives until impenetrable substrate (limestone) was encountered. The core drives were wrapped in plastic wrap and aluminum foil and enclosed in halved ABS plastic pipes for return to Bishop’s University. In the laboratory, the cores were kept in a refrigerator at approximately 6°C. Cores CJ01, CJ02, and CJ03 were all collected within 1 m of each other.

The perimeter of the cenote was mapped using a metered rope and compass due to the fact that hand-held Global Positioning Systems are not permitted or available in Cuba. A stationary point on the perimeter of the cenote was chosen, and from this location, a metered rope was extended to the opposite side of the cenote. At each degree, the distance in meters from the stationary point to the opposite side of the cenote was recorded. This was done at two stationary points on the southeast and southwest corners of the cenote in order to record the entire perimeter. The recorded lengths and degrees were then transcribed to paper and the points joined to create a perimeter map (Figure 1d).

A Hanna Instrument 9828 Multiparameter was used to measure the water chemistry characteristics of the cenote. After calibration in the field, measurements were taken at 55 cm intervals throughout the water column at 4 locations in the cenote, including the coring location (Figure 1d). Variables measured included temperature, pH, oxidation-reduction potential, dissolved oxygen, conductivity, total dissolved solids, salinity, density of seawater, and pressure.
2.2.2 Laboratory methods

2.2.2.1 Chronology

Lead-210 and 14C analyses were used to produce a chronology for the Cenote Jennifer sediments. Cores CJ01, CJ02 and CJ03 were stratigraphically correlated to generate a combined age-depth model for cores CJ01, CJ02, and CJ03 (Figure 5). The sediments of Cenote Jennifer have distinct laminations that enabled an extremely reliable stratigraphic correlation of all three cores. Nine bulk sediment samples from the upper 20 cm (alternating samples 1 cm thick from 0 to 5 cm and then every 5 cm until 20 cm) of core CJ02 were sent to Flett Research Limited (Winnipeg, Canada) for 210Pb dating. The base year from which 210Pb was calculated was 2011, the year core CJ02 was extracted. The sediment accumulation rate exhibits some variability over the length of the core, therefore the Constant Rate of Supply model was used to create an age vs. depth model for the upper 20 cm of core CJ02.

Fifteen samples consisting of leaves, sediment, wood, and a piece of bark from core CJ01 were sent to Beta Analytic (Miami, Florida) for AMS 14C dating. Nine samples consisting of small twigs, a leaf, and a piece of bark from core CJ03 were sent to DirectAMS (Seattle, Washington) for AMS 14C dating. The radiocarbon dates were calibrated using the package CLAM 2.2 (Blaauw 2010) and the IntCal13 dataset (Reimer et al. 2013). An age-depth model was plotted combining the 210Pb and 14C dates using the package CLAM 2.2 (Blaauw 2010) for R software (version 3.1.2, R Development Core Team, 2014). A linear interpolation was used between data points to generate age estimates for each depth interval.

2.2.2.2 Pollen Analysis

In the laboratory, the cores were split longitudinally using a thin wire. One-half of core CJ03 was archived. For pollen analysis, the other half was sampled every 5 cm throughout using core CJ01 from 0 – 60 cm and core CJ03 from 60 – 303 cm. A trial batch of samples was initially processed using a standard pollen processing protocol (Faegri and Iversen 1989). However, high amounts of organic detritus and clumped organic matter obscured the pollen grains. The standard pollen processing protocol was modified (see Appendix B for protocol) following information provided by other palynological studies in the Caribbean (Slayton 2010) and discussions with other experts in Caribbean palynology (Sally Horn, personal communication, August 2014).
One cubic centimeter of sediment was used for each sample. The samples were first sieved over 250 µm nylon mesh to remove shells and other large carbonate material, treated with dilute hydrochloric acid (HCl) to remove carbonates, treated with potassium hydroxide (KOH) to remove humic acids, sieved through 125 and retained on 10 µm mesh to remove coarse particles and clay, treated with glacial acetic acid and acetolysis to remove cellulose, treated with sodium metaphosphate (Na$_2$O$_3$P) to disaggregate the residue, and evaporated using tert-Butyl alcohol before being mounted on slides in silicone oil. One Lycopodium tablet containing a known number of exotic marker spores (1 tablet = 20848 ± 3457 spores) was added to each sample to determine concentrations and influx of pollen, spores, and charcoal on slides as described by Faegri and Iversen (1989). The KOH and Na$_2$O$_3$P treatments were added to the protocol as they produced aliquots that were clearer, had less obscuring organic matter, and were easier to count. Certain thin walled pollen grains (such as the Arecaceae family) may have been affected by these stronger treatments and thus the percentages of certain taxa may be underestimated. A minimum of 300 pollen grains and spores were counted for most samples, but those with low pollen concentrations were counted to a minimum of 100 grains where possible. Microscopic charcoal and dinoflagellate cysts were counted alongside pollen in the same transects. Particles were classified as charcoal only if fragments were black, completely opaque, and angular (Patterson et al. 1987; Clark 1988). Individual charcoal particles were counted to a minimum size of ~5 µm. Dinoflagellate cysts concentrations were determined using the known number of Lycopodium marker spores (Mertens et al. 2009). The differential preservation and possible degradation of dinoflagellate cyst was considered negligible due to the anoxic nature of the basin, and the good resistance or moderate sensitivity of the species found in the core (Mertens et al. 2009). Dinoflagellate cysts were identified according to Zonneveld and Pospelova (2015), Candel et al. (2012) and Mertens et al. (2013). Identifications were also aided and confirmed based on advice from experts in the field (Andrea Price and Vera Pospelova, personal communication, July 2015).

Several non-pollen palynomorphs (NPP) were recorded alongside the pollen, charcoal, and dinoflagellate cysts. However, the focus of this thesis was on vegetation reconstruction, and due to the chemical processing procedure required to isolate the pollen, counts of other NPPs are considered to be unreliable. General observations of NPPs noted a possible Pediastrum-like NPP in several samples (from 237 to 273 cm), whereas Glomus (a genus of fungi), and foraminiferal
test linings were also present throughout the core. Various fungal spores and three and two-celled ascospores were also recorded throughout the core, some of which were tentatively identified as *Neurospora crassa* and *Podospora*-type. NPPs were provisionally identified using published material from Chmura et al. (2006), Medeanic et al. (2008), Montoya et al. (2010), Cook et al. (2011), and van Geel et al. (2011).

The bottommost six samples of the core (from 276 to 303 cm) contained almost no pollen. A full slide was scanned from each sample, but based on the low pollen counts, it was decided that counting a second slide would not yield substantially higher pollen counts. Pollen was counted and identified at 400x magnification under transmitted light. Pollen grains were identified to the lowest possible taxonomic level using pollen reference collections from Grenada, Trinidad, and The Bahamas, as well as published keys from Palacios Chávez et al. (1991), Willard et al. (2004), Roubik and Moreno (1991), and the online *Key to the Pollen of The Bahamas* (Snyder et al. 2007). Identifications were also aided and confirmed based on advice from experts in the field.

Caribbean palynological studies were used to determine common conventions for reporting pollen types. For this reason, the Asteraceae family was grouped into short spine grains versus long spine grains. Likewise, certain pollen grains were identified based on the abundance of a specific plant found and the lack of producers of similar pollen. This was done primarily for *Iva spp.* (lack of *Ambrosia* on Cayo Coco), and *Typha domingensis* (lack of *Sparganium* in Cuba, and monad pollen grain).

### 2.2.2.3 Loss on Ignition and Magnetic Susceptibility

The proportion of organic matter (OM), calcium carbonate (CaCO₃), and silicate material (SiO₂) in the core was determined using a loss on ignition (LOI) procedure. The loss on ignition protocol followed Dean (1974) and Heiri et al. (2001). One cubic centimeter of sediment was sampled throughout the entire core at continuous 1-cm intervals. The samples were dried at 105°C for 14 hrs, and then allowed to cool in a desiccator before being weighed. They were then placed in a muffle furnace at 550°C for 2 hrs where the OM was combusted to ash and carbon dioxide. The LOI was then calculated using:

\[
\text{LOI}_{\text{OM}} = \left(\frac{\text{DW}_{105} - \text{DW}_{550}}{\text{DW}_{105}}\right) \times 100
\]
where LOI\textsubscript{OM} is the percent organic matter in the sample as a function of its dry weight (DW stands for dry weight of either 105°C or 550°C) in grams. Ashed samples were then combusted at 950°C for 2 hrs, cooled in a desiccator and weighed. In this step, the carbon dioxide is evolved from carbonate leaving calcium oxide (CaO), and LOI is calculated using:

\[
\text{LOI}_{\text{CaCO}_3} = \frac{((\text{DW}_{550}-\text{DW}_{950})/\text{DW}_{105}))/0.44*100}
\]

where LOI\textsubscript{CaCO\textsubscript{3}} stands for the percentage of carbonates in the sample as a function of its weight, and DW stands for dry weight of either 105°C, 550°C, or 950°C, all in grams. To calculate the weight of carbonates, the sample is divided by 0.44 to account for the fraction of CO\textsubscript{2} in CaCO\textsubscript{3} (Dean 1974). The loss of weight between the 550°C and 950°C burns is the amount of CO\textsubscript{2} evolved from carbonate materials, and the correction of dividing by 0.44 adjusts for the left over CaO. The final step was to calculate the residual from burning at 550°C and 950°C, using the following equation:

\[
\text{LOI}_{\text{Si}} = (100-(\text{LOI}_{\text{OM}}+\text{LOI}_{\text{CaCO}_3}))
\]

where LOI\textsubscript{Si} stands for the ash remaining after burning at 550°C and 950°C as a percentage. This was assumed to be silicate material. Now:

\[
(\text{LOI}_{\text{OM}}+\text{LOI}_{\text{CaCO}_3}+\text{LOI}_{\text{Si}}) = 100,
\]

assuming that all the material burned off in each sample is accounted for.

Magnetic susceptibility was measured at 1 cm increments on the whole core using a Bartington probe MS2C Sensor, following a protocol by Dearing (1999). The measurements of each core section were repeated four times. As the working environment can affect the measurements taken due to the magnetism of laboratory materials, each of the four measurements was performed in the same space that had been predetermined to minimize the amount of external magnetic measurements (Dearing 1999).

2.6.3 Data analysis

Zonation of the pollen diagram was undertaken both quantitatively and visually. First, stratigraphically constrained cluster analysis (Chord distance metric) was used in the program PAST to define levels with similar pollen assemblages (Hammer et al. 2001). The raw counts of all pollen taxa and no weighting were used for this analysis. Following this, the zones were
grouped visually to reduce their number and facilitate interpretation. To estimate pollen (and hence plant) diversity, Shannon’s Diversity Index was calculated in PAST on the pollen taxa, excluding the bottommost six samples, where pollen counts below 100 were obtained (Hammer et al. 2001).
Chapter 3: Results

3.1 \(^{210}\)Pb and \(^{14}\)C Chronologies

Lead-210 activities for nine sections of core CJ02 were obtained for the upper 20 cm of the core and are listed in Table 2. The values show an approximately exponential decrease in unsupported \(^{210}\)Pb activity as a function of depth. A linear regression model was initially applied to the logged activity which assumed that the \(^{210}\)Pb input and sedimentation rate were constant. Since these assumptions were false (sedimentation rate varied), the model could not be applied to the whole of core CJ02; however, it was applied to sections 0-17 cm where the sedimentation rate was relatively constant. The Constant Rate of Supply (CRS) model assumes a constant \(^{210}\)Pb input and that the core is long enough to include all of the measurable atmospheric \(^{210}\)Pb, but allows the sediment supply to vary, which is often the case in lake systems (Appleby 2008). The CRS model was applied assuming section 19-20 cm were below background level, and an age of 98.7 yrs was estimated for the 12-17 cm section. This was different from the 81.2 yrs age predicted by the linear regression model (Table 2). The good regression fit \((R^2 = 0.9899)\) suggests that some sediment may be missing from the core between sections 15 and 20 cm. This could arise if there was a hiatus in sedimentation at some time during the last 140 years, although it is unclear what could have caused this. If this were the case, it would produce a core with an incomplete \(^{210}\)Pb history which could not be properly handled by the CRS model. However, it is possible to calibrate the CRS model against the linear regression model, and therefore allow the CRS model to be used for the core history. The total atmospheric \(^{210}\)Pb input \((\text{Bq cm}^{-2})\) required in the CRS model calculation was chosen \((0.19 \text{ Bq cm}^{-2})\) such that the CRS model average sedimentation rate in sections 0-17 cm exactly matches the average accumulation rate \((0.0219 \text{ g cm}^{-2} \text{ yr}^{-1})\) calculated by the linear regression model. Once the CRS model was calibrated, it was used to calculate ages for sections 0-17 cm. The CRS model was preferred for the age-depth model (Figure 6) since it provides accurate age predictions at the bottom of each section, even though the sediment accumulation rate is changing with time. This does not, however, rule out the possibility of a hiatus; it only allows for better age estimation by combining the linear and CRS models.

Fifteen radiocarbon dates were obtained from cores CJ01 and CJ03 (Table 3). The calibrated radiocarbon ages display a generally linear trend when plotted against depth (Figure 7), with the most distinct changes in sedimentation rate occurring at ca. 1100 cal yr BP to the
present day, and between 4011-3883 cal yr BP (Figure 7). The lower part of the core, from 277-100 cm depth (9013-1100 cal yr BP), had a relatively slow sedimentation rate. A basal radiocarbon date of 9005 ±37 $^{14}$C yr BP was obtained on a twig at 277 cm depth. The 2-sigma calibrated age range for the basal date is 8997-9013 cal yr BP, indicating that sediments began to accumulate in the cenote prior to 9000 years ago. The most recent radiocarbon date of 180 ±30 $^{14}$C yr BP (calibrated as range 1-282 cal yr BP) was obtained on a leaf at a depth of 48.5 cm. Sample CJ03D 258.5-59.5 (Direct-007623) was dropped from the age-depth model and from the calculations for sedimentation rate since it resulted in an age inversion. The material dated (a twig) could reflect contamination of the core by a storm that may have remobilized older wood.

3.2 Lithology, loss on ignition, and magnetic susceptibility
The basal sediment consists of marl (carbonate mud; Munsell 10YR 8/2) from 303-240 cm (Figure 8). There is an abrupt change at 240 cm, where organic sediments begin to appear. A large fragment of tree bark was also found at 240 cm. The organic sediment (Munsell 10YR 6/3) has whole leaves and twigs preserved in it, and distinct laminations ranging from centimetre to submillimetre in thickness are present from 240 cm to the surface. Just above the transition at 240 cm is an upward-fining siliciclastic sand layer.

From 240 to 200 cm, carbonate clay (Munsell 10YR 8/3) alternates with light brown organic-rich layers (Munsell 10YR 3/1). From 200-175 cm, organic-rich sediments dominate (Munsell 10YR 3/1), with brown laminations (Munsell 10YR 86/3-10YR 6/6) throughout. A 5 cm by 3.5 cm fragment of limestone rock is present at 177 cm. At 173 cm, shell-dominated carbonate-rich laminations (Munsell 10YR 8/3) become common and continue to the surface of the core. These laminations are interspersed with organic laminations ranging from dark brown to greenish light brown in colour (Munsell 10YR 3/1-10YR 4/3). A coarse-grained carbonate-rich layer (Munsell 10YR 7/2) is notable from 120-116 cm and is enclosed by dark brown organic sediments (Munsell 10YR 4/2). At 125 cm, 112 cm, 109 cm, 81 cm and 39 cm, light brown to reddish fine-grained layers are present, and very distinct (Munsell 10YR 6/4).

The LOI results agree well with the visual description of the lithology. LOI revealed high percentages of carbonates throughout the core (Figure 8). The highest percentage of carbonates is found from 303 to 240 cm (~95% of dry weight of core), at which point carbonates slowly decrease from 240 to 180 cm to reach their lowest percentage (~40 %) at 180 cm. Carbonates
then increase to ~85% and fluctuate around that level to the surface. As the carbonates decrease from 240 to 180 cm, they are replaced by high percentages of organic matter (OM), with a peak of ~60% at 180 cm. OM follows the inverse trend of carbonates, decreasing from 180-120 cm to a low of ~10%, then increasing slightly to ~25% and remaining around this mark except for notable peaks of ~40% from 110-105 cm and 50-40 cm. Silicates are low throughout the core, averaging ~5% except for a peak of ~20% at 170 cm.

Magnetic susceptibility ($\kappa$) values (measured on a scale of -3 to 10) in the core are low, with average values below zero (Figure 8), indicating that most of the sample is comprised of minerals with weak to negative values of magnetic susceptibility. This is to be expected since most of the sediments comprise calcium carbonate or organic matter—both of which are diamagnetic substances (repelled by magnetic fields) containing no iron (Dearing 1999). From 303 to 240 cm, the section in the core comprised of carbonate clay, values of ~-2 $\kappa$ are present. At 230 cm are the first positive values of ~1 $\kappa$. From 230-192 cm values fluctuate between -1 and 3 $\kappa$, suggesting the presence of paramagnetic minerals (minerals attracted by an externally applied magnetic field) containing some iron commonly found in rocks and soils (Dearing 1999). There is a peak of 10 $\kappa$ at 192 cm, and then a decrease back to negative values of ~-2 $\kappa$ until 165 cm. From 165-127 cm there is a gradual increase to a peak of 9.5 $\kappa$ at 135 cm, at which point it decreases fairly abruptly again to values near 0 $\kappa$ until 100 cm where it dips in the negatives again until the surface of the core.

### 3.3 Pollen, charcoal, and dinoflagellate cysts

At least 86 different pollen taxa were identified in the Cenote Jennifer record. Of these, 69 were identified to species level, and 17 could not be identified taxonomically. Of the 69 identified, 20 taxa were considered specialists (exclusive to one habitat), and the other 49 were generalists (found in various habitats). Using definitions of ecoregions outlined by Borhidi (1996), ecological information on specialist taxa from published literature (e.g., Smith and Vankat 1992, Francis 2004), and information from online herbariums (e.g., Missouri Botanical Garden, Leon Levy Native Plant Preserve, Smithsonian Tropical Research Institute's Herbarium), six vegetation communities were identified as having occurred near Cenote Jennifer during the period spanning the Cenote Jennifer record. The succession of these six communities was
established using mainly specialist species and some generalist species found in the Cenote Jennifer record (Figure 9) (See Appendix C for complete pollen diagram).

The 71 levels in the pollen diagram (Appendix C) cover the period from 9013 cal yr BP to -53 cal yr BP (2003 CE) and form 6 zones.

Zone 0 (303-276 cm, >9000-8950 cal yr BP) has almost no pollen present, and for this reason, is not considered a pollen zone. Only Poaceae and Swartzia spp. (~2%), are present at this level and only 1-5 grains of each were identified (see Appendix D for list of common names of species discussed). Pollen influx is very low. Shannon’s diversity index (SDI) is 0 in this zone.

Zone 1 (276-240 cm, 8950-7600 cal yr BP) has high percentages of Typha sp. and Poaceae (~50%). Several other taxa are present, notably the shrub Buxus glomerata-type (~20%), Senna sp. (~10%), Diospyros sp. (~5%) and Swartzia spp. (~10%). Pollen influx is still low in this zone, although it begins to increase at the transition to zone 2. The SDI is also low, around 1.5.

Zone 2 (240-207 cm, 7600-6500 cal yr BP) is marked by an increase in B. glomerata-type to almost 60%, and an abrupt drop of Typha sp. to 0%. Poaceae decreases to ~25%. The first appearance of Picrorhiza baccata is in zone 2 around ~210 cm where it reaches a peak of almost 80% with a corresponding drop of B. glomerata-type to ~15%. B. glomerata-type quickly recovers to ~40% at 188 cm, making P. baccata decrease to ~10%. Other taxa, indicative of a dry scrubland forest, first appear such as Capparis spp. (~15%), Xylosma spp. (~10%), Solanum spp. (~3%), and Malpighia cubensis (~2%). There is more fluctuation in the pollen influx in zone 2, with two distinct peaks of ~2300 grains cm⁻² yr⁻¹. The SDI remains close to 1.5, but decreases midway in the zone to 0.9, coinciding with a high of Buxus glomerata-type.

Zone 3 (207-185 cm, 6500-5000 cal yr BP) is a zone which is alternately dominated by B. glomerata-type and P. baccatum. The latter reaches ~80% in most of zone 3 until it decreases to ~10% and is replaced by B. glomerata-type which reaches ~50% at the transition between zone 3 and 4. Poaceae is also present reaching ~10-15% throughout, and Swartzia spp is present (~5%). Of note is a spike in trilete fern spores, the highest recorded in the profile at 200 cm reaching almost 15%. Pollen influx remains fairly low throughout this zone, still around ~2300 grains cm⁻²
2 yr⁻¹, and decreases at the transition to zone 4. The SDI reaches its lowest level in zone 3, ~0.7. The low diversity coincides with high *P. baccatum*.

Zone 4 (185-128 cm, 5000-2500 cal yr BP) is characterized by the first appearance of microscopic charcoal and dinoflagellate cysts. Dinoflagellate cyst concentrations, composed of *Spiniferites sp.* and a spiny brown cyst provisionally identified as *Protoperidinium fukuyoi*, are high from ~178 to 172 cm. Concurrent to the dinoflagellate cyst peaks, charcoal is observed from 180 - 167 cm. Regarding pollen, this zone is dominated by *P. baccatum* (~70%), *Swartzia pp.* (~20%), *Phyllanthus epiphyllanthus* (~15%), Poaceae (~8%), and also the highest percentage of unidentified unknown pollen types (~40%). *P. baccatum* drops to almost 0% at 140 cm and is replaced by a combination of *Swartzia spp.* (~20%), *Xylosma spp.* (~15%), and unknowns (~40 %). There is an abrupt decline in *B. glomerata*-type at 180 cm, and it is virtually absent for the rest of the profile. A slight peak in charcoal is present at 140 cm, and two peaks in *Spiniferites sp.* are observed around ~143 cm and 133 cm. Zone 4 records a notable peak of *Spiniferites sp.* at 168 cm reaching almost 10000 cysts cm⁻² yr⁻¹. The SDI reappears at the beginning of zone 4, reaching 2 and fluctuates until it begins to increase at the end of zone 4 reaching a peak of 3.1.

Zone 5 (128-26 cm, 2500-100 cal yr BP) is dominated by mangroves and mangrove associates. *Conocarpus erectus* pollen first appears and *P. baccatum* is no longer dominant. *Conocarpus erectus* is present reaching ~50% for most of the zone except for two notable declines at 110 cm and 38 cm. The pollen of the mangroves *Rhizophora mangle* (~8%), *Avicennia germinans* (~3%), and *Laguncularia racemosa*. (~1%), first appears in zone 5. The first appearance of the mangrove fern *Acrostichum sp.* is also in this zone, with two peaks, one at 105-78 cm (~10%) and another at 38 cm. Some *P. baccatum* is still present at lower percentages (~20%), although this declines to ~3% when *C. erectus* is at its highest. *P. baccatum* briefly increases from 70 to 50 cm with a peak reaching 50%. Poaceae is also notable in this zone, remaining around ~15% except for a peak at 108 cm of almost 70%, the highest peak of Poaceae in the whole pollen profile. Several taxa appear at low percentages such as *Swartzia spp.* (~8%), *Trema spp.* (~3%), *Gymnanthes spp.* (~4%), and *Bursera simaruba* (~2%). Other grasses and herbs are also abundant in this zone, including Asteraceae (short and high spine) (~19%), Amaranthaceae (~3%), and *Senna spp.* which reappears with a maximum of nearly 25%. *Iva spp.* (~4%) is
present almost exclusively in zone 5. There are two dinoflagellate cyst maxima, one of a cyst provisionally identified as *Pyxidinopsis psilata*, and the other of *Spiniferites sp.* at 68 and 63 cm, respectively. There are also two small charcoal maxima present at 78 and 38 cm. Pollen influx is low at the start of zone 5, below 400 grains cm\(^{-2}\) yr\(^{-1}\), but slowly increasing to a peak at the transition to zone 6 reaching almost 17000 grains cm\(^{-2}\) yr\(^{-1}\), the highest influx recorded in the core. Diversity is variable fluctuating between 0.9 and 2.5.

Zone 6 (26-0 cm, 100 cal yr BP to present, 1900 to 2011 CE), the uppermost zone, is characterized by a marked increase in charcoal and *P. baccatum* (~60%) and a decrease in *C. erectus* to 5%, although it increases to 60% at the surface. Grasses (~10%) and herbs such as Asteraceae (~10%) and Amaranthaceae (~3%) are still present, as well as dry evergreen forest taxa including *Swartzia spp.* (~10%), *Trema spp.* (~3%), *Gymnanthes pp.* (~4%), and *Bursera simaruba*, the latter of which increases to ~25%, its highest percentage in the core. Pollen influx fluctuates from 17000 grains cm\(^{-2}\) yr\(^{-1}\) at the end of zone 5, then decreases to ~2000 grains cm\(^{-2}\) yr\(^{-1}\), and increases at the top of the zone to reach almost 9000 grains cm\(^{-2}\) yr\(^{-1}\). SDI continues to fluctuate from 1.5 to 2.7.
Chapter 4: Discussion

4.1 Paleoecological interpretation

This section provides an interpretation of the dominant vegetation communities in the Cenote Jennifer record, and how each changed over time based on the palynological data (see Appendix D for list of taxa found in core and common names). In the following discussion, disturbance vegetation has been identified as vegetation that thrives in areas that are repeatedly disturbed such as cleared or cropped lands, pastures, and along roadsides (Johnson and Miyanishi 2007). Pioneer vegetation consists of early successional species that colonize previously disturbed or disrupted sites (Brokaw 1985; Johnson and Miyanishi 2007).

4.1.1 Zone 0 (9050 – 8950 cal yr BP) – Early Holocene aridity

The early Holocene period at Cenote Jennifer has almost no pollen present, and as such cannot be considered a ‘true’ pollen zone, but was identified as zone 0 in the pollen diagram to facilitate discussion (Figure 9). The carbonate clay in the seven deepest samples (spanning ~9050-8950 cal yr BP), was likely an aerobic environment since at the time of deposition the cenote and surrounding area were dry due to lower sea level (Toscano and Macintyre 2003). Although pollen is more susceptible to degradation in aerobic environments (Bennett and Willis 2001), the pollen grains in these samples were in good condition, even though it is possible that more sensitive taxa were destroyed and only resistant taxa remained. This suggests that the low pollen concentration is due to low pollen production around Cenote Jennifer at this time.

4.1.2 Zone 1 (7600 - 8950 cal yr BP) – Cattail marsh (Figure 10a)

This zone represents a cattail marsh, as evidenced by the high percentages of *Typha sp.* (cattail) and Poaceae (grass) pollen which dominates the profile. The species of cattail is most likely *Typha domingensis* (southern cattail), which is found in the Caribbean (Plasencia Fraga and Kvet 1993). Cattail is often one of the first colonizers of newly exposed wet soil (Aona 2009), and *T. domingensis* normally favours fresh to slightly brackish (<5 ppt) salinity conditions (Beare and Zedler 1987). Its pollen and seeds are easily dispersed by the wind, and seeds buried in soil can survive for long periods and germinate in abundant sunlight (Aona 2009). The abundance of *T. domingensis* in Cenote Jennifer, and its light requirements suggests that Cenote Jennifer was open and that the bottom of the basin received adequate sunlight. The open cenote would have
provided the freshwater conditions required by cattails through precipitation directly into the cenote. Cattail is found today in small areas in the interior of Cayo Coco, particularly in surface depressions that hold moisture year round, often in association with grasses (Figure 11).

Cenote Jennifer’s zone 1 is similar to zone 1 at Laguna de la Leche, which also recorded high percentages of cattail at 6500 to ~4200 cal yr BP (Peros et al. 2007a). *Typha sp.* was also recorded in the Lake Miragoâne pollen record in Haiti by Higuera-Gundy et al. (1999) where it is present throughout the core in low abundance, but increases in zone P6 (550-200 cal yr BP), which was interpreted as marsh expansion that developed due to declining water levels.

Zone 1 at Cenote Jennifer is also characterized by the appearance of *Senna spp.*, a subshrub that grows in many habitats such as waterways, wetlands, scrublands, and disturbed sites (Holm et al. 1997; Palmer and Pullen 2001), thus *Senna spp.* could have been part of scrubland vegetation outside the cenote. The interpretation of scrubland vegetation is supported by the abundance of pollen of *Buxus glomerata*. This hardy shrub is generally restricted to dry areas, mainly growing in coastal thickets on limestone (González Gutiérrez 2014). The association of these two taxa likely represents the early stages of the development of an extensive thorny coastal scrubland community.

4.1.3 Zone 2 (7600 - 6500 cal yr BP) – Thorny coastal scrubland (Figure 10b)

The pollen assemblage of this zone suggests maturation of the thorny coastal scrubland vegetation community, dominated by *Buxus glomerata*, one of the most common *Buxus* species found in Cuban coastal environments (González Gutiérrez 2014). Today, *B. glomerata* grows on Cayo Coco in scrublands and coastal thickets, as well as on serpentine outcrops in other parts of Cuba (Bohridi 1996; González Gutiérrez 2014). Because *Buxus* species are ambophilous (pollinated through wind, insects, or both; González Gutiérrez 2014; Kohler 2014), it is difficult to determine whether the high percentages of *Buxus* pollen came from long distance transport. It is possible that *B. glomerata* both dominated the flora of the immediate area surrounding the cenote and grew elsewhere on Cayo Coco in coastal thickets. Surprisingly, *Buxus glomerata*-type pollen has not been reported in past Caribbean pollen studies.
4.1.4 Zone 3 (5000 - 6500 cal yr BP) – Dry evergreen forest/coastal scrubland (Figure 10c)
The appearance of *Picrodendron baccatum* could reflect the foundation of a dry evergreen forest. Today, this species is found in both established coastal scrublands and dry evergreen forest ecosystems of Cuba (Borhidi 1996), suggesting that zone 3 is a transitional habitat. This is further supported by the slight increase in *Trema* spp. and *Picramnia* spp., both of which are common in the evergreen forest (Borhidi 1996). *Picrodendron baccatum*, commonly known as Jamaican walnut, grows most often as a tree but can mature as a shrub (Esser 2010). Its pollen also is a dominant feature in palynological records in The Bahamas (Eric Kjellmark, personal communication, 2015). It may have been present around Laguna de la Leche in low percentages, having been previously identified as “Cayaponia” (Peros et al. 2007a; Matthew Peros, personal communication, 2016).

Palynological records elsewhere support the interpretation of an increase in tree pollen which corresponds to the dry evergreen forest of zone 3. Tree pollen found at Lake Miragoâne in Haiti from 6500 to 4250 cal yr BP was interpreted as representing generally moist conditions (Higuera-Gundy et al. 1999), and Laguna Saladilla, on the northern coast of Hispaniola, records tree pollen from 8030 to 5550 cal yr BP (Caffrey et al. 2015).

4.1.5 Zone 4 (5000 - 2500 cal yr BP) – Dry evergreen forest (Figure 10d)
Zone 4 is characterized by the establishment of dry evergreen forest, although a short duration (~200 year-long) increase in *B. glomerata* at the beginning of the zone suggests a short-term, temporary shift toward drier conditions allowed *B. glomerata* to expand at the detriment of *P. baccatum*. Nevertheless, *P. baccatum* dominates the remainder of this zone, and the appearance of taxa such as *Coccoloba*, *Exothea paniculata*, *Swietenia mahagoni*, *Celtis*, and *Picramnia* support the interpretation of the establishment of a dry evergreen forest around Cenote Jennifer and elsewhere on Cayo Coco. Today, dry evergreen forest habitat in Cuba is characterized by *Bucida spinose*, *Gymnanthes lucidus* (present in the Cenote Jennifer record in very small percentages), *Metopium toxiferum*, *Bursera simaruba*, *Coccoloba diversifolia*, *Swietenia mahagoni*, *P. baccatum*, and *Celtis trinervia* (Borhidi 1996). These forests have an understory of shrubs, succulents, herbs, epiphytes and lianas about 5-10 m high, and trees 12-15 m high with some palms reaching heights of 25 m (Borhidi 1996). The dry evergreen forest community found in zone 4 is similar to what would be found in dry evergreen forests in Cuba today.
4.1.6 Zone 5 (2500 – 40 cal yr BP (1900 CE)) – Mangrove zone (Figure 10e)
During this period, dry evergreen forests would still have existed on Cayo Coco, as is suggested by continuous low percentages of *P. baccatum* and other dry evergreen taxa. However, a decrease in the rate of sea level rise would have allowed the establishment of mangroves (Parkinson et al. 1994), which over time would have helped to trap sediments, stabilize the shorelines, and allow for the establishment of other mangrove species. *Conocarpus erectus* pollen dominates zone 5, and the appearance of the pollen of other mangrove vegetation suggests that mangroves would have been well established in the vicinity of Cenote Jennifer by ~2400 cal yr BP. It was not until ~500 cal yr BP that *Laguncularia racemosa, Avicennia germinans, and Rhizophora mangle* pollen first appear. This is not surprising, since *C. erectus* is the mangrove associate that normally grows farthest inland it would have been the first to establish near the site given the inland location of the cenote.

4.1.7 Zone 6 (1900 CE to present) – Secondary forest and human impact (Figure 10f)
This zone is characterized largely by evidence of human impact. Alcolado et al. (2007) reported that there were few permanent settlements on Cayo Coco until about 1920 CE when a small fishing village on the north shore was established. During the first half of the 20th century, the island was used as a fishing locale and as a site for mangrove harvests. Mangroves provide a choice wood for charcoal production (Alcolado et al. 2007). It is unclear how much of the vegetation on the island was cut, but it is believed that almost all the *C. erectus* would have been harvested to produce charcoal from the early 1900s to mid-1980s (Felipe Matos Pupo, personal communication 2014). Indeed, *C. erectus* pollen all but disappears at the beginning of zone 6, although abundances eventually increase. Charcoal fragments in this zone also peak at a level not seen anywhere else throughout the core. Land clearance would have allowed other secondary forest species, such as *Trema spp., Picramnia spp., Randia aculeata, and Bursera simaruba* to expand and their pollen percentages indeed peak during this time. Finally, a small percentage of rainforest pollen is present, but this most likely represents long distance pollen transport from the mainland.
4.2 Factors causing vegetation change on Cayo Coco

The pollen record from Cenote Jennifer permits an analysis of the causes driving long-term vegetation change on Cayo Coco. The main processes expected to cause these changes are relative sea level (RSL) rise, climate change, and human activities. In the sections that follow, these processes are discussed and weighed against the evidence from Cenote Jennifer to determine their relative importance at influencing long-term vegetation change at the site.

4.2.1 The role of relative sea level change

Evidence for past RSL change in the Caribbean comes from two main sources: inter-tidal mangrove peats and corals, both of which form at or near mean sea level, and can be $^{14}$C-dated to show change in local sea level over time. Corals, such as the species Acropora palmata, are submerged and often restricted to a depth range of $<1$ to $5$ m, whereas mangroves, typically R. mangle (red mangrove), grow in intertidal zones and thus provide a restriction for the upper limit of sea level. Combining data from both constrains the position of rising Holocene sea level positions (Toscano and Macintyre 2003).

Toscano and Macintyre (2003) synthesized a number of coral and mangrove based RSL records from the Caribbean and showed that RSL was $16$ m below its present position $9,000$ years ago, and that it rose until it reached its present level (Figure 12). Other studies from the Caribbean have indicated that late Pleistocene-Holocene RSL rise may have been punctuated by rapid catastrophic rise events, including one around $~7600$ cal yr BP, in which RSL rose by approximately $6.5$ m within a few years due to the final drainage of Glacial Lake Agassiz in North America (Blanchon and Shaw 1995).

The RSL curve in Figure 12 suggests that sea level at the beginning of the Cenote Jennifer record (ca. $9000$ cal yr BP) was $~17$ m below present level. The rise in sea level was rapid from $9000$ to $8000$ cal yr BP, reaching $~12$ m below current level by $8000$ cal yr BP. One of the consequences of a RSL position $~17$ m below its present level at $9000$ cal yr BP is that the area of Cayo Coco would have been substantially larger, and that Cayo Coco may have been connected to the mainland. The lower sea level position would have also meant that groundwater levels were substantially lower and the Cenote Jennifer basin would have been dry prior to $9000$ cal yr BP. Given the likelihood of a hydrological connection between Cenote Jennifer and the nearby ocean through one of the subterranean caverns identified by the SCUBA divers (Figure
the water level in the cenote has probably remained equivalent to or slightly above that of mean sea level once it reached the level of the cenote base. Thus, rising RSL during the Holocene was likely a key driver of water level rise in Cenote Jennifer. Indeed, a water depth of ~13 m at the core site, in addition to the core length of 2.77 m (i.e., 15.77 m, the depth of the earliest $^{14}$C date of ~9000 cal yr BP), is consistent with the Toscano and Macintyre RSL curve which shows Caribbean RSL ~17 m below present level at 9000 cal yr BP (Figure 12), validating the hypothesis of a hydrological connection between the ocean and the water level in Cenote Jennifer.

As RSL continued to rise, the water table on Cayo Coco would have increased, and by ~8700 cal yr BP Cenote Jennifer would have had permanent water in its basin, most likely from a combination of a higher groundwater table and accumulated rainfall. This would have created an opportunity for the establishment of vegetation in the basin, and around ~8700 cal yr BP marks the time when pollen (mostly *Typha sp.*) first became abundant in the core. From ~8700 cal yr BP onwards, the pollen influx increases in the core, suggesting an environment beneficial for sedimentation and pollen accumulation. It is also possible that some of the increase in pollen influx was due to pollen being transported from elsewhere on Cayo Coco by underground water transport.

The shift in core lithology and local vegetation communities around ~7600 cal yr BP may have been triggered by a catastrophic SLR event, as described above (Blanchon and Shaw 1995). The sudden increase in organic sediment coincides with a significant drop in *Typha sp.*, suggesting that rapid SLR increased the water level in the cenote, creating an environment no longer favorable for the growth of marsh vegetation. Furthermore, an increase in *Pinus spp.*, and indeterminate and unknown pollen grains supports the idea that storm surge transported various pollen taxa into the cenote. The notion of a catastrophic rise event in the core is also supported by the presence of an upward-fining siliciclastic sand layer in the core dating to ~7600 cal yr BP, since the size of the particles would have required high energy conditions to transport that material into the cenote.

By 4000 cal yr BP, RSL would have been 3-4 m below its present position (Figure 12; Toscano and Macintyre 2003). Mangroves are not present in the pollen profile until ~2400 cal yr BP, with the establishment of the dominant tree taxa switching from *Picrodendron baccatum* (common in evergreen forests) to *Conocarpus erectus* (Figure 13). The first appearance of the
pollen of *R. mangle, A. germinans, L. racemosa*, and *Achrosticum* at this time suggests continued rising sea level allowing these taxa to grow closer to Cenote Jennifer (Figure 13). The expansion of mangroves at Cenote Jennifer is also broadly consistent with that at other sites. For example, Peros et al. (2007a) reported an increase in mangroves beginning at 1700 cal yr BP at Laguna de la Leche. The difference in timing with Cenote Jennifer may be due to local differences in the systems recording the changes in RSL, as mangroves would already have been growing on Cayo Coco at an earlier period compared to in the vicinity of Laguna de la Leche (Alcolado et al. 2007).

### 4.2.2 The role of climate change

A number of proxy records of past precipitation change have been developed which inform us about the nature and timing of past climate change in the Caribbean. For example, a precipitation record from the Cariaco Basin, offshore northern Venezuela, spanning the last 14,000 years provides a detailed regional-scale picture of Caribbean climate change since the late Pleistocene. Sediment concentrations of iron (Fe) and titanium (Ti) (Figure 14) were interpreted as representing terrigenous input into the Cariaco Basin, with higher percentages of these elements denoting soil erosion during wetter periods, and lower percentages dry periods. The gradual decrease of both was attributed to the long-term southward migration of the ITCZ which resulted in a gradual drying over the northern Caribbean during the last 10,000 years (Peterson and Haug 2006). In addition, Fensterer et al. (2013) analyzed δ¹⁸O from a stalagmite collected in western Cuba, and found a wet early Holocene followed by drier conditions, and Hodell et al. (1991) recorded a wetter early Holocene followed by a drier later Holocene interpreted from the δ¹⁸O of ostracods at Lake Miragoâne, Haiti. Thus, while these records show similar overall trends, there still appears to be considerable local-scale variability throughout the Caribbean region.

The palynological data from Cenote Jennifer also provides evidence for wetter/warmer conditions during the early Holocene at Cayo Coco. The area was dominated by wetland vegetation (mainly *Typha domingensis*) in zone 1, which would support a wetter early Holocene since precipitation would have been needed to accumulate water in the cenote. The magnetic susceptibility results from the Cenote Jennifer core show very low values, suggesting diamagnetic materials were deposited in the core at this time (Dearing 1999), consistent with higher precipitation levels (Figure 14). The only parent material available in the catchment
erodible with surface runoff would have been the surrounding carbonate rocks, seen in the loss on ignition results (Figure 8).

Zone 3 represents a transition between thorny coastal scrubland and dry evergreen forests (Figure 14). The Cariaco Basin record shows a slightly decreasing trend in Ti, suggesting the start of a drying trend consistent with other Caribbean records (Peterson and Haug 2006; Fensterer et al. 2013). Interestingly, the magnetic susceptibility in zone 3 shows considerable variation at this time (Figure 8 and Figure 14), moreover, in addition to the LOI results—a spike in carbonates coupled with the presence of a large ostracode shell (Figure 8)—coincides with at least one large hurricane event inferred from a sediment core collected in the Great Bahama Bank (Figure 14) (Toomey et al. 2013). This suggests that a large hurricane may have passed Cenote Jennifer around the same time and may have deposited a large amount of non-local organic material and detritus into the cenote (Figure 14). However, dating uncertainties between both cores make it impossible to establish whether it was the same hurricane event that impacted both sites.

The beginning of Zone 4 is characterized by the first appearance of microscopic charcoal and dinoflagellate cysts (Figure 14). The appearance of dinoflagellate cysts suggests a possible change to a more saline environment in the cenote (Candel et al. 2012; Mertens et al. 2013). Records of microscopic charcoal in Puerto Rico and Hispaniola have been linked to increasing insolation (Caffrey and Horn 2014), and it is possible that the Cenote Jennifer microcharcoal evidence also reflects this (Figure 15). The Ti record from the Cariaco Basin shows a continuously decreasing trend until ~4,000 yr BP. There is a pronounced minimum around ~2,500 yr BP, consistent with a Holocene drying trend (Peterson and Haug 2006). Similarly, a drying trend was recorded using sediment Ti concentrations on the southwest coast of Cuba at two lagoons, Punta de Cartas and Playa Bailen (Gregory et al. 2015). A minimum was recorded at both sites from 1200–1100 yr BP, somewhat later than that of the Cariaco Basin, indicating drier conditions and less freshwater input.

However, the Cenote Jennifer record suggests increasing precipitation (with sustained positive values of κ indicating topsoil runoff) at the same time as the drying trend is recorded in the Cariaco Basin and southwest Cuban lagoons (Figure 14). The disagreement between Cenote Jennifer and the Cariaco Basin may be due to their locations in the Caribbean region; the Cariaco Basin is further south and could be recording lower precipitation due to a shift in the ITCZ which
would have meant an increase in precipitation in the northern Caribbean (Peterson and Haug 2006). The disagreement between Cenote Jennifer and the southwest Cuban lagoons may also be due to the nature of the deposits, as coastal lagoons would be subject to both terrestrial and marine inputs, whereas Cenote Jennifer would be confined mainly to terrestrial inputs given its location over 1 km inland. In addition, the radiocarbon dating at the southwest Cuban lagoons was done on bulk sediments that may have been susceptible to reservoir errors (Gregory et al. 2015), indicating that there may be chronological differences between the records.

Finally, the Cenote Jennifer site may record a moist LIA, as evidenced by an increase in tree species (such as *P. baccatum* and *Pinus* spp.) and a decrease in fire activity in the last 1000 years (Figure 16). An increase in tropical arboreal pollen and decrease in charcoal has previously been recorded as a possible LIA signal in lowland eastern Mesoamerica (Lozano-García et al. 2007), suggesting the region had higher moisture availability during this interval.

However, some sites in the Caribbean have recorded increased aridity during the LIA as well, consistent with a more southerly mean position of the ITCZ (Peterson and Haug 2006; Lane et al. 2011; Fensterer et al. 2012; Burn and Palmer 2013). Lozano-García et al. (2007) suggest that the potential reduction in summer precipitation was not great enough at Lago Verde to generate a moisture deficiency (and hence a change in vegetation detectable in the pollen record) since it is a particularly wet area (with a water surplus of 900 mm yr\(^{-1}\)). Areas that recorded drought conditions throughout the LIA are evident where evaporation greatly outbalances precipitation. With mean annual precipitation on Cayo Coco of \(~1076\) mm yr\(^{-1}\) (Alcolado et al. 1998), precipitation change during the LIA would only be recorded at Cenote Jennifer if the reduction in summer precipitation were great enough to create a moisture deficiency, similar to what was found by Lozano-García et al. (2007).

### 4.2.3 The role of humans

**Archaeology of Cuba**

The earliest known archaeological site in Cuba dates to \(~6000\) cal yr BP (Fitzpatrick and Keegan 2007; Cooper 2012). Cuba is thought to have been settled in three different waves of migration, although there is some contention with this model, and other possible settlement models have been proposed (Keegan 2006; Keegan and Carlson 2008; Colten et al. 2009; Cooper 2010; Cooper 2012). A map of the distribution of known archaeological sites in Cuba shows many
coastal sites, as access to water was vital for fishing as well as travel (Figure 17) (Keegan and Carlson 2008). Around ~6000 cal yr BP, the landscape of Cuba would have been considerably different due to lower sea levels. What are small islands today, like Cayo Coco, would have either been connected to the mainland or more accessible by canoe (Figure 17) (Keegan and Carlson 2008). Close to modern-day sea level would have been reached by approximately 4000 cal yr BP (Peltier 2002; Peros et al., submitted), allowing ~2000 years for the establishment of prehistoric humans on Cayo Coco and other neighboring islands of the archipelago before they were cut off by rising seas.

Even though Cuba was settled by 6000 cal yr BP (4050 BCE), these early populations would have likely been too small to have any marked impact on the vegetation of the surrounding area (Fitzpatrick and Keegan 2007). However, by ~2500 cal yr BP (550 BCE), several sites near Cayo Coco (both on the adjacent cays and mainland) were occupied by the Western Taino populations of incipient agriculturalists (Cooper 2010). These populations actively cleared land to plant crops, and may have been large enough to impact local vegetation through the burning of vegetation, thus having an impact on the charcoal record. One such example of a site is Los Buchillones, a Taino village occupied from 1220 to 1640 CE on the adjacent mainland to Cayo Coco (Peros et al. 2006). The Taino were agriculturalists who cleared the land and planted crops such as cassava, sweet potato and maize (Keegan and Carlson 2008). There are no known archaeological sites on Cayo Coco, however, this may be due more to a lack of archaeological survey rather than no prehistoric presence.

Cenotes held great importance to the indigenous peoples of the Caribbean islands and Yucatan peninsula, with these sites used both as sources of freshwater and also ritualistic activity (Keegan and Carlson 2008; Cooper 2010). Containing mostly freshwater, Cenote Jennifer would have been attractive as a focal point for human settlement on Cayo Coco, an island dominated by shallow saline lagoons. Even though no archaeological sites have been found on Cayo Coco, there are indicators in the pollen, microcharcoal, and sedimentary records that are consistent with human occupation on the island in the vicinity of the cenote. However, the evidence by itself is not sufficient to positively confirm prehistoric human activity on Cayo Coco, since microscopic charcoal, for example, can be linked to climatic change as well as human occupation (Kjellmark 1996; Caffrey and Horn 2014; Caffrey et al. 2015). Specifically, the Cenote Jennifer record presents evidence of possible prehistoric human impact as early as 850 BCE (2800 cal yr BP)
(Figure 18) occurring in three possible phases: (1) from ~850 to 50 BCE; (2) ~450 to 1350 CE; and (3) ~1850 to 1970 CE.

**Period 1: ~850 to 50 BCE (2800 to 2000 cal yr BP)**

From ~2800 to 2000 cal yr BP there is an increase in disturbance indicators, mainly *Senna* spp., *Sauvagesia* spp., Asteraceae and Amaranthaceae. *Senna* spp. is a sub-shrub that is opportunistic and grows well in disturbed sites, cropped lands and roadsides, and is well adapted to a range of soil types. Pioneer species such as *Trema* spp. that grow well in open areas and disturbed sites, are also present at this time, as are *Picramania* spp. a large shrub or small tree often found in secondary forests, which is pollinated by honeybees and insects, suggesting pollen accumulated in the sediment was locally derived. *Randia aculeata* is a species moderately intolerant of shade and grows best in open areas; it also invades abandoned and disturbed lands and is prominent in secondary forests after clearing for pastures or agriculture (Francis 2004). The presence of these taxa and a decline in species making up the dry evergreen forest habitat (including a large decrease in *Picrodendron baccatum*) suggests that the forest was cleared, possibly for agriculture. A charcoal peak around ~920 BCE also supports the idea that land was burned for clearing.

Further supporting the view of early occupation on Cayo Coco is the possible appearance of sweet potato (*Ipomoea batatas*) pollen around ~250 BCE. Several types of *Ipomoea* species are present throughout the core. However, the pollen found downcore resembles other non-domesticated *Ipomoea* species (such as *Ipomoea pes-caprae, Ipomoea indica, Ipomoea microdactyla*), based on pollen morphology. The pollen grains of *Ipomoea* around ~250 BCE are distinct and have echinate spines with conical to rounded tips on short domed bases that closely resemble *Ipomoea batatas* (see Figure 19). The presence of sweet potato pollen, if confirmed through scanning electron microscopy, would be a strong indicator of early human occupation since it is known as a cultivated species and a staple of the diet of early Caribbean populations (Keegan and Carlson 2008). In addition, another plant indicator occurs between 850 and 450 BCE, *Agave americana* (century plant), whose fibers were commonly used by the Taino to weave hammocks (Keegan and Carlson 2008). This plant may not have been cultivated per se, but its growth might have been encouraged and the plant protected for human use.
Period 2: ~450 to 1350 CE (1500 to 600 cal yr BP)
By ~450 CE the pattern of disturbance vegetation re-emerges, although the pioneer vegetation is not as pronounced. *Senna spp.*, *Sauvagesia spp.*, and Asteraceae again dominate the disturbance indicators, although the addition of *Acrostichum sp.*, a large, fast-growing fern that is opportunistic and colonizes disturbed areas, suggest the possibility of marshland or coastal areas being cleared since this species requires water or moist soils to grow (Medina 1999). The pioneer vegetation is represented mainly by *Trema spp.* and *Picramania spp.*. The absence of *Ipomoea sp.* could suggest a smaller agricultural presence or land clearance for habitation rather than agriculture. A charcoal peak is present towards the end of this phase, around ~1350 CE, after which time mainly grasses and herbs (from Asteraceae) as well as *Trema spp.* and *Picramania spp.*, suggest the start of the establishment of a secondary forest. At 900 CE, the sedimentation rate increases and stays high until the present, presumably due to land clearance and burning, an increase in precipitation, or both.

By 1520 CE the pre-Columbian populations on most islands were wiped-out as Spanish colonialists killed, enslaved and overworked the indigenous populations, and most significantly exposed them to European diseases (Keegan and Carlson 2008). The recovery of *P. baccatum* pollen occurs at 1500 CE, around the time of the Conquest, suggesting a potential depopulation of Cayo Coco. However, other taxa, such as *Trema spp.*, *Picramania spp.*, and Asteraceae persisted through this period suggesting that a mixed evergreen secondary forest was established (Figure 18). Furthermore, the disappearance of *Agave sp.* suggests that it was no longer cultivated and left to be outcompeted by other plants.

Period 3: ~1850 to 1970 CE (Historic human impact)
Lastly, a clear indication of modern human impact on Cayo Coco is recorded in the Cenote Jennifer core. From ~1850 to 1970 CE, the core records a sudden increase in charcoal, with the highest amount recorded around ~1970 CE. As mentioned, a known permanent village was present on Cayo Coco beginning in 1920 CE, composed mainly of fishers and charcoal producers (Alcolado et al. 2003). However, prior to this, the island was inhabited during the fishing season and for charcoal production a few months each year, most likely starting in the late 1800s. There are several accounts of large parts of the island being burned for charcoal production in the early to mid-1900s CE, with *Conocarpus erectus* being a prime charcoal source.
(Alcolado et al. 2003; Felipe Matos Pupo, personal communication 2014). Indeed, a sharp decrease in *C. erectus* pollen is evident around ~1900 CE, followed by its gradual re-establishment as charcoal production slowed (Figure 18).

4.3 Evaluation of factors causing changes in vegetation and implications for future research

In section 4.2, the main factors responsible for causing vegetation change on Cayo Coco during the Holocene were assessed, with a goal to evaluate their relative importance. There is evidence that RSL rise, climate change, and human activity played a role in causing vegetation change at this site, but the importance of each varied over time. The rate of relative sea level rise was most important during the early Holocene, which is not surprising given that this is when rates were highest (Figure 12). While at this time a minor role of a wetter climate could have encouraged the growth of *Typha* in the basin, RSL rise was likely the main factor at Cenote Jennifer and responsible for the transitions in early Holocene vegetation communities. Indeed, the pollen data shows essentially complete species turnover on three occasions, underscoring the importance of RSL change as a driver of vegetation change in low island karst-based environments. This has implications for vegetation communities today situated along tropical coastlines with rising sea levels; while the rate of RSL today (~3 mm yr\(^{-1}\); Nurse et al. 2014) is much less than that of the early Holocene, it suggests that tropical coastlines are still sensitive to changes in RSL position.

Climate change also likely played a limited role in causing vegetation change, although its effect was probably more important during the middle to late Holocene, and the changes to vegetation that it triggered were subtler. For example, there is some evidence for the LIA in the Cenote Jennifer record, both in the pollen percentages and in the microcharcoal counts, but additional palynological and charcoal data through this section of the core is needed to better define the timing of these changes. Further research would better define how this climate event was characterized in the Caribbean (i.e., warm/wet or cool/dry), which is the subject of much current debate (Lozano-García et al. 2007; Lane et al. 2011; Fensterer et al. 2012; Burn and Palmer 2013).

In addition, the microcharcoal record, which essentially consists of data from 5000 cal yr BP to the present, does not conclusively record the same long-term drying trend as documented elsewhere (Peterson and Haug 2006; Gregory et al. 2015), although some of the charcoal signal might be related to human activity. Given that this long-term drying is less evident in the pollen
percentages, it could mean that coastal vegetation communities in the tropics are less sensitive to long-term climate change and reflect fire activity. Generation of additional, long-term palynological records from Caribbean sites is required to answer this question.

Finally, there is strong evidence for historic human impact and some indirect evidence for prehistoric human impact at Cenote Jennifer. Both these impacts occur in the late Holocene when humans were most likely to be living near Cenote Jennifer. The data suggest that humans may have been on Cayo Coco several thousand years earlier than previously realized (Fitzpatrick and Keegan 2007; Cooper 2012; Siegel et al. 2015) and that they had a sufficient impact on the vegetation to be detectable in the pollen and charcoal records. If human activity can be confirmed through the positive identification of *I. batatas* pollen, this will have important implications for Caribbean archaeology and provide new data to help understand the diffusion of cultigens between islands. The use of paleoecological techniques has also been shown to be useful at identifying early human activity in areas where archaeological surveys have not been undertaken. Thus paleoecology can help direct archaeological studies to new locations.
Chapter 5: Conclusions and Recommendations

The thesis attempts to answer the following research questions: (1) how has the vegetation on Cayo Coco changed over the course of the Holocene?; (2) is there any evidence for human activity in the sedimentary/pollen record?; (3) what have been the main processes (i.e., sea level change, climate change, human impacts) that have caused changes in vegetation on Cayo Coco, and how has the relative importance of each changed with time?; and (4), how does the Cayo Coco record compare to other Caribbean paleoecological records? Cenote Jennifer was an excellent site to answer these questions. Changes in pollen, charcoal, dinoflagellate cysts and sediment accumulation reflect changes in relative sea level and prehistoric and human impact, as well as changes in climate, from 9000 cal yr BP to present.

Sea level rise was the primary driver of changes in vegetation from ~9000 to 5000 cal yr BP as evidenced by fossil pollen. A catastrophic rise event around ~7600 cal y BP recognized by Blanchon and Shaw (1995) also was recorded at Cenote Jennifer, supporting their interpretation of rapid sea level rise in the Caribbean. Cenote Jennifer was surrounding by an arid, low vegetation environment in the early Holocene. Throughout the early Holocene, sea level rise drove vegetation changes on Cayo Coco. The first abundant pollen signal in the core shows the establishment of a wetland within the cenote itself. An increase in the regional groundwater level caused the level of water in the cenote to increase and the vegetation of the surrounding area to shift from an arid low vegetation environment to a thorny coastal scrubland. Further changes in vegetation were identified by shifts from dry evergreen forest, with the main species *Picrodendron baccatum* dominating from ~6500 to ~2500 cal yr BP, to a mangrove and associate expansion around ~2400 cal yr BP, particularly *Conocarpus erectus* and *Acrostichum sp*.

The length of the Cenote Jennifer record makes it an important site for reconstructing past environmental changes and provides a basis for comparison to other Holocene-length Caribbean paleoenvironmental records. The Cenote Jennifer record broadly agrees with general climatic trends elsewhere in the Caribbean, such as a wetter early Holocene (Higuera-Gundy et al. 1999; Peterson and Haug 2006). However, a drying trend during the Holocene recorded at other sites such as the Cariaco Basin, is not evident at Cenote Jennifer or at other Cuban sites (see Fensterer et al. 2013; Peros et al. 2015). The coastal position of Cenote Jennifer makes it less affected by climate and more by sea-level changes and human impacts. Thus no drying trend
was clearly recorded in vegetation changes. Furthermore, microscopic charcoal data at Cenote Jennifer follows the trend of increasing insolation in the Caribbean after ~5000 cal yr BP recorded at sites such as Lake Miragoâne, Haiti, and Laguna Saladilla, Dominican Republic. Cenote Jennifer also recorded a moist Little Ice Age, unlike elsewhere in the Caribbean where this event is typically represented by dry conditions. This finding reinforces the notion that complex local responses to climate signals are present in individual island settings (Nurse et al. 2014).

Human impacts were identified by three periods of occupation near Cenote Jennifer based on the pollen of disturbance taxa, microcharcoal, and the possible appearance of Ipomoea batatas (sweet potato) pollen. These periods were identified from ~2800 to 2000 cal yr BP, ~1500 to 600 cal yr BP, and 1850-1970 CE.

This research signifies the importance and viability of using cenotes as archives of paleoenvironmental proxies. The identification of long-term paleoenvironmental changes from cenotes can fill a void in this region lacking in lakes. However, little is known of the underground hydrology connecting cenotes to each other, aquifers, and the ocean on Cayo Coco. Our understanding of water transport is limited, and it is necessary to establish a better understanding of connectivity, particle movement, and whether these are closed or open systems, as these factors can influence the paleoecological record. Furthermore, while the Cenote Jennifer core is generally well-dated, other studies from cenotes have had dating problems, such as inversions (Kjellmark 1996; Kovacs et al. 2013), which may limit chronological integrity of their sedimentary records. Despite these limitations, cenotes hold valuable information that can aid in our understanding of the importance of past climate changes in tropical regions, past changes in sea level, human occupation and archaeology.

Further research should focus on more records from cenotes, and greater high-resolution data to capture centennial-length events such as the Little Ice Age, Medieval Climate Anomaly, short-term droughts, and prehistoric land use signals. Based on the information in this thesis, it is clear that the tropics cannot be considered as a region which responds unidirectionally to change, but instead consists of complex patterns of climate and sea level variability that offers new scenarios to assess the impacts of recent and future climate changes at a more regional and island based level.

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References


Alcolado PM, García EE, Arellano-Acosta M, editors. 2007. Ecosistema Sabana-Camagüey: estado actual, avances y desafíos en la protección y uso sostenible de la biodiversidad. La Habana (Cuba): Editorial Academia.


Table 1: Water chemistry data for Cenote Jennifer.

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<th>Surface</th>
<th>Bottom</th>
<th>Mean</th>
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<td>6.45–7.30</td>
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<td>1.80</td>
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<td>23460.0–40710.0</td>
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<td>19710</td>
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<td>Pressure (mbar)</td>
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Table 2: $^{210}$Pb data for Cenote Jennifer (CJ02-D0) from Flett Research Laboratory, Winnipeg, Canada.

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<th>Extrapolated Section Depth (cm)</th>
<th>Weight of Sample Counted (g)</th>
<th>$^{210}$Po Total Activity (DPM/g)</th>
<th>Error $^{210}$Po ± 1 S.D. (DPM/g)</th>
<th>$^{210}$Po Unsupported Activity (DPM/g)</th>
<th>CRS Model</th>
<th>Linear Regression Model</th>
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<td>1</td>
<td>0-1</td>
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<td>0.97</td>
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<td>1.5-3.5</td>
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<td>3.5-5</td>
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<td>6-7</td>
<td>6-7</td>
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<td>7-8.5</td>
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<td>0.39</td>
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<td>8.5-12</td>
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<td>2.54</td>
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<td>12-17</td>
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<td>17-20</td>
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Table 3: Radiocarbon dates for Cenote Jennifer sediment profile from Direct AMS and Beta Analytic laboratories.

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<th>Sample</th>
<th>lab number</th>
<th>depth in core (cm)</th>
<th>material</th>
<th>$\delta^{13}$C</th>
<th>conventional $^{14}$C age (yr BP)</th>
<th>2σ calibrated intercepts (cal yr BP) (proportion under calibration curve in brackets)</th>
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<tr>
<td>CJ01D0 48-49</td>
<td>Beta</td>
<td>48.5</td>
<td>Leaf</td>
<td>-25.4</td>
<td>180 ±30</td>
<td>1 – 12 (0.203) 148 – 153 (0.078) 168 – 187 (0.402) 208 – 211 (0.015) 269 – 282 (0.302)</td>
</tr>
<tr>
<td>CJ03D2 58.5-59.5</td>
<td>Direct-007623</td>
<td>59</td>
<td>Twig</td>
<td>-25.5</td>
<td>153 ± 18</td>
<td>11 – 23 (0.267) 141 – 149 (0.129) 561 – 574 (0.240) 576 – 596 (0.355) 634 – 653 (0.404)</td>
</tr>
<tr>
<td>CJ01D1 29-30</td>
<td>Beta</td>
<td>74.5</td>
<td>Leaf</td>
<td>-25.4</td>
<td>630 ± 30</td>
<td>1058 – 1094 (0.480) 1101 – 1148 (0.304) 1159 – 1173 (0.216) 1995 – 2061 (0.962) 2091 – 2103 (0.038)</td>
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<tr>
<td>CJ03D3 100-101</td>
<td>Direct-007624</td>
<td>100.5</td>
<td>Twig</td>
<td>-23.7</td>
<td>1172 ± 17</td>
<td>2881 – 2911 (0.303) 2919 – 2961 (0.697) 3865 – 3927 (0.905) 3947 – 3962 (0.095)</td>
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<tr>
<td>CJ01D2 7-8</td>
<td>Beta</td>
<td>111</td>
<td>Sediment</td>
<td>-28.2</td>
<td>2070 ± 30</td>
<td>1995 – 2061 (0.962) 2091 – 2103 (0.038) 2881 – 2911 (0.303) 2919 – 2961 (0.697)</td>
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<tr>
<td>CJ01D2 41-42</td>
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<td>Leaf</td>
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<tr>
<td>CJ03D3 169-170</td>
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<td>Leaf</td>
<td>-28.6</td>
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<td>174</td>
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<tr>
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<td>Direct-007626</td>
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<td>5916 – 5941 (0.961) 5975 – 5982 (0.039) 5916 – 5941 (0.961) 5975 – 5982 (0.039)</td>
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<tr>
<td>Sample</td>
<td>lab number</td>
<td>depth in core (cm)</td>
<td>material</td>
<td>δ(\textsuperscript{13}C)</td>
<td>conventional \textsuperscript{14}C age (yr BP)</td>
<td>2σ calibrated intercepts (cal yr BP) (proportion under calibration curve in brackets)</td>
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<td>CJ03D4 210-211</td>
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<td>208.5</td>
<td>Twig</td>
<td>-27.5</td>
<td>5778 ± 31</td>
<td>6543 – 6636 (1.000)</td>
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<tr>
<td>CJ01D6 10-11</td>
<td>Beta</td>
<td>234.5</td>
<td>Wood</td>
<td>-27.6</td>
<td>6450 +/- 40</td>
<td>7327 – 7398 (0.844) 7411 – 7423 (0.156)</td>
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<td>CJ03D4 237.5-238.5</td>
<td>Direct-007627</td>
<td>238</td>
<td>Bark</td>
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<td>6558 ± 23</td>
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<tr>
<td>CJ01D6 34-35</td>
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<td>CJ03D4 279-280</td>
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<td>8068 ± 37</td>
<td>8997 – 9013 (1.000)</td>
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Figure 1: a) Location of Cayo Coco in white square in relation to Cuba. b) Location of Cenote Jennifer in white square on Cayo Coco. c) Cenote Jennifer in white square in relation to coastline. d) Perimeter map of Cenote Jennifer. Black dots denote location of cores used in this study. Hollow dots denote locations of multiparameter readings. Arrows are positioned to show the direction of the pictures in Figure 2. Caves are at 10 m water depth.
**Figure 2:** a) Cenote Jennifer, looking north from limestone outcrop, b) Looking north to lowered limestone shelf, c) Looking south to elevated limestone outcrop, d) Looking west, note exposed high limestone ledge to the left of the picture.
Figure 3: Water chemistry measurements for Cenote Jennifer. The black line denotes normal marine salinity (~52400 µS/cm) and the red line denotes a change to highly brackish conditions (~30000 µS/cm) on the conductivity plot. On the dissolved oxygen plot, the black line denotes hypoxic conditions, and the red line denotes anoxic conditions of below 0.5 µg/L, based on USGS definitions (Zogorski et al. 2006).
Figure 4: Coring Cenote Jennifer July 2014
**Figure 5:** Stratigraphic and chronological correlations of cores CJ01, CJ02 and CJ03. CJ01-D4 and CJ01-D3 were not used due to errors associated with the coring or labeling process while in the field, which were identified after radiocarbon dating results were returned.
Figure 6: CJ02-D0 lead-210 age-depth model for Cenote Jennifer, CRS Model vs. Linear Regression Model.
Figure 7: Age-depth model for Cenote Jennifer. The lithology does not rule out a possible hiatus; however, we are confident with the age-depth model which combined the linear and CRS models presented here.
Figure 8: Core stratigraphy, loss on ignition, and magnetic susceptibility for Cenote Jennifer. Note percent scale change on x-axis. Pollen zones are delimited on right.
Figure 9: Pollen diagram of vegetation communities established using specialist species. Note percent scale change on x-axis. Red line denotes 3x exaggeration multiplier on *Pinus spp* and influxes. Pollen zones are delimited on right.
Figure 10: Evolution of Cenote Jennifer. Black dash on y-axis denotes position of relative sea level.
Figure 11: *Typha domingensis* growing in a depression on Cayo Coco.
Figure 12: Toscano and Macintyre (2003) RSL curve with Cenote Jennifer basal date plotted.
Figure 13: Pollen diagram for Cenote Jennifer showing key taxa associated with SLR and dinoflagellate cyst concentrations. Note percent scale change on x-axis. Red line denotes 3x exaggeration multiplier on *Pinus* spp and influxes. Pollen zones are delimited on right.
Figure 14: Comparison of Cenote Jennifer record to other records. Percentages of pollen and plant spores grouped by source vegetation in Cenote Jennifer, with data on loss on ignition, dinoflagellate cyst concentrations, charcoal and pollen influx, and magnetic susceptibility (κ). Note percent scale change on x-axis. Red line denotes 3x exaggeration multiplier on Pinus spp and influxes. Cariaco Basin Ti data from Peterson and Haug 2006, and Bahamas grain size data from Toomey et al. 2013. Pollen zones are delimited on right.
Figure 15: Comparison of charcoal influx at Cenote Jennifer and Laguna Saladilla, Dominican Republic. Red line denotes 4x exaggeration multiplier on charcoal influxes. Pollen zones are delimited on right.
Figure 16: Pollen and charcoal evidence for the Little Ice Age at Cenote Jennifer. Red line denotes 3x exaggeration multiplier on *Pinus* spp and influxes.
Figure 17: Archaeological sites on Cuba denoted by red dots with present day shorelines outlined in black, and 6000 yr BP shorelines in green. Adapted from: Cooper 2012
Figure 18: Pollen and charcoal evidence for human occupation periods on Cayo Coco. Red and green line denote 3x exaggeration multiplier on Pinus spp, Agave spp, Ipomoea spp, and influxes.
Figure 19: Various types (1-3) of Ipomoea spp found in Cenote Jennifer core. Type 4 is the pollen provisionally identified as *Ipomoea batatas* until better resolution photographs can be taken. Grain found at 132-133 cm, ~2613 cal yr BP. Size: ~90 by 90-70 µm, note apertures and shape of spines with conical to rounded tips on short domed bases in inset ph
Appendix A. Main northern hemisphere paleoenvironment events alongside Cuban and Caribbean events discussed in the literature review. Delineation for Northern Hemisphere events were identified from Dansgaard et al. (1989) and Fairbanks (1989) for the Younger Dryas, Renssen et al. (2009) for the Holocene Thermal Maximum, Bond et al. (1997) for the Bond Events (BE), Alley et al. (1997) for the 8.2 kyr cooling event, and Mann et al. (2009) for the Little Ice Age and Medieval Warm Period (MWP). Caribbean and Cuban events are listed in the literature review section. Other abbreviations used are as follows: Olig. – Oligohaline; Polyhl – Polyhaline; Euhl - Euhaline; Mngs – Mangroves; Co – Colombia; STX –St. Croix UVI; BB, Barbados; TT – Trinidad and Tobago; CRE – Catastrophic rise event.

<table>
<thead>
<tr>
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<th>Northern Hemisphere</th>
<th>Cuban records</th>
<th>General Caribbean records</th>
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<td>Lagoon SC01</td>
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<tr>
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<td>Freshening to present</td>
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<td>Holocene Thermal Maximum</td>
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<tr>
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<tr>
<td>12</td>
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</table>

- **CRE 7.6ky**: CRE 7.6ky
- **Mngs begin, BB**: Mngs begin, BB
- **Mng**: Mng
- **Warm and wet**: Warm and wet
- **Cool**: Cool
- **Abrupt warming**: Abrupt warming
Appendix B. Modified Caribbean Pollen Processing Protocol

This is the protocol for Caribbean fossil pollen used in the Climate and Environmental Change Laboratory at Bishop’s University. Samples were processed in 15 ml Nalgene® polypropylene centrifuge tubes. The centrifuge was programmed for 5 m at 3000 RPMs.

**Sediment preparation**

1. Transfer sub-samples of 1 cubic centimeter from sediment core into 15 mL centrifuge tubes.
2. Fill tubes 1/2 way with hot distilled water, stir, pour through 250 μm coarse sieve, collecting liquid in a 600 ml labeled beaker underneath.
3. Centrifuge and decant material from the beaker back into the tube.
4. Add 1 Lycopodium tablet to each centrifuge tube as an exotic spike.
5. Add a few drops of 10% HCl, stir gently and let reaction proceed. Continue this process until tubes are filled half way.
6. Next day, keep adding HCl slowly until there is 10 mL in each tube. Stir, centrifuge and decant. Add new 10% HCl to samples that have not yet stabilized. Continue slowly adding 10% HCl and stirring until all samples have stopped reacting. Centrifuge and decant.
7. Wash 2-3 times with hot distilled water. Centrifuge and decant after each wash.

*Note: A maximum of 4 KOH washes can be done.*

8. Add 10 mL 10% KOH, stir, and place in boiling bath for 15 minutes, stirring after 5 minutes and removing stir stick. Let cool for 5 minutes, stir, centrifuge and decant. Repeat if necessary.
9. Wash 3-4 times with hot distilled water. Centrifuge and decant after each wash.
10. Fill tubes 1/2 way with distilled water, stir, and pour through 125 μm coarse sieve, collecting liquid in a labeled beaker underneath.
11. Pour contents through a 10 μm fine sieve. Transfer from fine sieve to centrifuge tube. Centrifuge and decant.
12. Add 10 mL glacial acetic acid, stir, centrifuge and decant.
13. Make acetolysis mixture by mixing together 9 parts acetic anhydride and 1 part concentrated sulfuric acid.
14. Add 10 mL to each tube and stir. Remove stirring sticks and place in boiling bath for 15 minutes. Stir after 5 minutes. Let tubes cool down for 5 minutes. Centrifuge and decant.
15. Add 10 mL glacial acetic acid, stir, centrifuge and decant. Wash with hot distilled water, stir, centrifuge and decant.
16. Add 10 mL hot 10% Sodium Metaphosphate solution to each tube. Stir well just before placing in sonicator bath for 2 minutes. Let sit for 5 minutes. Centrifuge and decant.
17. Add 10 mL hot distilled water, centrifuge, and decant for a total of 2-3 washes.
18. Add 5 drops 1% safranin stain to each tube. Use vortex mixer for 10 seconds. Add 10 mL of distilled water. Stir, centrifuge, and decant.
19. Add a few mL tert-Butyl alcohol (TBA), use vortex mixer for 10 seconds. Fill to 10 mL with TBA, stir, centrifuge, and decant.
20. Transfer to vials using a spatula and TBA. Centrifuge down vials to remove extra TBA. Evaporate rest of TBA by putting vials directly on a hotplate at a temperature between 30°C-40°C.
21. Add several drops of silicone oil. Stir with a toothpick, put on vortex mixer for 20-30 seconds. Leave vials open overnight in the fume hood to allow leftover TBA to evaporate.
Appendix C. Stratigraphic pollen diagram from Cenote Jennifer showing all taxa, unknowns, dinoflagellate cysts, Shannon’s diversity index and charcoal and pollen influxes.
**Appendix D:** Taxa found in Cenote Jennifer core. Species name in bracket denotes the most likely occurrence, based on local vegetation present.

<table>
<thead>
<tr>
<th>Family</th>
<th>Species (most likely)</th>
<th>Common Name</th>
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</thead>
<tbody>
<tr>
<td><strong>Mangroves and associates</strong></td>
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<tr>
<td>Acanthaceae</td>
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<td>Black mangrove</td>
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<tr>
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<td><em>Conocarpus erectus</em></td>
<td>Silver buttonwood, Button mangrove, Grey mangrove</td>
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<tr>
<td></td>
<td><em>Laguncularia spp (racemosa)</em></td>
<td>White mangrove</td>
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<tr>
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<td><em>Acrostichum sp</em></td>
<td>Golden leather fern</td>
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<td><em>Alchornea latifolia</em></td>
<td>Dovewood, Aguacatillo</td>
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<tr>
<td>Fabaceae Caesalpinioideae</td>
<td><em>Swartzia spp. (cubensis)</em></td>
<td>Katalox, Mexican royal ebony</td>
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<tr>
<td>Juglandaceae</td>
<td><em>Juglans</em></td>
<td>West Indian Walnut</td>
</tr>
<tr>
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<td><em>Polypodiaceae</em></td>
<td>epiphyte</td>
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<tr>
<td><strong>Disturbance vegetation and pioneers</strong></td>
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<td>Sunflower family</td>
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<td><em>Rhynchosia spp.</em></td>
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<td>Fabaceae Caesalpinioideae</td>
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<td>Sicklepod</td>
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<td><em>Tetrapterys spp.</em></td>
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<td><em>Triumfetta spp.</em></td>
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<td><strong>Bursera simaruba</strong> Gumbo Limbo, Tourist tree</td>
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<td><strong>Terminalia</strong> Chicharrón</td>
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<td><strong>Jacquemontia (pentanthos)</strong> Clustervine</td>
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<td><strong>Gymnanthes lucidus</strong> Crabwood, Oysterwood</td>
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**Thorny coastal scrubland**

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<td>Buxus glomerata type</td>
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<td>Capparis spp.</td>
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**Marshes and Coastal**

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**Pan-tropical**

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