



The Legacy of Pre-Columbian Fire on the Pine-Oak Forests of Upland Guatemala

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Mountain tropical forests of the Southern Maya Area (Pacific Chiapas and Guatemala, El Salvador, and Northern Honduras) predominantly comprise pine and oak formations, which form intricate mosaics and complex successional interactions following large-scale fire. These forests have been transformed by the peoples of the Maya civilization through practices of horticulture, agriculture, and architectural developments over thousands of years. Anthropogenic impacts and the extent of early human interaction with these upland forests is currently poorly understood. In this study we identify: (i) the natural baseline vegetation of the region; (ii) when human impact and agrarian practices began in the Maya uplands; and (iii) what impacts the Maya had on forest structure, composition, and successional regeneration. Past vegetation, anthropogenic use of fire, and faunal abundance were reconstructed using proxy analysis of fossil pollen, macroscopic charcoal, microscopic charcoal, and dung fungal spores (*Sporormiella*). Three phases of forest succession were identified from 4000B.C.E. to 1522CE that broadly overlap with the well-defined archaeological periods of (i) the Archaic (10,000–2000B.C.E.); (ii) Pre-Classic (2000B.C.E.–100C.E.); (iii) Terminal Pre-Classic (100–250C.E.); (iv) Classic (250–950C.E.); and (v) Post-Classic (950–1522C.E.). These results also include the earliest evidence for agriculture within the Southern Maya Area through presence of peppers (*Capsicum*) from 3850B.C.E. and the rise of maize cultivation (*Zea mays*) from 970B.C.E. Persistent high intensity burning driven by agricultural practices and lime production during the Late-Pre-Classic (400–100B.C.E.) to Classic Period resulted in a compositional change of forest structure c.150B.C.E. from oak (*Quercus*) dominated forests to pine (*Pinus*) dominated forests. The legacy of Pre-Columbian anthropogenically driven fire in these mountain tropical forests demonstrates the resilience and thresholds for fire driven succession. These findings are particularly relevant for addressing current land use and management strategies involving agriculture, fire, and forest management in the mountain tropical forests of the Southern Maya Area.

Keywords: fire, pine-oak forest, *Zea mays*, early agriculture, *Capsicum*, *Sporormiella*, palaeoecology, Maya

INTRODUCTION

Unlike the Amazon or boreal regions, Central America does not have large tracts of intact forests (Watson et al., 2018), and further reductions in the extent of intact forests are a concern. Potapov et al. (2017), for example, determined that forest cover declined by 13.3% in Guatemala between 2000 and 2013 C.E. Mountain tropical forests (MTF) are important for the provision of ecosystem services, particularly biodiversity and water (Martínez et al., 2009), and loss of intactness has serious implications for these ecosystem services. Given the current high international interest in the effects of human actions that cause degradation of forests and subsequent loss of ecological function, the development of long-term ecological data will provide insight on how forests were influenced by anthropogenic and natural factors during pre-history and thereby help inform potential future responses to similar actions and/or occurrences. For Central America such long-term ecological datasets are scarce and are rarely considered in modern conservation discussions (Jeffers et al., 2015). In particular, the Middle to Late Holocene (6000–2000 B.C.E.) vegetation history of the Central American uplands (>1,000 m.a.s.l.) is not well-documented but is essential to our understanding of early human impacts and prehistoric land use across the Maya Area (Neff et al., 2006). Filling these temporal and spatial gaps in knowledge is essential for understanding the function and protection of intact forests in this region and more generally.

The Maya occupied three separate areas: the Southern Uplands, and the Central, and Northern Lowlands (<1,000 m) (Figure 1). Our research area lies within the Southern Uplands, which includes the highlands of Guatemala and adjacent Chiapas (Coe and Houston, 1966). There are altitudinal gradients in temperature and precipitation, with annual mean temperatures ranging between 14 and 25°C and annual rainfall ranging between 900 and 3,700 mm per year (Kappelle, 2006). The vegetation inhabiting this upland area typically comprises tropical and subtropical mixed deciduous and coniferous forests, known as mountain tropical forest (MTF) formations, which start in the Sierra Madre de Chiapas (Southern Mexico) and extend down to Northern Nicaragua (Dinerstein et al., 2017).

PREVIOUS WORK IN THE MAYA AREA

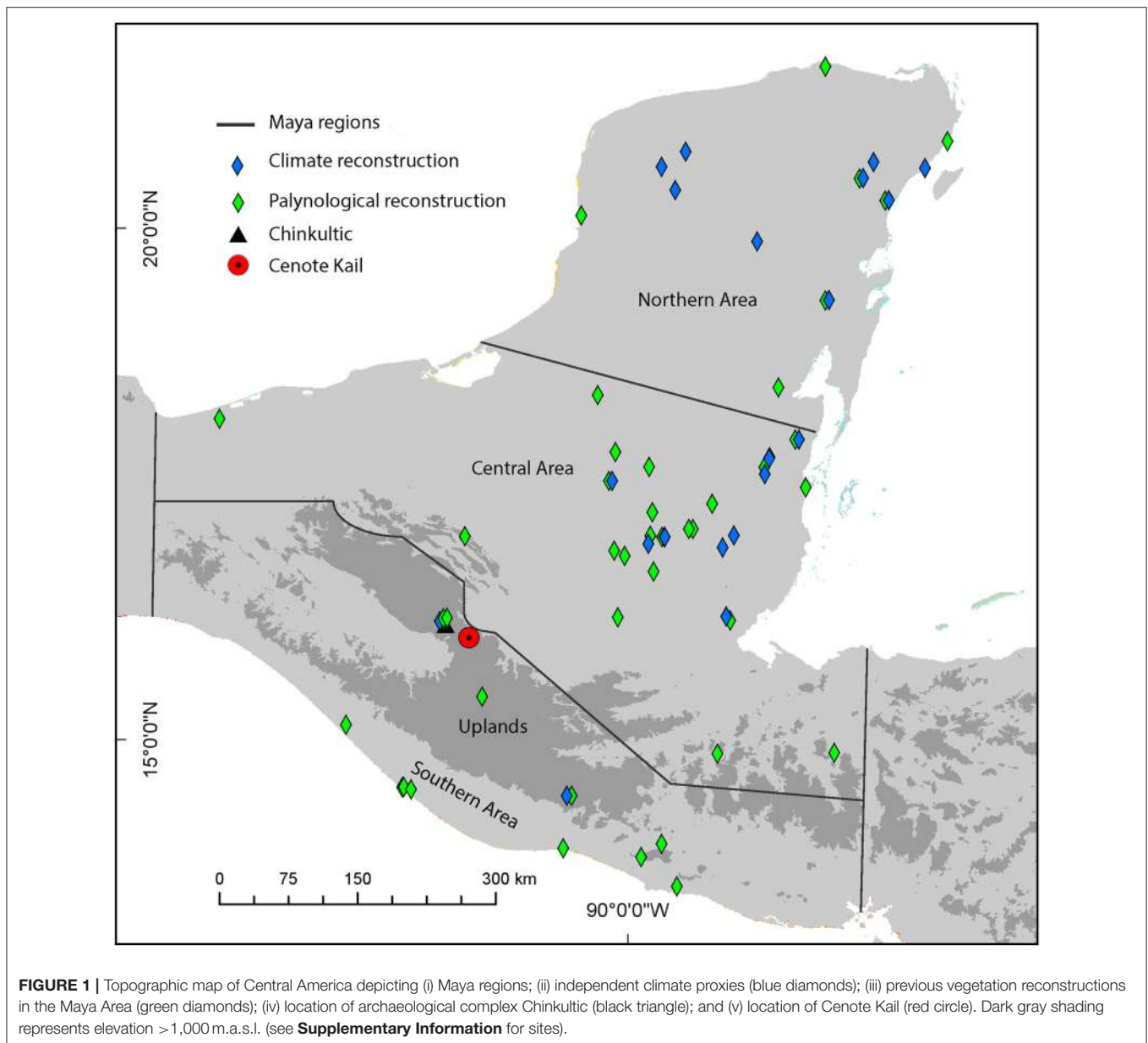
Early human populations across Central America are suggested to have increasingly interacted with their surrounding environment from 6000 B.C.E., aided by progressively more favorable climatic conditions (Turner and Miksicek, 1984; Colunga-GarcíaMarín and Zizumbo-Villarreal, 2004; Ford and Nigh, 2009). In palaeoecology records from Maya sites, anthropogenic impacts to vegetation are typically inferred from the: (i) presence of known cultigens, such as *Capsicum* (peppers), Cucurbitaceae (gourds), *Maranta arundinacea* (arrowroot), *Phaseolus* (beans), and *Zea mays* (Maize) (White, 1999); (ii) presence of “weedy taxa,” such as, Amarathaceae, Compositae, and *Polygonum* (Dull, 2004a; Franco-Gaviria et al., 2018); (iii) reductions in all or select arboreal taxa, such as *Quercus* (Dull, 2004a,b, 2007; Velez et al., 2011); and (iv)

increases in local and regional burning (e.g., Dull, 2004a,b, 2007; Anderson and Wahl, 2016).

Archaic (10,000–2000 B.C.E.) anthropogenic impacts and the extent of early human interaction with the upland forests of the Maya Area are currently poorly understood. There have been 11 palaeopalynological studies conducted in the southern Maya Area (Figures 1, 2), and only five of these reconstructions have been undertaken in the uplands (Dull, 2004a; Caffrey et al., 2011; Velez et al., 2011; Franco-Gaviria et al., 2018). Interpretations of fossil pollen and charcoal records from Laguna Verde (El Salvador) and Lago Amatitlan (Guatemala) identify extensive human alteration of the upland vegetation between 2550 and 625 B.C.E. (Dull, 2004a; Velez et al., 2011). Likewise, records from Lake San Lorenzo and Lake Esmeralda (Chiapas) provide evidence that anthropogenic and climatic impacts drove vegetation changes from c.450 B.C.E. (Franco-Gaviria et al., 2018). In contrast, palynological data from Miquil Meadow (Guatemala) indicates that climate is the sole driver of vegetation change (Caffrey et al., 2011). These records are mostly low in resolution (more than 200 years between samples: e.g., Laguna Verde and Miquil Meadow) and poorly chronologically constrained (e.g., Miquil Meadow), limitations that prevent conclusive assessment of questions related to the timing of events. In order to reconstruct the impacts of disturbance events in MTF and forest succession, palaeoecological datasets must be sampled at a resolution higher than that of the rate of succession, which is up to 200 years in MTF (Kappelle, 2006). In addition, many of these studies rely on geographically distant proxy records to infer the impacts of climate on vegetation dynamics (e.g., La Yeguada, Panama: (Bush et al., 1992) and Peten Itza, Guatemala: Islebe et al., 1996). Given the spatial heterogeneity in precipitation patterns across Central America through time (e.g., Metcalfe et al., 2015), it is critical to include local palaeoclimate records for comparison with vegetation reconstructions.

FOREST SUCCESSION

Currently the arboreal canopy of MTF predominantly comprise a combination of coniferous forest taxa (e.g., *Pinus* and *Abies*) and mixed hardwood forest (MHWF) taxa (e.g., *Quercus*, *Alnus*, and *Liquidambar*), which are well-adapted to variable climatic conditions and natural fires (Corrales et al., 2015). These MTF are a combination of pine forests (PF), pine-oak forests (POF), mountain-pine-oak forests (MPOF), oak forests (OF), pine-oak-*Liquidambar* forests (POLF), mountain rain forests (MRF), and cloud forests (CF) (Kappelle, 2006). These typically overlap in floristic composition but vary in species abundance (Miranda, 1952; Breedlove, 1981; Kappelle, 2006; Figueroa-Rangel et al., 2008, 2010, 2012). POF form intricate mosaics and complex successional interactions, especially at higher elevations, which extend up into the broad-leaved evergreen CF (Rzedowski, 2006). Altitudinally, MPOF in Chiapas are found above 1,500 m, while POF have an extensive range from 500 to 3,400 m.a.s.l., with strong turnovers between species along altitudinal gradients (Kappelle, 2006). There are over 150 species of *Pinus* and *Quercus* that can be found across the uplands of Guatemala

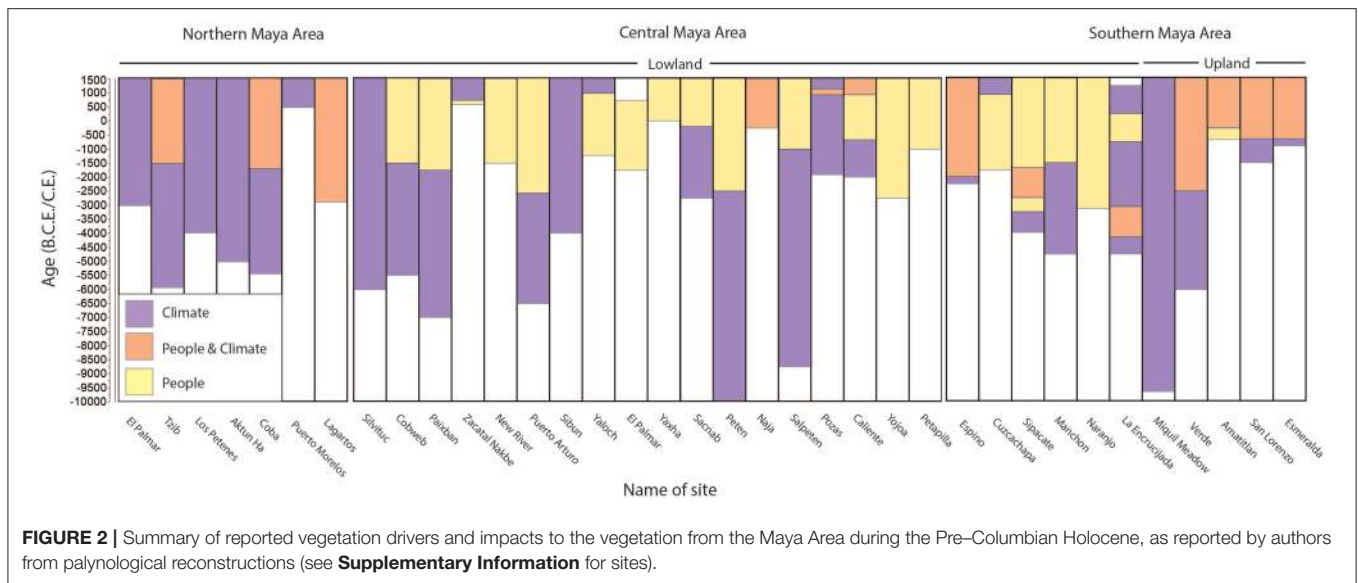


(Muller, 1942; Kappelle, 2006). Only 47% of forest cover (1990–2000 C.E.) remains, and it is highly fragmented due to high human population densities and land modification for subsistence farming (Corrales et al., 2015).

Drivers of POF dynamics have been previously investigated in upland Guatemala (Velez et al., 2011), neighboring Chiapas (Domínguez-Vázquez and Islebe, 2008), Pacific Mexico (Figueroa-Rangel et al., 2008, 2010, 2012) and Costa Rica (Islebe and Hooghiemstra, 1997), detailing the climatic and anthropogenic mechanisms that contribute toward changes in POF composition through time (Kappelle, 2006). In these studies fire has been identified as the dominant driver of structural and successive turnover within POF systems. However, there is disagreement as to what factors are driving these fires, changes

in burning are controlled by complex interactions of fire, fuel load, climate, and humans (Cochrane and Barber, 2009; Bowman et al., 2011; Anderson and Wahl, 2016). While it is not possible wholly to differentiate between anthropogenic and naturally occurring fires (Anderson and Wahl, 2016), inferences can be made by combining multiple lines of evidence such as fossil charcoal with the presence of known agricultural grains (e.g., *Zea mays*) (Dull, 2004a,b, 2007), or with climatic proxy data, to infer known shifts in precipitation, which can impact fuel loads and ignitions (Bowman et al., 2011).

Research conducted on the Pacific coast of Mexico (Figueroa-Rangel et al., 2008, 2010, 2012) and in Costa Rica (Islebe and Hooghiemstra, 1997) suggests that fire within POF are primarily climatically driven; whereas palynological work in



Guatemala and Chiapas (Domínguez-Vázquez and Islebe, 2008; Velez et al., 2011) indicates a more intertwined relationship of climate and people. Other factors considered to affect the structure and successional regeneration of POF are overall climate (temperature and precipitation), soil (type, nutrient availability), and anthropogenic activities (timber extraction and agriculture) (Kappelle, 2006). In addition, herbivory can cause deviations in successional pathways through sapling browsing and seed dispersal (Baker et al., 2016; Arroyo-Rodríguez et al., 2017).

It has been suggested that without further disturbances natural recovery will return a fallow field to a POF within c.80 years (Figueroa-Rangel et al., 2008). Sustained low-intensity and long-duration human disturbance leads to a deviation from this natural sequence resulting in slowed recovery, and more intensive anthropogenic or climatic disturbances can reverse or reset recovery times (Kappelle, 2006). However, these are theoretical timelines and to date there is very little evidence on recovery rates from different types of disturbances (fire, human, climate) in this region, nor on how this varies according to altitude.

This study seeks to identify (i) the natural baseline vegetation of the region; (ii) when human impact and agrarian practices began in the Maya uplands; and (iii) what impacts the Maya had on forest structure, composition, and successional regeneration. To address the potential impacts of anthropogenic influences and herbivory upon the biota of upland Guatemala, a proxy reconstruction of changes in vegetation, burning, and animal populations from 4000B.C.E. to 1522C.E. was developed using fossil pollen, macroscopic charcoal (>150 μm), microscopic charcoal (<150 μm), and fossil dung fungal spore (*Sporormiella*), from Cenote Kail, a lake situated in the uplands of the Southern Maya Area. These records were then compared with local and regional climatic archives and information on human population dynamics collected from nearby archaeological sites.

METHODS

Study Site: Cenote Kail

Cenote Kail (150 m diameter) is located within the uplands of the Southern Maya Area (N16°00′00.0″W91°33′14.4, 1,534 m.a.s.l.) and situated 28 km away from the well-documented archaeological complex Chinkultic (Ball, 1980; Figure 1). This city was established sometime between 50B.C.E and 75C.E. and occupied until 300–350C.E. The city was then abandoned between 350 and 700C.E. before being occupied again from 700 to 1,250C.E. (Ball, 1980). The lake is presently surrounded by a coniferous forest mosaic best described as POF or MPOF. Vegetation is distributed between densely populated mixed deciduous and coniferous forested patches, and large open shrub/grasslands.

Field and Sampling Techniques

In 2015 a 545 cm-long composite sediment core, with overlapping sections, was extracted from Cenote Kail using a Livingstone piston corer (Livingstone, 1955). Forty-six samples (1g wet weight) were extracted at 10 cm intervals for biological proxy analysis of macroscopic charcoal (>150 μm), microscopic charcoal (<150 μm), pollen, and coprophilous fungal spores (*Sporormiella*).

Chronology

An age depth model was constructed using 38 calibrated radiocarbon dates obtained from charcoal and terrestrial leaf fragments, which represent a single event or from one to two seasons of growth (Table 1). Samples were pre-treated using standard acid–base–acid protocols (Abbott and Stafford, 1996). Radiocarbon dates were generated at the W.M. Keck Carbon Cycle Accelerator Mass Spectrometry Laboratory at the University of California, Irvine. The IntCal13 radiocarbon

TABLE 1 | Measured, calibrated, and modeled radiocarbon ages for Cenote Kail.

Lab#	Measured age (C14 B.P.)		Depth	2 σ Calibrated age range (B.C.E./C.E.)		Median 2 σ calibrated age (B.C.E./C.E.)	OxCal 2 σ modeled age (B.C.E./C.E.)		Median 2 σ modeled age (B.C.E./C.E.)	Model agreement index
146795	385	±20	106.5	1,445	1,620	1,532.5	1,560	1,633	1,596.5	99.9
209175	260	±20	118.75	1,528	1,797	1,662.5	1,515	1,595	1,555	99.2
209176	560	±25	138.75	1,311	1,425	1,368	1,312	1,425	1,368.5	105.7
209177	870	±20	160.75	1,052	1,220	1,136	1,061	1,224	1,142.5	102.3
146797	1,080	±30	192	894	1,018	956	895	1,017	956	114.4
169170	1,380	±80	229.8	433	865	649	431	767	599	107.3
146798/ 146799	1,975/2,115	±20/45	267	-44	53	4.5	-40	61	10.5	55.9
209178	2,070	±30	299.25	-174	-1	-87.5	-188	-50	-119	85.5
209179	2,235	±25	318.75	-385	-206	-295.5	-389	-210	-2,995	103
209180	2,515	±25	332.75	-791	-543	-667	-789	-543	-666	101.2
146800	2,585	±20	342	-805	-772	-788.5	-806	-770	-788	64.8
209181	2,990	±50	355.75	-1,391	-1,054	-1,222.5	-1,371	-1,023	-1,197	116.6
209182	3,220	±20	378.75	-1,527	-1,439	-1,483	-1,596	-1,436	-1,516	130.8
209183	3,350	±35	382.75	-1,739	-1,531	-1,635	-1,728	-1,529	-1,628.5	118.4
209184	3,405	±20	387.75	-1,749	-1,642	-1,695.5	-1,745	-1,654	-1,699.5	102.9
209185	3,415	±20	390.75	-1,767	-1,658	-1,712.5	-1,757	-1,667	-1,712	110.1
209186	3,590	±20	394.5	-2,018	-1,889	-1,953.5	-2,015	-1,886	-1,950.5	106.8
209188	3,700	±60	407.75	-2,284	-1,928	-2,106	-2,196	-1,984	-2,090	103.9
209189	3,750	±40	412.75	-2,286	-2,035	-2,160.5	-2,270	-2,046	-2,158	95.6
209190	3,750	±25	413.75	-2,278	-2,041	-2,159.5	-2,273	-2,052	-2,162.5	100.4
146802	3,940	±25	428.5	-2,561	-2,345	-2,453	-2,466	-2,310	-2,388	98.9
209191	3,875	±25	431.25	-2,465	-2,286	-2,375.5	-2,468	-2,343	-2,405.5	101.1
209193	4,315	±30	467.25	-3,013	-2,888	-2,950.5	-3,011	-2,888	-2,949.5	96.1
209195	4,475	±25	484.25	-3,338	-3,030	-3,184	-3,303	-3,025	-3,164	93
209196	4,570	±25	498.25	-3,491	-3,119	-3,305	-3,361	-3,118	-3,239.5	92.6
193048	4,545	±25	508.8	-3,366	-3,106	-3,236	-3,367	-3,146	-3,256.5	102.5
146803	4,570	±20	519	-3,485	-3,126	-3,305.5	-3,659	-3,194	-3,426.5	100.8
193050	4,900	±25	521.7	-3,709	-3,643	-3,676	-3,708	-3,642	-3,675	106.9
193051	4,995	±25	532.9	-3,927	-3,704	-3,815.5	-3,913	-3,705	-3,809	100.7
193052	5,100	±20	536.9	-3,965	-3,804	-3,884.5	-3,961	-3,798	-3,879.5	13.9
193054	5,130	±30	543.7	-3,990	-3,804	-3,897	-3,989	-3,811	-3,900	66
*209187	3,485	±25	404.75	-1,886	-1,703	-1,794.5	-2,164	-1,759	-1,961.5	42
*209192	4,275	±25	438.25	-2,916	-2,879	-2,897.5	-2,916	-2,369	-2,642.5	28.1
*209194	4,185	±40	472.25	-2,892	-2,633	-2,762.5	-3,145	-2,755	-2,950	22.8
*209197	5,020	±60	499.25	-3,958	-3,674	-3,816	-3,386	-3,116	-3,251	6.9
*193049	5,090	±20	516.33	-3,961	-3,801	-3,881	-3,872	-3,281	-3,576.5	16.5
*193053	5,330	±25	541.3333	-4,245	-4,051	-4,148	-4,197	-3,805	-4,001	19.8

*Omitted dates identified by the general outlier model.

dataset (Reimer et al., 2013) was used to calibrate the measured radiocarbon dates, and OxCal (v.4.3) was used to construct an age–depth model applying a Bayesian approach (Ramsey, 2009). Outliers were identified using the general outlier model implementing an outlier probability of 0.05 (Ramsey, 2008). Sedimentation rates were calculated using this age–depth model.

Fossil Pollen and Sporormiella Analysis

Fossil pollen was used to reconstruct the abundance and composition of past vegetation dynamics. Fossil pollen extraction

and preparation followed standard palynological procedures applying the Oxford Long–Term Ecology Laboratory (OxLEL) protocol (OxLEL, 2016). Silicone oil was used as the mounting agent to allow for the rotation of grains, easing identification. Samples were spiked with known concentrations of an exotic marker, *Lycopodium* spores (batch No. 20848 or 9666), to calculate pollen accumulation rates. Pollen influx was calculated using pollen accumulation rates and sedimentation rate (Bennett and Willis, 2001). Counting and identification of pollen grains were conducted at 400x and 1000x magnification. For each

level a minimum of 300 terrestrial pollen grains were counted (**Data Sheet 1**). Morphological identification was achieved using (i) pollen databases (APSA, 2007; Bush and Weng, 2007; Martin and Harvey, 2017); (ii) published plates: (Roubik and Moreno, 1991; Willard et al., 2004); and (iii) botanical reference materials from the OxLEL reference collection. In order to interpret the relative composition of the forest, coniferous and mixed—hard—wood forest (MHWF) canopy taxa were compared as a ratio. The abundance of *Sporormiella* spores was used to indicate herbivorous animal presence and abundance. *Sporormiella* spores were counted and morphologically identified on the same slides (Davis and Shafer, 2006; Baker et al., 2016).

Charcoal Analysis

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

Microscopic charcoal (<150 μm), representing a regional signal of up to 100 km (see Clark, 1988), were also counted on the same slides, applying the point counting method at 400x magnification (Clark, 1982). Microscopic charcoal counts were recorded until a minimum of 50 *Lycopodium* spores and 200 fields of view were encountered for each level to allow for influx of microscopic charcoal (cm^2 per year) to be calculated.

Data Handling

Pollen counts were converted to percentages, while *Sporormiella*, macroscopic, and microscopic charcoal are presented as annual influx (Maher, 1981; Bennett, 1994; Bennett and Willis, 2001; Whitlock and Larsen, 2002; Baker et al., 2016). To identify discrete zones in the resulting palynological diagrams, constrained hierarchical clustering upon the palynological assemblage was applied following the broken stick model (Bennett, 1996).

Statistical analysis and presentation of data were performed using packages Vegan (Oksanen et al., 2015) and Rioja (Juggins, 2009) in base R (R. Core Team, 2012). Before performing all ordination analyses, the percentage data were square-root transformed to normalize the distribution and for variance stabilization (Bennett and Willis, 2001; Legendre and Legendre, 2012). A square root transform was chosen because it can be applied to data sets containing zero values. Detrended Correspondence Analysis (DCA) was conducted upon the palynological assemblage data to check if it was appropriate to apply a linear or unimodal ordination method (Ter Braak and Prentice, 1988). The site scores for the first axis of the DCA were then extracted to calculate the species turnover. Next, a Principal Component Analysis (PCA) was used to infer similarities between samples and the change in trajectories of composition of taxa through time, applying a singular value decomposition of the centered, but not scaled, data matrix. Finally, a Canonical Correspondence Analysis (CCA) was performed to quantify the relationship between environmental

variables (fire and herbivory) and the palynological assemblage data. Ellipses representing the discrete Zones were calculated using standard parameterization ($\cos(\theta + d/2)$, $\cos(\theta - d/2)$), where $\cos(d)$ is the correlation of the parameters (see Murdoch and Chow, 1996).

RESULTS

Chronology and Resolution

The age–depth model indicates that the sediment sequence (545–105 cm) continuously (i.e., without hiatus) spans 4000B.C.E. to 1522C.E. (**Figure 3**). The general outlier model (see Ramsey, 2008) identified six dates as outliers and thus were removed from the overall age–depth model (**Table 1**). The overall model agreement index was high (96.7), indicating there is very little variance between the modeled ages and the observational data. The sedimentation rate is on average 1.2 mm per year.

Palaeoecological Trends

Three statistically significant Zones were identified using the broken stick model (**Figures 4, 5**). Seventy-six taxa were recognized in the palynological sequence extracted from Cenote Kail (see **Supplementary Information**). Throughout this sequence *Pinus*, *Quercus* and *Morella cerifera* dominate the arboreal component while Compositae and Poaceae are the most abundant herbaceous taxa (**Figure 5**). Temporal spacing between samples is as follows: (i) Zone 1 represents an average spacing of 130 years spanning 1800 years (with a range of 68–415 years); (ii) Zone 2 represents an average spacing of 137 years spanning 2300 years (with a range of 53–192 years); and, (iii) Zone 3 represents an average of 90 years spanning 1400 years (with a range of 68–160 years).

Results from the CCA show that microscopic and macroscopic charcoal are significant environmental variables most associated with Zones 2 and 3, while *Sporormiella* is most associated with Zone 1 and is not statistically significant (**Figure 4A**). The PCA displays a distinct gradient and several associations between taxa and samples (**Figure 4B**). The first axis represents 20.2% of the variation, while axis two represents 10.5% of the variation. The arch between samples suggests that there is only one clear gradient. When the independently calculated palynological Zones are superimposed upon these quadrants, the top, and bottom right quadrants are most associated with Zone 1, the top left quadrant is most associated with Zone 2 and the bottom left quadrant is most associated with Zone 3 (**Figure 4B**). The first taxonomic association comprises canopy taxa *Quercus*, understory taxa Leguminosae, *Myrica*, Ericaceae, and the herbaceous and agrarian taxa *Capsicum*, which is most associated with Zone 1. The second taxonomic association comprises of understory taxa *Juniperus* and *Terminalia*, herbaceous taxa Polygalaceae, Apiaceae, Compositae *Aphelandra*, and agrarian taxa *Capsicum* most associated with Zone 2. The third taxonomic association comprises canopy taxa *Pinus*, *Alnus*, and *Liquidambar* together with understory taxa *Morella cerifera*, and herbaceous taxa Poaceae, and Campanulaceae, which is most associated with Zone 3 (**Figure 4B**).

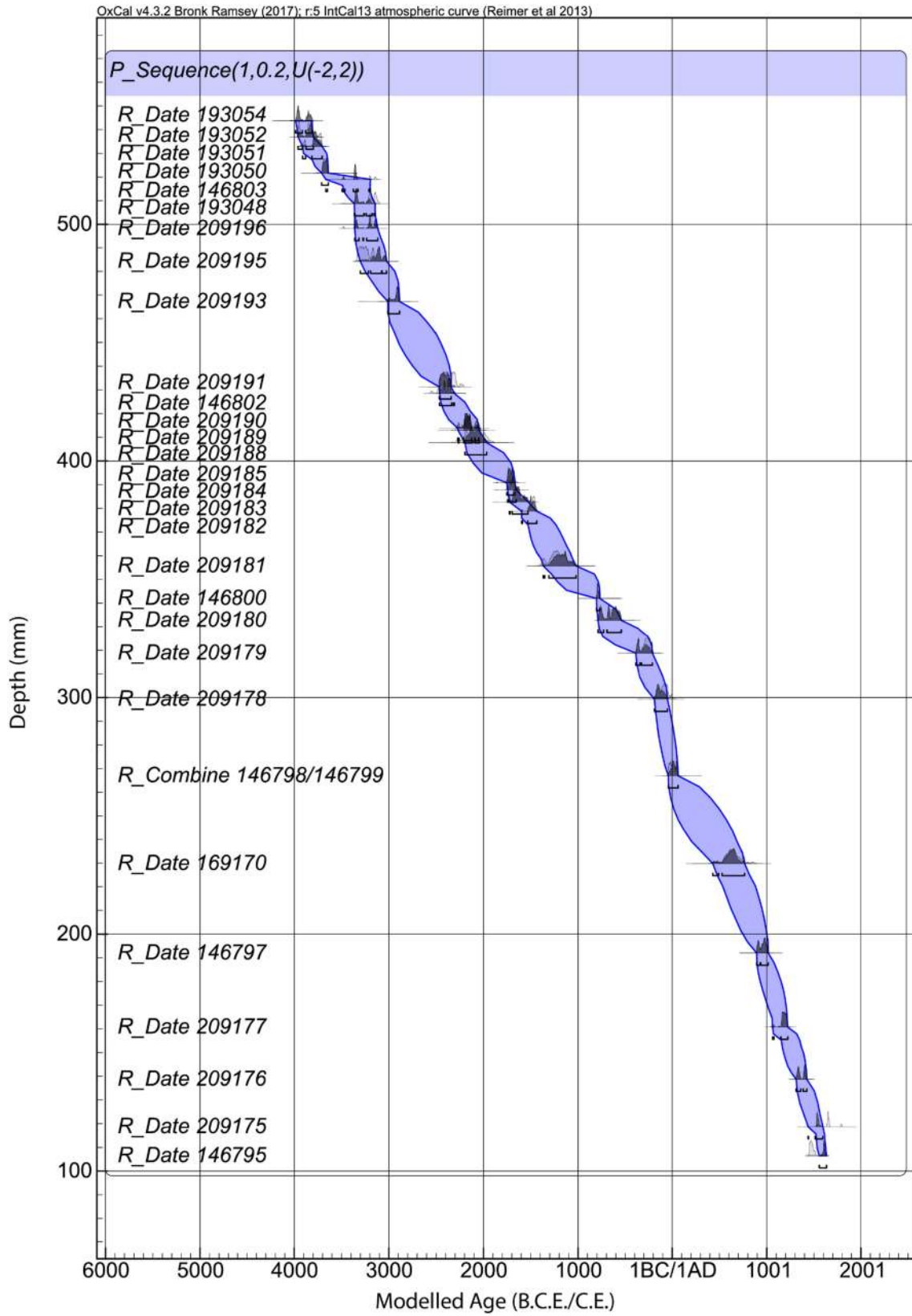


FIGURE 3 | Age depth model for Cenote Kail.

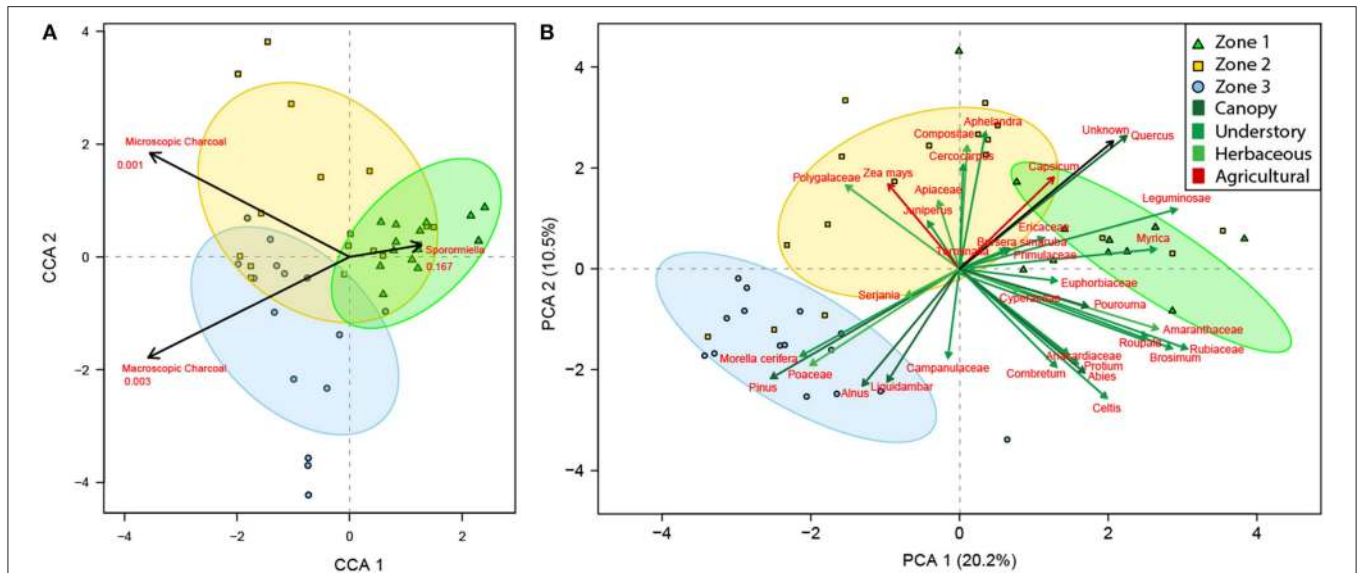


FIGURE 4 | Canonical correspondence analysis of the palaeopollinological data set ordinated against independent environmental indicators of local fire (macroscopic charcoal), regional fire (microscopic charcoal), and herbivory (*Sporormiella*) (A). Principal component analysis of the palaeopollinological data set (B). Zones are derived from the broken stick model and are represented by ellipses at a confidence of 95%. Zone 1 = green triangles; Zone 2 = yellow squares; Zone 3 = blue circles.

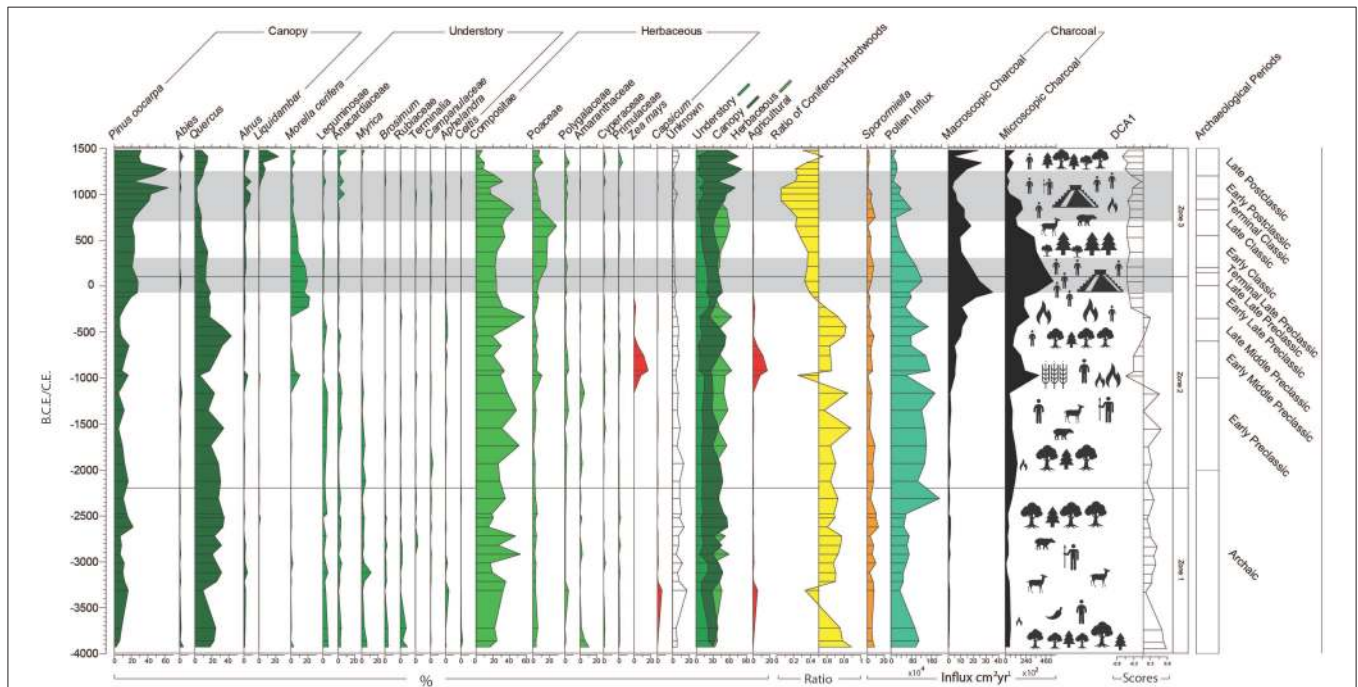


FIGURE 5 | Palynological percentage diagram of taxa appearing in an abundance >2%; forest structure; coniferous to hardwood ratio; pollen influx; macroscopic and microscopic influx; DCA axis 1; and Occupation of Chinkultic (dark bands). The palynological data are expressed as a percentage of total land pollen.

Zone 1 (545.75–421 cm, 14 samples, 4000–2200B.C.E.) spans c.1800 years concurrent with the last 2000 years of the Archaic Period (10,000–2000B.C.E.) (Figure 5). This Zone is predominantly defined by POF taxa *Quercus* (25.9%) and *Pinus* (11%) alongside herbaceous taxa *Compositae* (27.6%). Between 4000 and 3300 B.C.E. there is evidence for a decline

in canopy taxa (from 61.3 to 37.3% of the total pollen sum), particularly *Quercus* (18–9.7%). In contrast, *Pinus* became abundant during this period, rising from 4000B.C.E. (2.3%) to 3300B.C.E. (16.7%). *Myrica* and *Alnus* are mostly present throughout this Zone, peaking at 3100B.C.E. (15.3%). *Brosimum* (0–4.3%), *Anacardiaceae* (0.3–4.3%), *Leguminosae* (0–6.3%),

Morella cerifera, and Rubiaceae (0–9%) are present in low abundance and on average decrease from 4000 to 2200B.C.E. The ratio of coniferous to MHWF is on average 30:70. The coniferous to MHWF ratio changes from 25:75 to 66:34 between 3700 and 3300B.C.E. Compositae abundance increases between 4000 and 3200B.C.E. (17.3–35.3%) and peaks at 2900B.C.E. (53.3%) and 2700B.C.E. (47.3%). Amaranthaceae is present at 10.3% from 4000B.C.E. but subsequently declines leading up to 3700B.C.E. (1.3%). *Capsicum* appears and increases from 3850 to 3300 B.C.E. (0.3–5.3%), and Polygalaceae follows a similar trend, peaking at 3300B.C.E. (4.3%). Poaceae is stable and in low abundance throughout the record (2.3–5.6%). Pollen influx is low, decreasing from 4000 to 3300B.C.E. (965–344 grains $\times 10^3$ cm^2 per year) and increasing after 2300B.C.E. (1,919 grains $\times 10^4$ cm^2 per year). *Sporormiella* abundance is relatively high and stable (2.6–10.5%), falling below 4% abundance at 3100B.C.E. (2.6%), 2700B.C.E. (2.9%), and 2320B.C.E. (3.8%); there is a sustained high abundance of >10% between 2600 and 2500B.C.E. (10.2–13.3%). Macroscopic and microscopic charcoal are relatively low, decreasing between 4000 and 3000B.C.E. (macroscopic charcoal: 0.44–0.32 particles cm^2 per year; and, microscopic charcoal: 552–86 particles $\text{cm}^2\text{yr}^{-1}$) then increasing through to 2300B.C.E. (macroscopic: 1.2 particles cm^2 per year; and, microscopic: 770 particles cm^2 per year).

Zone 2 (412–263.5cm, 17 samples, 2200B.C.E.–100C.E.) spans 2100 years, including the Early, Middle, and Late Pre-Classic Periods (2000–B.C.E.–100C.E.) and is defined by arboreal taxa *Quercus*, *Pinus* and *Morella cerifera* and herbaceous taxa Compositae, Poaceae, and *Zea mays* (Figure 5). *Quercus* continues to dominate the arboreal component (23%) but decreases between 1550 and 970B.C.E. (34–6%). After 970B.C.E. (6%) *Quercus* recovers until 550B.C.E. (43%) before decreasing rapidly by 350C.E. (17.3%) and stabilizing by 100C.E. (13%). *Pinus* continues to be persistently present and in stable abundance with slight increases between 1550 and 650B.C.E. (4.6–17.7%) and a larger increase from 340B.C.E.–100C.E. (6.3–28.3%). The low ratio of coniferous to MHWF taxa indicates relatively abundant MHWF, particularly *Quercus* (47:63), with a turnover to more coniferous taxa between 1150 and 970B.C.E. (17:83–74:26) and 230B.C.E.–50C.E. (4:6–7:3). *Morella cerifera* first substantially enters the record from 970B.C.E. (10.3%) but does not establish until 230B.C.E. where it rises to the second most abundant forest taxa through to 100C.E. (19.7%). Prior to the arrival of *Zea mays* (c.1000B.C.E.), Amaranthaceae abundance briefly increases c.1150B.C.E. (5.3%). The rise of *Zea mays* from 970B.C.E. (8.6%) peaks at 930B.C.E. (17%) and is abundant until 650B.C.E. (4.6%). Polygalaceae re-establishes between 1350 and 750B.C.E. (4–3.3%). Poaceae begins to increase from 1150B.C.E. (2%) through to 100C.E. (11.5%), while Compositae remains the dominant herbaceous taxa (33.1%). Pollen influx is high overall during this Zone, peaking at 1150B.C.E. (175×10^4 grains cm^2 per year), with the exception of lower values at 970B.C.E. (577×10^3 grains cm^2 per year) and again between 650 and 550B.C.E. ($810\text{--}781 \times 10^3$ grains cm^2 per year) and 340–130B.C.E. ($881\text{--}98 \times 10^3$ grains cm^2 per year). Macroscopic charcoal rises substantially after 1150B.C.E. (1.25 particles cm^2 per year) until 50C.E. (24.9 particles cm^2 per year).

Microscopic charcoal follows a similar trend; however, it begins to increase from the beginning of this Zone (1,163 particles cm^2 per year) and peaks at 970B.C.E. (4,004 particles cm^2 per year), increasing again from 650 B.C.E. to 50C.E. (911–5,660 particles cm^2 per year). *Sporormiella* continues to be high in abundance and remains stable (0.6–8.8%) but on average is lower (4.4%) than in Zone 1 (7.2%). There are particularly high abundances of *Sporormiella* from 2100B.C.E. (7.4%) to 1750B.C.E. (8.8%), 930B.C.E. (6.5%), and at 550B.C.E. (7.7%).

Zone 3 (254.5–114 cm, 15 samples, 100–1,522C.E.) encompasses c.1400 years and is defined by the arboreal components: *Pinus*, *Quercus*, *Morella cerifera*, and *Liquidambar*, and herbaceous components: Compositae and Poaceae (Figure 5). This zone is representative of the Terminal Preclassic (150–250C.E.), Classic (250–950C.E.) and Post-Classic Periods (950–1,522C.E.). *Quercus* and *Morella cerifera* decline between 200 and 1,070C.E. (30–4.7%) while *Pinus* increases (21.3–64%). *Liquidambar* establishes and rises from 1070C.E. (0.7%) through to 1522C.E. (9.3%). Of the remaining MHWF canopy taxa, *Alnus* increases after 850C.E. (1.3%) through to 1150C.E. (6.3%) and then again from 1200 to 1,522E. (0.7–6.3%). The coniferous to MHWF ratio increases between 100 and 1,522C.E. (78:22) in favor of coniferous taxa. Compositae remains in high abundance (22.9%) but decreases after 850C.E. (45.3%) through to 1522C.E. (7.7%). Poaceae increases from 200 to 650C.E. (15.7–28%). Pollen influx decreases from 200C.E. through to 1522C.E. (10 to 20×10^4 grains cm^2 per year). *Sporormiella* abundance increases from 70B.C.E. (0.9%) through to 200C.E. (7.1%) then decreases until the end of this Zone (4.1%). Overall *Sporormiella* abundance is comparatively lower (3.3%) than in Zone 2 (4.4%). Influx of macroscopic and microscopic charcoal decreases from 200 to 1000C.E. (macroscopic charcoal: 0.44–0.32 particles cm^2 per year; and, microscopic charcoal: 552–86 particles cm^2 per year).

DISCUSSION

The Natural Baseline Vegetation

This palaeoenvironmental sequence represents the vegetation dynamics of the Maya uplands of Guatemala from 4000B.C.E. to 1522C.E. Our data indicate that the natural baseline of this region is best described as OF to MPOF. This deciduous coniferous mosaic of oak dominated forests largely persisted from 4000 to 230B.C.E. after which, the vegetation assemblage deviates away from the natural baseline toward pine dominated forests. Deviation from the natural baseline was attributed to extensive and prolonged anthropogenic settlement and activities surrounding agrarian practices and use of fire for architectural developments (Anderson and Wahl, 2016). While our record suggests that this region has been predominantly forested through time, there is clear evidence for compositional changes in flora as a direct result of anthropogenic activities, particularly between 3700 and 3300B.C.E. and from 1000B.C.E.–1522C.E. (Figure 5). For example, the transition from MPOF in Zone 1 (4000–2200B.C.E.) through to PFs in Zone 3 (100–1522C.E.) is reflected in the taxonomic associations of the PCA and the environmental drivers presented in the CCA (Figure 4).

Anthropogenic Impacts and Agrarian Practices

Archaeological records have widely found that village farming became firmly established across the wider Maya Area after c.1800B.C.E. (Neff et al., 2006). This is reflected in the interpretations of the reconstructed palynological assemblages for both the Maya lowlands and the upland areas (Figure 2). Disturbance driven by anthropogenic activities, such as: (i) agricultural practices (e.g., Dull, 2004a,b, 2007); (ii) rearing livestock (Lovell, 1985); (iii) timber extraction (e.g., Dull, 2004a,b, 2007; Velez et al., 2011); and (iv) lime production (Anderson and Wahl, 2016), can initiate or maintain local vegetation succession impacting: (i) forest composition, (ii) structure, and (iii) regeneration (González-Espinosa et al., 1991).

Archaic populations from the Maya Area combined agriculture (e.g., pepper, beans, maize, squash, and chili) with hunting and gathering from as early as 5200B.C.E. (Pope et al., 2001). Evidence for agriculture from Centote Kail is first indicated by vegetation changes from 4000B.C.E. The observed changes include (i) a decline in canopy and understory taxa; (ii) increases in weedy disturbance taxa; (iii) a very small increase in local and regional burning; (iv) and the presence of cultivated taxa such as *Capsicum* (White, 1999), between c.3850 and 3300B.C.E. or *Zea mays* between c.970 and 550B.C.E. (Figure 5). A mixture of traditional hunter-gather practices combined with limited agriculture is exemplified by the abundance and variety of edible fruits and nuts (e.g., *Brosimum*, *Myrica*, and *Anacardiaceae*) and high abundance of fauna as indicated by the influx of *Sporormiella*.

Little is known about the Pre-Columbian human habitation of the upland Maya Areas, particularly during the Archaic, due to a scant archaeological record (MacNeish, 1982; Clark and Cheetham, 2002; Lohse et al., 2006; Lohse, 2009). Evidence from Centote Kail suggests that people were manipulating the uplands of Guatemala from at least c.4000B.C.E. and practicing agriculture from c.3850B.C.E. This is the earliest palynological evidence for agriculture in the Southern Maya Area, preceding evidence from lowland Pacific Guatemala and from El Salvador, which all indicate agrarian practices established from c.3500B.C.E. (Dull, 2004a; Neff et al., 2006). Based on this evidence, we hypothesize that agriculture in the Southern Maya Area started in the uplands and spread to the lowlands, driven by increasingly favorable climatic conditions in the lowlands during the Holocene Thermal Maximum (6000–3000BC.E.) (Ford and Nigh, 2009). Human populations dispersed with the expansion of the lowland forests (Rosenmeier et al., 2002; Hillesheim et al., 2005; Neff et al., 2006; Wahl et al., 2006, 2014; Bush et al., 2009; Mueller et al., 2009; Escobar et al., 2012), increasingly interacting with the tropical forest ecosystem and gaining ethnobotanical knowledge (Ford and Nigh, 2009).

The start of the Pre-Classic (2000B.C.E.) is marked by the first appearance of state level settlements and an increased reliance on domesticated crops, particularly *Zea mays* (Neff et al., 2006). Settlements and agriculture were concentrated around water bodies, such as Cenotes, which provided reliable access to fresh water for sustenance and agriculture (Lucero et al., 2014). Although pollen records have been used to document the spread of maize agriculture in the Maya Area, most of these records are from the lowlands (Figure 1). Consequently, our

understanding of the initial arrival of maize in the uplands of Central America is poor. Results from Centote Kail are filling this gap. For example, traditional *Zea mays* agriculture is evident from 970B.C.E. in the Centote Kail record. This is late compared to the uplands of El Salvador, c.2500B.C.E. (Dull, 2004a); however, the relative palynological abundance of *Zea mays* found in Centote Kail, suggests that the expanse of agriculture in the Guatemala highlands was much greater. *Zea mays* agriculture is typically associated with *Milpa* (e.g., Dull, 2004a,b, 2007), which entails a 5–10 year cycle between periods of cultivation and fallow (Cowgill, 1962). Intensification of milpa cycling due to increasing human populations commonly leads to the depletion of nutrients in the soil (Ford and Nigh, 2009). We suggest that after 550B.C.E. the agricultural settlement surrounding Centote Kail was abandoned in favor of more productive soils in the lowlands.

By c.350B.C.E. large pyramids were being built across the Maya Area including the establishment of Chinkultic c.50B.C.E. (Ball, 1980). These pyramids were typically covered in plaster for architectural as well as decorative purposes (Anderson and Wahl, 2016). The production of this lime plaster involved the burning of powdered limestone (Oates, 2008). Monuments built during the Pre-Classic period were covered in this plaster (Hansen, 2001, 2012; Anderson and Wahl, 2016). Hansen (2012) reports that floor thickness alone could exceed 13cm. Anderson and Wahl (2016) explore the amount of fuel required to produce sufficient lime to meet the demands of this monument building and the impact that this might have had on the forest environment. They calculate 192 km² of forest would have been required for burning to create enough plaster for the construction of El Mirador in the central Maya Area. While Chinkultic is significantly smaller than El Mirador, the required plaster to create the complex of temples and ball courts would have been extensive. Agriculture in the Guatemala highlands culminated c.400 years before the Chinkultic settlement was established (Ball, 1980). Therefore, we suggest that the large increase of macroscopic and microscopic charcoal from c.200B.C.E. in Centote Kail might relate to the production of lime plaster at Chinkultic, coinciding with its founding. The extraction of wood from the surrounding forests for burning is reflected in the structure of these POF as well as patterns for local and regional burning.

Forest Structure, Composition, and Successional Regeneration

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

Weedy disturbance taxa (e.g., *Amaranthaceae*), reductions in canopy taxa (e.g., *Quercus*) and the creation of more open habitats exemplify anthropogenic disturbance prior to the agrarian establishment of *Zea mays* (e.g., Dull, 2004a,b,

2007). Anthropogenic impacts, as indicated by agricultural grains and reductions in forest taxa in Zone 1 occur at Cenote Kail between c.4000 and 3300B.C.E. Disturbance to the natural vegetation baseline was likely caused by settlement and agrarian practices directly surrounding Cenote Kail. After 3300B.C.E. cultivation ceases and arboreal taxa (understory and canopy) re-establish within c.100 years (3200–3100B.C.E.). This follows the expected recovery time of c.80 years for POF (Kappelle, 2006; Figueroa-Rangel et al., 2008). By 2600B.C.E. the mature structure of the POF are well-established and persist in relative equilibrium until further anthropogenic disturbance at 1150C.E. Deforestation, agrarian cultivar, and increased regional burning surrounding Cenote Kail all coincide at c.1000B.C.E. (Figure 5), and are attributed to the expansion and development of the Pre-Classic Maya (e.g., Neff et al., 2006). Increases in local and regional burning from the onset of Pre-Classic agriculture marks the sustained decline and eventual transition of POF to Pine dominated forests.

Plant community composition after burning is often explained by: (i) the sprouting ability of dominant species, (ii) the ability of subdominant species to increase in numbers, and (iii) the failure of invasive species to become established (Elliott et al., 1999; McDonald et al., 2003). Many species of oak rapidly sprout from their root collar after burning (e.g., *Quercus insignis*, *Q. skinneri*), dominating early successional stands (Barnes and Van Lear, 1998; Kirby and Watkins, 2015). However, several species of pine have also adapted to fire through the development of thick bark, serotiny, rapid growth, and sprouting, including *Pinus teocote* and *P. pseudostrobus* (Richardson, 2000; Rodríguez-Trejo and Fulé, 2003). The early successional formation of oak dominance is evident between 970 and 550B.C.E. (Figure 5). As the forest becomes more established, oak abundance typically diminishes under faster-growing conifers (Sheffer, 2012).

Extraction of wood, sustained land clearance, and most importantly burning has changed the structure of the POF from oak-dominated to pine-dominated (Figure 5). Additionally, herbivores, such as the white-tailed deer (*Odocoileus virginianus*) may also have impacted forest composition and regeneration through selective browsing on young saplings and individual species (Vera, 2000; Kirby and Watkins, 2015). We suggest that the coppice systems created by the Maya are particularly vulnerable to browsing from medium and large sized herbivores (Joys et al., 2004). Pines have been found to be preferentially browsed compared with other arboreal taxa (Blair and Brunett, 1980). While overall herbivore abundance decreases through time, their browsing impacts upon forest structure may have been particularly important to recovery after prolonged disturbance (Joys et al., 2004).

The pine-dominated forests become increasingly established between 150B.C.E. and 1070C.E. (Figure 5). When coniferous forests form closed stands, they change the environment beneath them. The most substantial changes involve the greater uptake of soil water and decrease of light reaching the ground (Jucker et al., 2014). The combination of these factors makes it almost impossible for other arboreal taxa to establish and grow (Kappelle, 2006). For example, most species of oak suffer increased reproductive failure under closed canopy conditions

(Jucker et al., 2014), relying on the dispersal of acorns to forest edges or clearings through animal transport (Lopez-Barrera, 2003; Kappelle, 2006). Large herbivores, such as the Baird tapir (*Tapirus bairdii*), are important to the structure and diversity of recovering POF due to their role as long distance seed dispersers, ingesting whole seeds and dropping them intact with their feces (Bodmer, 1991; Rodrigues et al., 1993; Fragoso, 1997; Olmos, 1997; Lawton, 2000). The reduction of herbivore abundance during the transition of oak dominated POF to pine dominated POF at Cenote Kail (c.220B.C.E.) is likely to have contributed to the established rise in pine. Coniferous forest stands remain dominant until they are removed through felling or die of disease, insect attack or old age (Jones, 1974). The transition from pine dominated coniferous forests to MHWF is gradual and relies upon the breakup of the coniferous forest canopy to allow for secondary canopy taxa to rise through (Jones, 1974). The establishment of *Quercus*, *Liquidambar* and *Alnus* at Cenote Kail after c.850C.E. demonstrates this final transition back to MHWF dominance (Figure 5).

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

Terrestrial hydroclimatic reconstructions from the upland Maya Area suggest that only modest changes in precipitation amounts occurred over the last several millennia. Climatic evidence from Lago Amatitlan indicates lower lake levels from 250B.C.E. to 125C.E. and 875 to 1375C.E., which has been attributed to a decline in water level resulting from either a drier climate and/or reforestation after anthropogenic abandonment (Velez et al., 2011). Also, evidence from San Lorenzo (Chiapas) indicates generally wetter conditions from c.1400–700B.C.E., 500–850B.C.E., and c.1200–1522C.E. interrupted by periods of drought from c.700–500B.C.E. and c.850–1200C.E. (Franco-Gaviria et al., 2018). These records suggest that although climate may have played an abetting role in driving forest dynamics, the timing of these hydroclimatic changes do not reflect the forest and fire dynamics reconstructed from Cenote Kail. Our findings suggest that anthropogenic activities revolving around agriculture and architectural developments have initiated and maintained successive regeneration of vegetation from mixed oak dominated forests to pine dominated forests. However, further work investigating past hydroclimate changes for this region will be required to fully understand the role of climate as an independent driver of the vegetation surrounding Cenote Kail.

CONCLUSIONS

The sedimentary sequence from Cenote Kail was continuously deposited from 4000B.C.E. to 1522C.E. and provides a record of past changes in vegetation and human impacts. We have found that POF within the Southern Maya area were transformed by Pre-Columbian human populations through practices of agriculture and architectural developments over thousands of years extending back into the Archaic Period (Betz, 1997; Piperno and Pearsall, 1998; Smith, 1998; Dull, 2004a; Neff et al., 2006). Three successional phases can be discerned following a combination of natural and anthropogenically modified successional pathways. The Archaic period is defined by light anthropogenic disturbance, centered around some land clearance for agriculture. *Zea mays* cultivation is prevalent from 970 to 550B.C.E., after which time sedentary agriculture does not appear to be widely practiced. Herbivorous animals, such as deer and tapir, are likely to have played an important role in forest recovery after disturbance; however, discerning their individual impacts would require further research. Persistent high intensity burning for lime production during the Late-Pre-Classic to Classic Period are suggested to have resulted in a turnover of forest structure c.150B.C.E. from oak-dominated POF to pine-dominated POF. Evidence for the fragmentation, degradation and subsequent recovery of these MTF over the past c.6000 years provides a valuable comparison for the present-day anthropogenic activities that are driving current changes in this region. To protect the remaining intact fragments of these MTF and to encourage the recovery of areas that have suffered past compositional or structural shifts, fire needs to be carefully managed.

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AUTHOR CONTRIBUTIONS

WH conceived the presented idea with input from SN, KW, and GP. WH conducted all palaeoecological lab work, statistical analysis, and age-depth modeling. SN and KW verified the analytical methods. NS and BS conducted the field work. NS carried out the radiocarbon dating. KW, SN, NS, and GP helped supervise the project. WH drafted the final manuscript. All authors discussed the results contributing to the final manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/ffgc.2019.00034/full#supplementary-material>

Supplementary Table 1 | Sites represented on **Figures 1** and **2**.

Supplementary Table 2 | Images of palynological taxa at 400x magnification identified from Cenote Kail.

Data Sheet 1 | Raw Palaeoecological Data.

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