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The development of early farming diets and population change in the Maya region and their climate context

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ABSTRACT

We explore the impact of a millennium-long period of decreased rainfall during the transition from the Middle to Late Holocene on human diet and population dynamics in the northern neotropical Maya Lowlands. To do so, we use a nearby paleo-precipitation reconstruction to evaluate the timing of this period of reduced rainfall and compare those data to population proxies and stable isotopes of carbon and nitrogen from directly dated human bone spanning the interval of interest. Our results show that decreased precipitation coincided with archaeological and isotopic evidence for increasing reliance on maize as a dietary staple. Two rockshelter sites located in Southern Belize have produced a mortuary assemblage that spans the Holocene. These assemblages provide a unique opportunity to examine how early farmers during the transition to agriculture may have been affected by Middle to Late Holocene climate change. Between 5600 and 4200 cal BP lowland populations were already consuming significant amounts of maize reflected in proxies for the protein and the whole diet portions, suggesting the establishment of farming communities at least 800–2200 years before the emergence of public architecture. We demonstrate that increasing reliance on maize shows the resilience of farming populations to climate variability during this crucial period just prior to massive demographic change and the emergence of complex economic institutions.

1. Introduction

The boundary between the Middle and Late Holocene at ca. 4200 cal BP is an important transition associated with hydroclimatic changes in many regions (Walker et al., 2012; Weiss, 2016; Zanchetta et al., 2016). By comparing global climate records across this interval, researchers identified regional differences in precipitation. Equatorial and mid-northern latitudes experienced reduced rainfall while other regions experienced increased rainfall (Railsback et al., 2018). In regions of reduced precipitation, changes have been attributed to a southward translocation of the Intertropical Convergence Zone (ITCZ), the equatorial moisture belt that delivers seasonal moisture to lower latitude regions (Zanchetta et al., 2016; Railsback et al., 2018; Bini et al., 2019). The collapse of political systems in early civilizations and agricultural innovations have also been attributed, at least in part, to precipitation reduction during this period (Weiss et al., 1993; Weiss, 2016; Railsback et al., 2018; Lawrence et al., 2021; Giesche et al., 2023). In other places, dry conditions are difficult to define or there is not clear evidence of human impacts from drying (Greenberg and Höflmayer, 2017; Jaffe and Hein, 2021).

There have been relatively few mentions of this climate excursion in the literature of the northern neotropics. Recently, it has been hypothesized that a drying interval at 4200 cal BP was the catalyst for a 3-century-long period of agricultural intensification, increasing sedentism, the first Mesoamerican ceramic containers, and conditions for emergent social stratification (Rosenswig, 2021). Limited climate data from the neotropics has made it difficult for researchers to assess the impacts of a hypothesized dry period at the end of the Middle Holocene on local populations. Few climate records in the region extend to the period of interest with reliable dating and high enough resolution to resolve a

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centuries-long dry interval. Aside from the archaeological sites in this paper there are no stratigraphically intact well-dated mortuary sites in Central America that have a continuous occupation history with sufficient preservation of human remains extending into the Middle Holocene to facilitate dietary reconstructions (Prufer et al., 2021).

Using climate, demographic, and diet proxies, we can ask the following questions for the interval around 4200 cal BP in lowland Mesoamerica: 1) was this an interval of significantly reduced rainfall that impacted the ability of humans to farm and/or the quality of their diets; 2) did population sizes grow, remain stable, or contract across this period of hypothesized climatic uncertainty; and 3) how do aspects of diet at the end of the Middle Holocene compare to those of the Late Holocene Classic Period? To explore these questions, we conducted analyses across two time periods. First, we explore the relationship between diet, population and climate across the transition from the Middle to Late Holocene. From 5600 to 4000 cal BP we specifically assess the impact of reduced rainfall on diet. Next, we compare diet between the previous period to that of farmers who lived between 3750 and 1000 cal BP. The latter allows us to assess changes in diet that accompanied a major demographic transition starting ca. 3500 cal BP, just centuries prior to the emergence of public architecture (Inomata et al., 2020) and markers of institutional hierarchies in the archaeological record (Pugh, 2022).

Discussions of the influence of climate on past human societies are multi-faceted and complex and require careful evaluation to account for environmental variability, spatiotemporal heterogeneity of past climate, and flexible human responses (Degroot et al., 2021; Kennett et al., 2022). To better understand past relationships between climate and culturally mediated changes we evaluate relevant datasets through quantitative analyses to model the relationships between climate, diet, and relative population proxies anchored to reliable chronologies. In this paper we use multi-proxy evidence to explore the potential climatic influence on human societies during a period of profound cultural change, including the increasing reliance on agriculture and early expansions of populations in the Maya Lowlands prior to the rise of complex political systems and economic networks. We develop dietary reconstructions of directly dated burials along with a regional climate record to explore the relationship between overall diet quality, the increasing importance of maize as a cereal grain, and population change all within the context of climatic variability in the final centuries of the Middle Holocene and between the transition from the Middle to Late Holocene and the later growth of Maya cultural formations.

2. Regional setting

In northern Central America there are few climate records spanning the Middle to Late Holocene. For the Late Holocene, precipitation proxies based on speleothems from Yok Balum cave have been linked to a suite of drivers of climate variability, specifically the intertropical convergence zone (ITCZ), ENSO, and Atlantic cyclone activity, which still drive most variation today (Kennett et al., 2012; Ridley et al., 2015; Asmerom et al., 2020; Braun et al., 2023). To the south, off the coast of Venezuela in the anoxic marine sediments of the Cariaco Basin, elemental Ti analysis of varved deposits is thought to reflect a regional precipitation record reflecting local changes in the position of the ITCZ across the Holocene (Haug et al., 2001). This record shows a slight drying trend from 5000 to 4000 cal BP, and a more extreme drying event at 3800 cal BP. To the west of the Maya Lowlands in Guerrero, Mexico in the Balsas River drainage the Cueva del Diablo speleothem rainfall record primarily reflects convection linked to monsoonal circulation at the northernmost extent of ITCZ and shows modest drying just before 4000 cal BP (Lachniet et al., 2013). The Balsas region consists of seasonal tropical forests and mean annual rainfall of 1100 mm and is the location of the earliest domesticated maize at 8700 cal BP (Piperno et al., 2009). Closer to the northern neotropics of Belize, the GU-RM1 $\delta^{18}O$ speleothem record from Grutas del Rey Marcos in the Guatemalan Highlands (15.42°N, 90.28°W, 1460 masl) spans the Holocene, making it ideal for this analysis. Precipitation in the region is linked to ITCZ dynamics after ~9000 cal BP, with a convective regime favored by warming Caribbean and North Atlantic sea surface temperatures (SST) regulating moisture in the region in the Middle and Late Holocene. However, the exact mechanics of climate evolution remains murky. GU-RM1 shows a protracted period of reduced rainfall and several pronounced events between 5000 and 4000 cal BP prior to a gradual drying trend from 3800 to 400 cal BP. The differences in the timing of reduced rainfall reflected in GU-RM1 and the Cariaco records have been attributed to latitudinal differences (Winter et al., 2020). The location of Grutas del Rey Marcos and the Maya lowlands at the northern margin of the ITCZ suggests more distant records may not accurately reflect rainfall evolution over this region. Additionally, $\delta^{234}U_i$ (initial uranium isotope concentration) in GU-RM1 positively covaries with $\delta^{18}O$. Since $\delta^{234}U_i$ signal is a proxy for local soil infiltration and residence time in the aquifer feeding the drip, this is strong evidence that the GU-RM1 reflects past rainfall along the eastern slope of the Guatemalan highlands in Alta Verapaz (Bernal et al., 2023), comparable to precipitation regimes in southern Belize (Kennett et al., 2012). No other contemporaneous high resolution isotopic paleo-precipitation records exist for this region. Therefore, Rey Marcos is the most appropriate record for our comparison.

The study area for this paper is the northern extent of the neotropics, a lowland region with subtropical conditions now known as the southern Maya Lowlands in reference to Late Holocene cultural developments. The greater neotropics is a region of warm lowland broadleaf forests and savannas with cooler highlands stretching from southern Mexico through greater Amazonia (Prufer et al., 2021). During the Early through Middle Holocene, this region is characterized by shared cultural developments that preceded highly networked emergent social formations during the Late Holocene. These include very early evidence of plant domestication (~11,500 cal BP), land clearing (7000 cal BP) (Piperno, 2011; Iriarte et al., 2020; Lombardo et al., 2020), and foodways leading to the initial adoption of maize as a staple grain in South America (~6000-5500 cal BP, Tung et al., 2020) followed by the Maya lowlands about 1500 years later (Kennett et al., 2020; Tung et al., 2020). In the Maya region, micro- and macrobotanical evidence for early maize comes primarily in the form of pollen from wetland excavations (Pope et al., 2001; Pohl et al., 2007), starch grains from stone tools (Rosenswig et al., 2014) (both around 6000–6500 cal BP), and well-preserved corn cobs from El Gigante Cave in Honduras by 4300 cal BP (Kennett et al., 2017, 2023).

These agricultural developments followed changes in stone tool technologies consistent with increased reliance on plant resources including the abandonment of bifacial chipped tool technologies at ~8000 cal BP (Prufer et al., 2019; Prufer and Kennett, 2020; Ranere and Cooke, 2021). Four millennia later, after 4000 cal BP, we see the construction of public architecture consistent with varying degrees of emergent complexity in both South and North America (Iriarte et al., 2004; Šprajc et al., 2023). New evidence points to a possible south-to-north spread of people, cultigens, and horticultural knowledge (Kennett et al., 2022). Ceramic containers first appear in Amazonia by 7000 cal BP (Iriarte et al., 2020), then later in Panama perhaps by 5000 cal BP (Cooke, 1985), in Costa Rica by 4000 BP, and in Honduras by 3600 cal BP (Joyce and Henderson, 2017). The initial ceramic producing villages appear in west Mexico perhaps as early as 3850 cal BP (Rosenswig, 2008, 2012; Kennett et al., 2021), roughly coincident with demographic changes discussed below.

This general northward movement of developments related to increasing plant consumption during the Middle Holocene is supported by both genetic and isotopic data (Kennett et al., 2022). Maize was domesticated in central-west Mexico by 8700 years ago and rapidly spread southward to the Amazon before 7000 cal BP (Piperno et al., 2009). Early selection for traits found in later land races may have been hampered by introgression and improved varieties outside of the range of teosinte and likely included a suite of traits that characterize more productive varieties (Kistler et al., 2018, 2020). This may be related to a northward migration of people from the Isthmo-Columbian region to the Maya Lowlands prior to 5300 cal BP, based on genetic data that is consistent with the arrival of improved maize varieties into the region (Kennett et al., 2022). In southern Belize, maize is adopted as a staple grain by 4000 cal BP following a period of increasing consumption (Kennett et al., 2020). This suggests that maize was a staple grain for farming communities long before the advent of stone architectural construction and public ceremonial spaces, which first appear in the Maya area just prior to 3000 cal BP (Inomata et al., 2020; Awe et al., 2021).

For this paper, dietary data come from two rockshelter sites, Mayahak Cab Pek and Saki Tzul (16.49° N, 88.91° W; ~430 masl), located in the southern Maya Mountains in modern day Belize (Fig. 1). These two sites have a long history of use for animal processing, stone tool use, and as mortuary sites (Kennett et al., 2020; Prufer and Kennett, 2020; Prufer et al., 2021). As previously discussed, genetic data from the region suggest that the earliest occupants are likely linked to the earliest dispersals of humans in the Late Pleistocene. However, later populations are genetically related to this earlier group, but also populations from lower Central America and northern South America (Kennett et al., 2022). For the humans in the latter population, maize was a substantial component of their diet by 4700 cal BP and comprised more than 50% of their diet by 4000 cal BP (Kennett et al., 2020).

3. Material and methods

3.1. Diet proxies

Measurements of δ^{13}C and δ^{15}N from bone collagen and bone apatite have long been used as proxies for diet (DeNiro and Epstein, 1978, 1981; Schoeninger and DeNiro, 1984; Lee-Thorp et al., 1989; Ambrose and Norr, 1993; Tieszen and Fagre, 1993; Jim et al., 2006). Carbon from the protein portion of the diet is preferentially routed to form bone collagen and other proteinaceous tissues. Whereas $\delta^{13}C_{apatite}$ is representative of carbon in the whole diet – i.e., primarily carbohydrates, but also lipids, and some proteins dependent on diet quality or food availability. Nitrogen, on the other hand, is only incorporated into proteinaceous tissues with enrichment between trophic levels. Nitrogen values increase at a rate of ~3.4‰ per trophic level. $\delta^{15}N_{collagen}$ values can also be used to assess diet quality. In this context, a high-quality diet indicates that the macromolecular composition of the diet is similar to that of the consumer.

Some edible plant species that are currently grown in the region have been sampled for bulk carbon stable isotope analysis in order to establish a modern baseline. Carbon values for some C_3 plants from this region range from −25.43‰ to −30.95‰ (mean = −28.5‰, sd = 1.78). For maize varieties and other C_4 plants, there is a greater abundance of the heavier Carbon-13 isotope with δ^{13}C values ranging from −12.07‰ to −11.56‰ (mean = −11.87, sd = 0.21). Nitrogen is 0‰ when compared with atmospheric air and for most plants in terrestrial ecosystems, the value is near 0‰ except for some nitrogen fixers and nitrogen-fixing symbionts. Marine ecosystems vary both in terms of carbon and nitrogen baseline values, but previous research has demonstrated that none of our individuals are consuming significant amounts of marine resources (Kennett et al., 2020).

Bone collagen and bone apatite samples from twenty-six previously published individuals within the interval of interest were used to assess C_4-plant consumption, diet change, and overall diet quality (Kennett et al., 2020). Collagen samples were previously assessed for quality using C:N ratios (Supplemental Appendix 1). Apatite samples were assessed for quality using FTIR analyses (Kennett et al., 2020: Supplemental Figures S7-S10).The sample includes individuals of all ages. Infants with bone $\delta^{15}N_{collagen}$ values elevated more than 3‰ above the minimum for the time period were removed prior to statistical analysis. Lab analysis identified 17 adults, 2 juveniles between ages 6–15, and 5 infants with $\delta^{15}N_{collagen}$ values within an acceptable range. Two additional samples come from isolated adult remains of unknown age at death. Males (n = 5) and females (n = 7) are represented among the individuals with 14 unidentified.

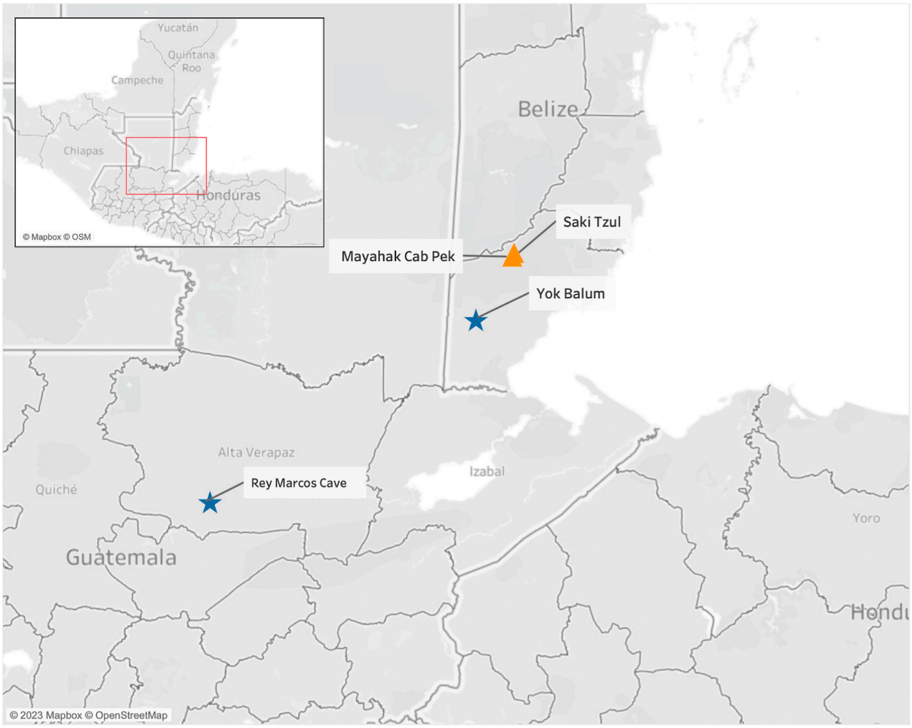


Fig. 1. Map showing the location of the rockshelter sites of Mayahak Cab Pek and Saki Tzul in southern Belize in relation to the two paleoclimate records from Yok Balum Cave and Rey Marcos Cave.

3.2. Proxies for demographic change

We built a population proxy for the Maya Lowlands based on a compendium of 974 published radiocarbon dates (Hoggarth et al., 2021), combined with the following dates (n = 1526). For Southern Belize, a subset of 552 AMS dates from bone collagen (n = 144) and charcoal (n = 408) was compiled from 32 different sites including the two rockshelter sites and the Classic period site of Uxbenká (Prufer et al., 2022; Braun et al., 2023). Most bone dates for southern Belize come from Saki Tzul (n = 50) and Mayahak Cab Pek (n = 68). All dates were calibrated using IntCal20 and binned into 100-year bins (Reimer et al., 2020). Calibrated samples whose median date falls within 100 years of another from the same site are averaged together to reduce potential sampling bias through the process of binning. The resulting probability distributions of the binned and calibrated dates were summed to create the SPD. A composite Kernel Density Estimate (cKDE) model was also created using a bootstrapping method by which calendar dates are randomly sampled from each calibrated date (Brown, 2017). This process was repeated with 1000 MC simulations. The model also included dates outside the period of interest (7000–200 cal BP) to reduce edge effects (Crema, 2022). Finally the model for the Maya Lowlands was corrected for taphonomic bias, because older charcoal dates from surface sites are less likely to be preserved in the archaeological record (Surovell et al., 2009; Crema and Bevan, 2021). The model for Southern Belize was not corrected for taphonomic bias because the majority of dates come from the rockshelters and therefore the correction would overestimate population in the earliest time periods. The cKDE model was ultimately used for further analysis because it reduced some of the noise inherent in the SPD. KDE models can be used to look at population aggregation through time since the radiocarbon samples often come from habitation sites. All the dates for southern Belize prior to 2000 cal BP are from the rockshelters, which are not sites of habitation but rather sites of mortuary significance to the surrounding communities. Thus, this suggests, that the cKDE model is a useful metric for looking at changes in relative population size in the region as individuals from multiple settlements were likely interred in these two sites prior to 2000 cal BP (Supplemental Appendix 1).

3.3. Paleo-precipitation proxy

Grutas del Rey Marcos is located approximately 175 km to the southwest of the two rockshelter sites (Winter et al., 2020). The GU-RM1 record consists of 520 δ^{18}O and δ^{13}C carbonate measurements and a 12, 435 year-long chronology modeled using COPRA (Breitenbach et al., 2012) based on 21 Uranium-series dates and a median sampling resolution of 12 years. The age model uncertainty over the 5000–4000 cal BP interval is approximately ±140 years (CI = 95%). The δ^{18}O and δ^{13}C values, expressed in per-mil deviation from the VPDB standard, do not covary over the Holocene, indicating that kinetic fractionation did not play a role in the isotopic values and δ^{18}O sample values are a good proxy for precipitation. This record indicates that there were three major climate phases, a dry to wet interval from 11000 to 9000 cal BP representing increasing monsoon strength, a stable but wetter phase from 9000 to 5000 cal BP, and our period of interest, a centennial scale period of reduced rainfall between 5000 and 4000 cal BP. The period from 9000 to 5000 cal BP is arguably the wettest interval in the Holocene with a median δ^{18}O value of −6.2‰ (±0.16‰). The 5000-4000 cal BP interval spanning the transition from the Middle to Late Holocene consisted of distinct episodes of decreased precipitation (Winter et al., 2020). From about 5000 to 4500 cal BP δ^{18}O sample values suggest precipitation was variable but a similar median value(-6.1‰ ± 0.22‰). From 4500 to 4000 cal BP δ^{18}O values were consistently but only slightly higher, suggesting a sustained period of somewhat less precipitation (−5.96‰ ± 0.16‰). The ~0.27‰ difference between the driest interval of 4500-4000 yr BP is about 19% of the magnitude of the deglacial δ^{18}O decrease from 11,400 cal BP ($\delta^{18}O_c$ = −4.77‰ VPDB) into the 9000-5000 cal BP wet interval. These are not large differences and are lighter than median modern values reflected in meteoric rainfall.

3.4. Statistical analyses

To identify potentially relevant subgroups within our sample of twenty-six archaeological humans, we employed a hierarchical cluster analysis using the paired $\delta^{13}C_{collagen}$, $\delta^{15}N_{collagen}$, and $\delta^{13}C_{apatite}$ measures. We then used linear discriminant analysis to determine the statistical validity of the groups and to identify which variables were the primary drivers of group differentiation. Multiple linear regressions were used to test if changes in relative population and/or precipitation significantly predict three measures of diet, $\delta^{13}C_{collagen}$, $\delta^{15}N_{collagen}$, and % C_4 (the latter calculated using a simple linear regression ((−25-($\delta^{13}C_{apatite}$-9.7))/-16) based on $\delta^{13}C_{apatite}$ from 5600 to 1000 cal BP (Model Set B) (Schwarcz, 1991; Kennett et al., 2020). These three isotope-derived variables represent different aspects of diet, therefore changes in each may signify different strategies in response to external pressures such as changes in climate or population. To investigate a potential temporally isolated relationship between the three measures of diet and the precipitation proxy, we used bivariate regression models (linear and quadratic) from 5600 to 4000 cal BP (Model Set A). Lastly, we used two-sample tests (Students t-test, or Wilcoxon Mann-Whitney Rank Sum Tests) to evaluate potential dietary differences between the transitional and agricultural groups identified in the hierarchical cluster analysis.

For the regressions and visualizations, we assigned each individual a median date generated by 10,000 Monte Carlo simulations weighted based on the probability density of the respective calibrated radiocarbon date. We assigned individuals mean $\delta^{18}O_{carbonate}$ (precipitation variable) and cKDE (relative population variable) values based on their median date ± 25 years. We extracted the $\delta^{18}O_{carbonate}$ values from the GU-RM1 record and the population values from the Maya Lowlands cKDE model. We tested all model assumptions using a combination of visual and statistical aids. Extreme outliers were identified using Cook's Distance and leverage and were removed from the models. In order to meet the assumptions of residual linearity in the multiple linear regression models, we performed a logarithmic transformation of the predictor variable (cKDE).

All the statistical analyses were conducted in the R open-source statistical software package (Rstudio Team, 2020) with some code modified from (Wilson et al., 2022). The modified code is clearly labeled with references to the original authors and is available as a supplement (Supplemental Appendix 2).

4. Results

4.1. Diet

After testing four different clustering methods, a Ward type cluster was employed (coefficient = 0.949). The average silhouette width method indicated that three clusters were the optimal number of diet groups (Fig. 2). Group 1 (n = 12) likely represents individuals transitioning from foraging to agriculture, classified by consumption of low levels of C_4 plants (0%–25.6%, sd = 8.2) and likely higher quality diet as indicated by the mean $\delta^{15}N_{collagen}$ value of 9‰ (Table 1). The mean $\delta^{13}C_{collagen}$ value for these individuals was −20.3‰, and the mean $\delta^{13}C_{apatite}$ value was −13.5‰. Group 3 (n = 11) consists of agriculturalists who consumed high levels of C_4 resources (31.3%–68.8%, sd = 10.6; consistent with the consumption of maize) with a mean $\delta^{13}C_{collagen}$ value of −10.3‰, a mean $\delta^{13}C_{apatite}$ value of −6.7‰, and a mean $\delta^{15}N_{collagen}$ value of 7.7‰. Group 2 (n = 3) consists of individuals who had a high level of C_4 consumption with a range in their % C_4 values of 53.1%–62.5%, but with a potentially higher quality diet as indicated by their mean $\delta^{15}N_{collagen}$ value of 10‰. Sample size for Group 2 is small (n = 3) and crosscuts diet groups and time periods previously identified

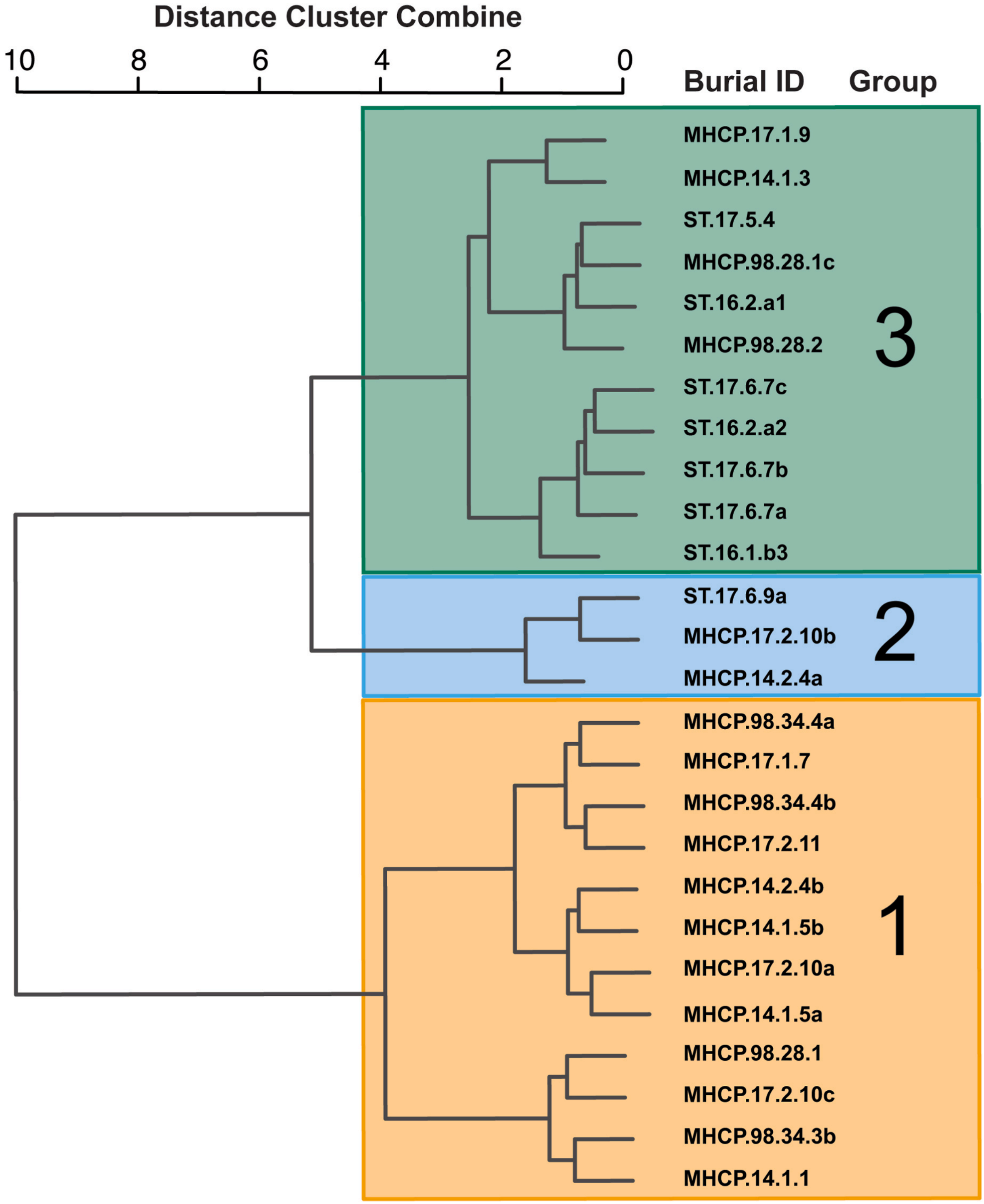


Fig. 2. Individuals clustered using Ward type clusters into three groups based on diet. Group 1 (Orange): Transitional Individuals Group 2 (Blue): Possible outliers, Group 3 (Green): Agriculturalists.

(Kennett et al., 2020) and may consist of potential outliers from the other groups. Plots of the groups raw $\delta^{13}C_{col}$, $\delta^{13}C_{ap}$, and $\delta^{15}N_{col}$ along with available modern plants and archaeological animal data are available in the supplemental (Supplemental Appendix 3).

The overall reclassification rate for the LDA (Fig. 3) was 92.5% suggesting that these are distinct diet groups. Groups 1 and 3 had high reclassification rates of 100% and 90.9% respectively. Some individuals from Group 2 were classified as Group 1 leading to a reclassification rate of 66.6% (Table 2). In part, this is likely due to a small sample size, but also because these individuals occupy a dietary space between the other two distinct groups (Fig. 4). These could also be outliers and thus were excluded from further analysis. $\delta^{15}N_{collagen}$ and $\delta^{13}C_{collagen}$ are the largest drivers of variation in LD1, while $\delta^{15}N_{collagen}$ and $\delta^{13}C_{apatite}$ are the largest drivers of variation in LD2 (Table 3).

Dietary trends between 5600 and 4000 cal BP indicate increased consumption of C_4 resources and no significant changes in diet quality. Individual values of $\delta^{13}C_{collagen}$ increase over time beginning around 5000 cal BP ($\rho = 0.6$, p-value = 0.03), however $\delta^{13}C_{apatite}$ ($r = 0.73$, p-value <0.01) values indicating increasing contribution of C_4 plants likely increase before 5600 cal BP. $\delta^{15}N_{collagen}$ values ($r = 0.41$, p-value

Table 1
Summary statistics for each dietary group identified using hierarchical cluster analysis.

Group	Variable	Minimum	Maximum	Median	Mean	Std. deviation
1 (*n* = 12)	$\delta^{15}N_{collagen}$	7.8	10.5	8.85	9.0	0.9
	$\delta^{13}C_{collagen}$	−21.1	−17.2	−20.6	−20.3	1.1
	$\delta^{13}C_{apatite}$	−15.4	−11.3	−13.4	−13.6	1.3
	% C_4	0	25.6	12.5	11.4	8.2
2 (*n* = 3)	$\delta^{15}N_{collagen}$	9.9	10.2	10.1	10.1	0.2
	$\delta^{13}C_{collagen}$	−16.9	−11.1	−11.5	−13.2	3.2
	$\delta^{13}C_{apatite}$	−6.9	−5.4	−6.6	−6.3	0.8
	% C_4	53.1	62.5	55	56.9	5.0
3 (*n* = 11)	$\delta^{15}N_{collagen}$	6.8	8.6	7.7	7.7	0.6
	$\delta^{13}C_{collagen}$	−13.1	−8.7	−10.5	−10.3	1.4
	$\delta^{13}C_{apatite}$	−10.4	−4.4	−6.3	−6.7	1.7
	% C_4	31.3	68.8	56.9	54.1	10.6

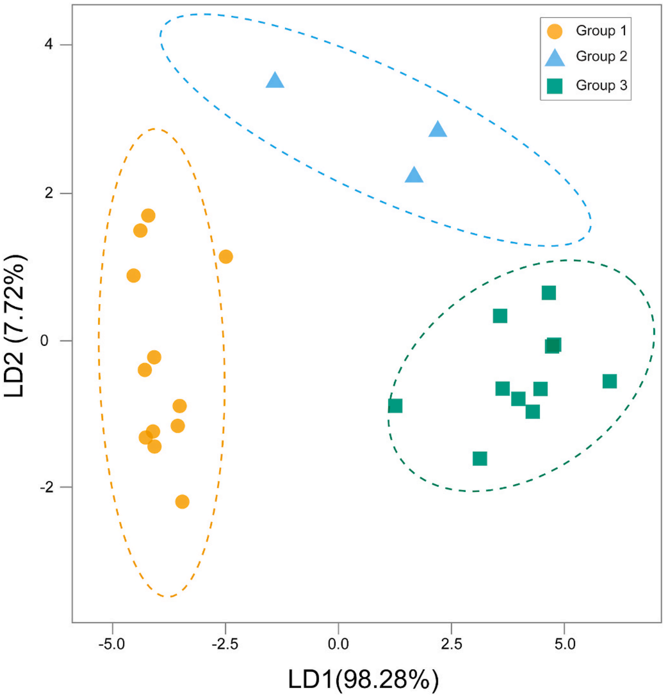


Fig. 3. LDA classifying individuals into 3 diet groups. Based on $\delta^{13}C_{apatite}$, $\delta^{13}C_{collagen}$, and $\delta^{15}N_{collagen}$. Group 1 (Orange): Transitional Individuals, Group 2 (Blue): Possible outliers, Group 3 (Green): Agriculturalists.

Table 2
Classification table for diet groups derived from hierarchical cluster analysis generated using the leave-one-out, cross validation method in linear discriminant analysis. The rows represent the actual groups, and the columns represent the groups the LDA model classified the observations into. The correct reclassifications are bolded and the total percent of observations the LDA model correctly reclassified are listed in the rightmost column.

	Group 1	Group 2	Group 3	Successful reclassification (%)
Group 1	12	0	0	100
Group 2	1	**2**	0	66.7
Group 3	0	1	10	90.9

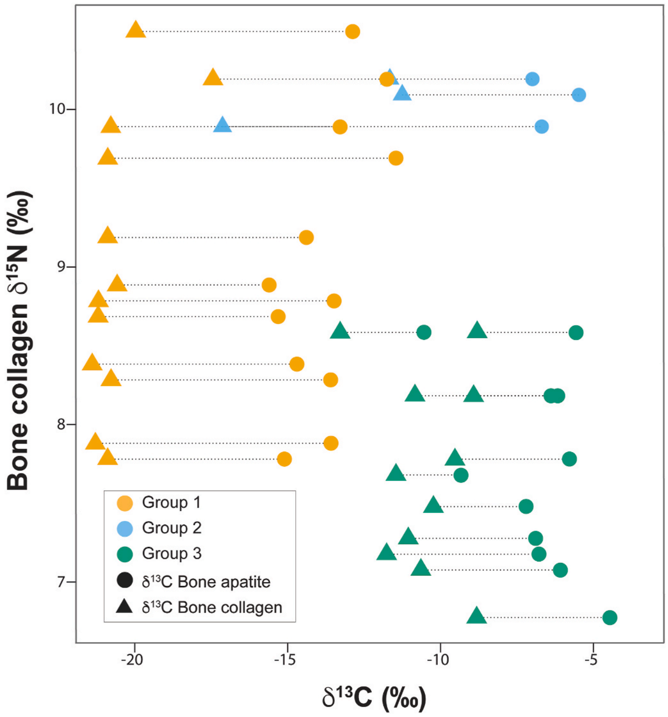


Fig. 4. Spacing plot demonstrating the differences in dietary isotopes between the three diet groups identified in the hierarchical cluster analysis.

Table 3
Coefficients of the linear discriminants (LD1, LD2) from the linear discriminant analysis on the dietary-based stable isotopes values ($\delta^{13}C_{collagen}$, $\delta^{15}N_{collagen}$, $\delta^{13}C_{apatite}$) for the 3 diet groups identified in the hierarchical cluster analysis.

	LD1	LD2
$\delta^{13}C_{collagen}$	−0.5831125	0.2606065
$\delta^{15}N_{collagen}$	0.6290126	−0.9933447
$\delta^{13}C_{apatite}$	−0.1335094	−0.5441911

= 0.14), have no statistically significant differences through time.

Two-sample tests between diet groups and $\delta^{13}C_{collagen}$, $\delta^{13}C_{apatite}$, and $\delta^{15}N_{collagen}$ reveal significant differences in all three measures between Groups 1 and 3. A Mann-Whitney *U* test for $\delta^{13}C_{collagen}$ values (W = 164, p-value <0.001) and $\delta^{13}C_{apatite}$ values (W = 159, p-value <0.001) show statistically significant differences between groups. A student's t-test (t = −3.57, p-value = 0.002) demonstrates that differences also exist between groups for $\delta^{15}N_{collagen}$ values.

4.2. *Population stability and precipitation*

The cKDE model for the Maya Lowlands shows that population levels were relatively low until about 5000 cal BP after which there was a slow increase in population size until about 3700 cal BP. After which population size rapidly increased. For southern Belize, the cKDE shows an increase in relative population prior to 6000 cal BP with some relative decline until about 3000 cal BP. The population appears to have been mostly stable between 5000 and 4000 cal BP. A slow decline appears towards the end of the period and then remains stable until populations increased coincident with the Late Preclassic (~2400 cal BP).

We used three multiple linear regression models to investigate the potential relationships between diet (response variable), and population and climate (predictor variables) across the Middle to Late Holocene (Fig. 5). All three regression models were significant (Table 4). However, in all three models we found that the relative population proxy was significantly associated with changes in each response variable while the climate proxy was not statistically significant (Table 5) (see Fig. 6).

Model Set A: We explored the relationships between the diet variables and precipitation between 5600 and 4000 cal BP (Table 4, Model Set A) using separate regression models for each diet variable and the precipitation proxy. However, we must note that these models are only applicable to this interval and cannot be accurately applied to other time periods. For the $\delta^{13}C_{collagen}$ model, there was a significant relationship between higher $\delta^{18}O$ values (less rainfall) and higher $\delta^{13}C_{collagen}$ ($r^2 = 0.8$, p-value <0.001). The relationship between $\%C_4$ and $\delta^{18}O$ values ($r^2 = 0.45$, p-value <0.01) also demonstrate a positive relationship between $\delta^{18}O$ (less precipitation) and $\delta^{13}C_{apatite}$ (C_4 consumption proxy). The regression between $\delta^{15}N$ and climate ($r^2 = 0.07$, p-value = 0.18) demonstrates no statistically significant relationship.

Model Set B: The adjusted r^2 values and the standard errors indicate that overall the model with the best fit was the $\delta^{13}C_{collagen}$ model, which had a high adjusted r^2 value (0.96) and a low standard error value (1.01), indicating that 96% of the variation in $\delta^{13}C_{collagen}$ can be explained by the model, more specifically by the relative population proxy variable, and that 96% of the actual observations $\delta^{13}C_{collagen}$ values fall within roughly ± 2‰ of the regression line. Whereas the $\delta^{13}C_{apatite}$ model has a high adjusted r^2 value (0.93) but also has an elevated standard error value (6.55), indicating that although 93% of the variation in % C_4 can be explained by the model, 95% of the actual observations % C_4 values fall within ±13.1% of the regression line. Conversely, the $\delta^{15}N_{collagen}$ model has a moderately low adjusted r^2 value (0.45), but also a fairly low standard error (0.76) indicating that 45% of the variation in $\delta^{15}N_{collagen}$ can be explained by the model, but that 95% of the actual observations $\delta^{15}N_{collagen}$ values fall within ±1.52‰ of the regression.

5. Discussion

5.1. 5600-4000 cal BP as a period of reduced rainfall

Maize is a crop that is vulnerable to drought and its increasing use across the period of reduced rainfall at the end of the Middle Holocene raises important questions regarding human behavior in the context of changing environments, increasing selection of plants with traits favorable for domestication, and social processes leading to the establishment of farming communities. Maize is less vulnerable to drought than its progenitor teosinte, particularly in terms of root architecture necessary to access moisture during annual dry seasons or longer dry intervals (Lopez-Valdivia et al., 2022). The C_4 photosynthetic pathway provides maize with a higher water-use efficiency compared to C_3 plants and some capacity for water conservation (Ehleringer and Monson, 1993).

Of the Mesoamerican dietary triad including beans and squash, maize is the only crop that can withstand a short-duration drought of less than one year where the dry season is extended by three or more months, depending on landrace, planting location, and timing of planting relative to rainfall. In a moderate or severe drought, maize cannot be grown (Fedick and Santiago, 2022). Regardless of landrace, maize is also vulnerable to even shorter dry intervals, particularly if they occur during flowering (Fischer et al., 1982) and moisture deficits lasting 1–2 days during tasseling or pollination can cause as much as a 22% reduction in yield (Robins and Domingo, 1953).

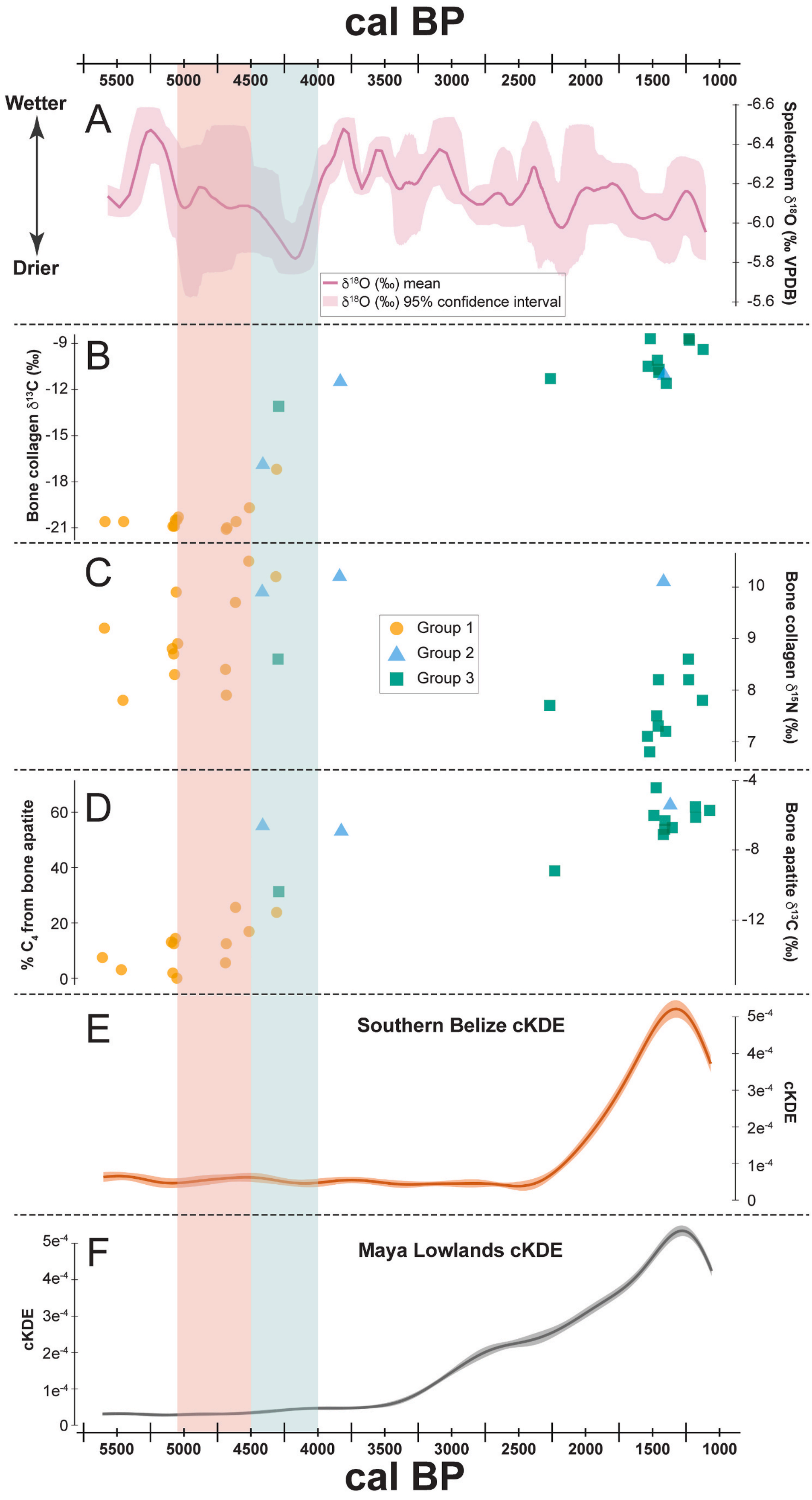
Early maize from Coxcatlán cave, Tehuacan, Mexico at 5300-4970 cal BP was analogous to progenitor teosinte in lacking root architecture necessary for drought resistance, though some selection for those traits may have been underway (Lopez-Valdivia et al., 2022). This raises particularly interesting questions regarding the movement of improved varieties of maize from South American back to the Maya area where it would have bred with existing landraces (Kistler et al., 2018, 2020), and which is hypothesized to have been related to migrations of likely farmers from the Isthmo-Colombian region prior to 5300 cal BP (Kennett et al., 2022).

The role of geography in the Maya Lowlands may also have had an impact on early maize farming. The Maya Lowlands have been described as a “seasonal desert” (Haug et al., 2001), with evapotranspiration exceeding precipitation in some dry season months (Ridley et al., 2015). Upland maize farming is very much conditioned by dependence on the timing of the seasonal distribution of rainfall (Braun et al., 2023). In the Maya Lowlands, evidence of maize farming prior to 4000 cal BP is primarily from identifications of maize pollens and/or starch grains recovered from or near perennial wetlands (Pohl et al., 1996; Wahl et al., 2006; Rosenswig et al., 2014). It is plausible that early agriculturists focused their cultivation efforts on perennial wetlands, alongside lakes, or in alluvium of perennial watercourses, providing an additional hedge against the risk of drought. Today, Chontal Maya subsistence maize farmers living in Tabasco, Mexico, practice traditional recessive flood agriculture, where wetlands are cultivated during the dry season. Both maize and squash are inter-cropped, though unlike most Classic Maya wetland farming systems no effort is made at landscape modifications such as raised or drained fields. Flood recession agriculture takes advantage of a falling water table during the dry season and relies on residual moisture and natural fertility of wetland soils. The Chotal use maize seeds selected for resilience to moisture during germination and crops are harvested before the onset of the rainy season and the seasonal flood cycle. (Peraza-Villarreal et al., 2019).

The same wetlands are the location where some of the earliest maize pollens suggest cultivation at 6000 cal BP (Pope et al., 2001; Pohl et al., 2007; Kennett et al., 2010). This system of farming produces yields similar to both rainy season upland maize farming and winter farming cycles without any fertilization of conditioning for soil fertility, and with low incidence of weeds, and substantial soil moisture (Aguirre-Rivera et al., 2019). Wetland farming in the absence of landscape modifications is highly susceptible to the timing of the onset of the dry season (for planting) and the rainy season (when harvest must be completed) to avoid crop inundation. While it is beyond the scope of this study, there is significant evidence that seasonal predictably negatively impacted maize productivity at different times in the past (Braun et al., 2023), perhaps creating risks unfavorable for later large scale surplus farming that charaterized the Late Holocene Classic Maya.

Values of $\delta^{13}C_{apatite}$ (representing carbohydrate, lipid, and some protein sources of carbon in the diet) from individuals in the Middle Holocene (5600–4000 cal BP) show a clear and increasing contribution of C_4 plants, most likely maize (Kennett et al., 2020). By 5000 cal BP we see higher $\delta^{13}C_{collagen}$ values. The $\delta^{15}N_{collagen}$ values do not indicate a change in the trophic level at which people were eating nor is there a change in diet quality. When combined with $\delta^{13}C_{collagen}$ and $\delta^{13}C_{apatite}$ data, this suggests that people started to eat C_4-consuming animals by 5000 cal BP (For ealiest direct evidence of C4 consumption see White et al., 2001; Thornton et al., 2012). The trajectory of increasing C_4 plant consumption across this period began prior to 5000 cal BP, before the onset of the dry period (Fig. 5d). Whereas the trend toward increasing consumption of C_4-consuming animals began by 5000 cal BP, the onset of the dry period.

There is also a gradual increase in relative population across this interval. Combined these may reflect a significant reduction in residential mobility as farming became the dominant subsistence strategy. Archaeologists have yet to identify the remains of residential dwellings



(caption on next page)

Fig. 5. Climate, Population, and Diet through time. A.) carbonate values from Winter et al., 2020., B.) Bone Collagen $\delta^{13}C$, C.) Bone Collagen $\delta^{15}N$, D.) %C_4 estimation from Bone Apatite, E.) SPD and KDE from Southern Belize and Maya Lowlands. Orange shading represents the SPD from Southern Belize with the dark brown line showing the posterior probability, the dark orange line is the smoothed KDE model. Gray shading represents the cKDE from the Maya Lowlands and the dark gray line is the posterior distribution for the Maya Lowlands.

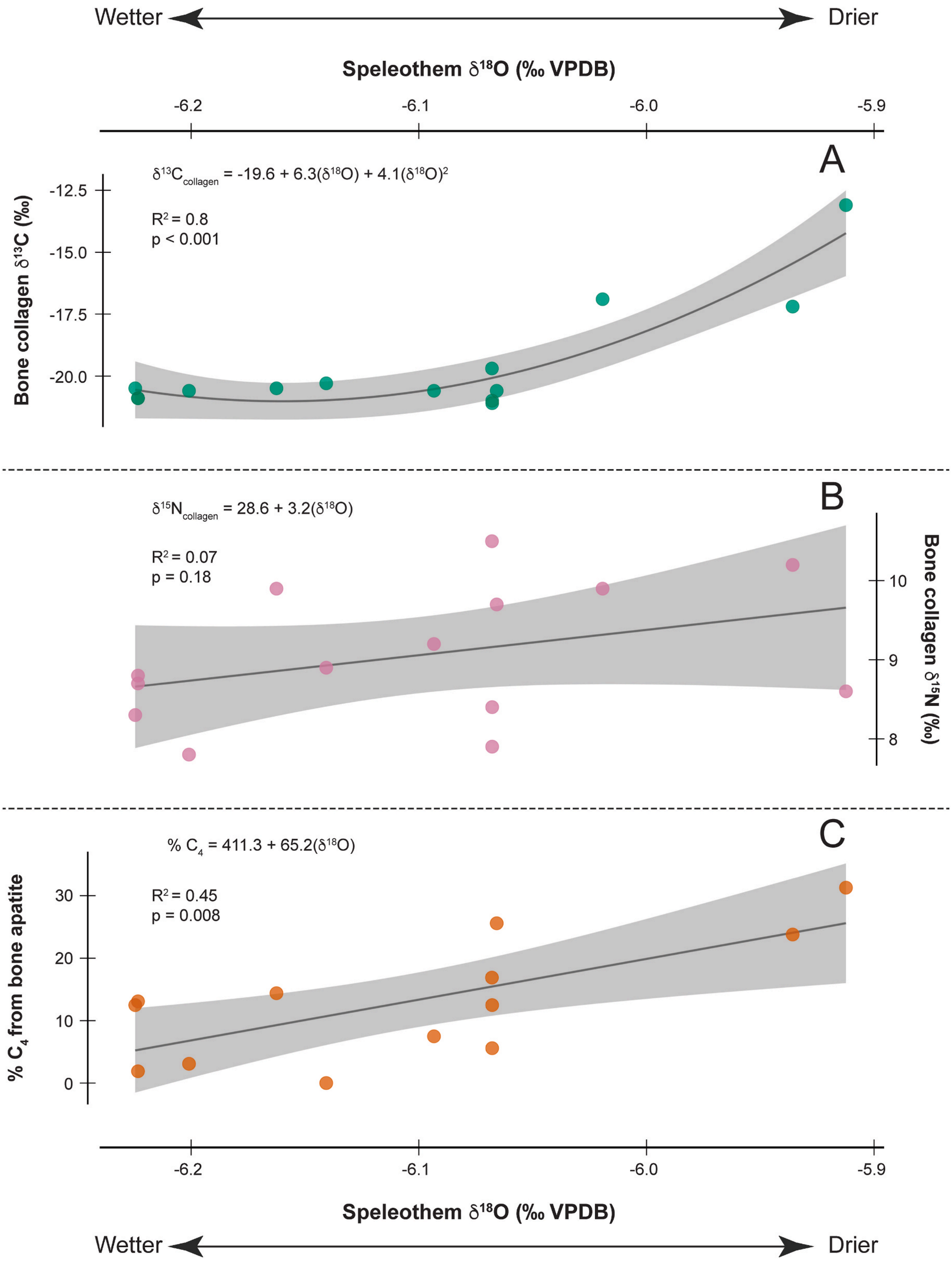


Fig. 6. Results and visualization of model set A comparing the three diet measures with the precipitation proxy. A) $\delta^{13}C_{collagen}$, the model of best fit was a quadratic regression, B) $\delta^{15}N_{collagen}$, the model of best fit was a linear regression, there is no statistically significant relationship, C) $\delta^{13}C_{apatite}$, the model of best was a linear regression.

Table 4

Regression model results testing relative population and climate proxies. A. Set of simple regression models testing the relationship between the three diet variables and climate and population from 5600 to 4000 cal BP, B. Set of multiple linear regression models testing the relationship between the three diet variables and climate and population from 5600 to 1000 cal BP.

Statistic/model	% C_4		$\delta^{13}C_{collagen}$		$\delta^{15}N_{collagen}$	
	Model Set B	Model Set A	Model Set B	Model Set A	Model Set B	Model Set A
Models	5600–1000	5600–4000	5600–1000	5600–4000	5600–1000	5600–4000
Multiple R-squared	0.94	0.49	0.95	0.83	0.29	0.14
Adjusted R squared	0.94	0.45	0.95	0.80	0.22	0.07
p-value	0.00	0.01	0.00	0.00	0.02	0.18
Degrees of freedom	20	11	22	11	22	12
F-statistic	161.3	10.67	215.2	27.29	4.47	2.02
Standard error	6.22	7.13	1.17	1.02	0.93	0.83
Error rate	18.7%	55.1%	7.5%	5.2%	10.9%	9.1%

Table 5

Results of multiple linear regression models by predictor variables. Statistically significant variables at $\alpha < 0.05$ are bolded. In each model population is significant and climate is not.

Model	Variable	Coefficient	Std. Error	t-value	p-value
% C_4	*(Intercept)*	4.88	127.22	0.04	0.97
	Population	**11.45**	**0.86**	**13.29**	**0*****
	Climate	−9.68	21.2	−0.46	0.653
$\delta^{13}C_{collagen}$	*(Intercept)*	−31.12	23.06	−1.35	0.19
	Population	**2.52**	**0.16**	**16.07**	**0*****
	Climate	−3.69	3.84	−0.96	0.35
$\delta^{15}N_{collagen}$	*(Intercept)*	28.61	15.72	1.82	0.08
	Population	**−0.34**	**0.11**	**−2.95**	**0.01****
	Climate	3.46	2.62	1.32	0.2

prior to ~3000 cal BP in the Maya Lowlands. However, non-elevated and perishable structures without stone foundations are difficult to locate given vegetation cover, high rainfall, erosion, and later Formative and Classic Period modifications to the built environment. Subsistence maize farming is also a labor and time-intensive activity, requiring significant time for clearing, planting, tending, harvesting, and processing (Kramer and Boone, 2002), which is likely incompatible with itinerant subsistence strategies.

Although generally, populations are low compared to later periods, during the period from 5600 to 4000 cal BP, we see evidence for very gradual population increase beginning by 4500 cal BP. This is reflected in both the southern Belize cKDE and the Maya Lowlands cKDE. Across this period consumption of C_4 (maize) and maize-eating animals increased as populations increased, as reflected in higher $\delta^{13}C_{collagen}$ values.

It might also be that slightly drier conditions in the lowlands favored maize production in contrast to the slightly wetter period from 9000 to 5000 BP. Would minor changes in rainfall and wetter soil conditions disfavor maize production? The GU-RM1 record would suggest that rainfall during the period 4500-4000 cal BP (median $\delta^{18}O$ −5.95‰, ±0.16‰) might have been only slightly reduced from that of the Classic Period from 2000 to 1000 cal BP (median $\delta^{18}O$ −6.1‰ ± 0.14‰), when maize production for surplus storage and consumption was arguably at its peak.

If C_4 production was hampered by drought during this period, we would expect to see either: 1) significant population declines suggesting that people may have been forced to move elsewhere (as seen in other regions of the world) (Petraglia et al., 2020; Schug et al., 2023); or 2) decreased C_4 consumption. Since our data show that populations were relatively stable and diet shifted toward increasing rather than decreasing C_4 consumption, overall maize production was not impeded by this event.

On the other hand, if small variations in rainfall across the period from 5100 to 4000 cal BP had little effect on the ability of people to produce maize, then increasing consumption of maize might be linked to other social processes, including changes in the availability of improved maize varieties (Kistler et al., 2018, 2020), demic diffusion of people with knowledge of farming and farming technologies into the region (Kennett et al., 2022), changes in dietary preferences (Tung et al., 2020), or the appeal and collective benefits of more sedentary lifeways linked to plant management and subsequent demographic growth, as seen in South America in the centuries after maize domestication (Souza and Riris, 2021).

5.2. Changes in diet and population from 4000 to 1000 cal BP

Population change in the Maya Lowlands was much more pronounced after the thousand-year-long dry interval. There is a significant demographic shift between 3500 and 2500 cal BP (Fig. 5f) coincident with the emergence of archaeologically documented population centers, increasingly diverse ceramic assemblages, and institutional hierarchies. Likewise, diets were significantly changed by 3500 cal BP. Statistically significant differences were observed in $\delta^{13}C_{collagen}$, $\delta^{13}C_{apatite}$, and $\delta^{15}N_{collagen}$ clearly demonstrating that the individuals from 5600 to 4000 cal BP have distinctly different diets than the Classic Maya. While this should not be surprising, it emphasizes the fact that the individuals living during the driest part of the Middle Holocene were farmers who were already transitioning to a more maize-reliant diet but had not yet become full-fledged agriculturalists. In southern Belize this demographic increase comes later, at 2500 cal BP. Reasons for this late development may be related to an emphasis on collective actions of small urban centers to the north of this region, or to the stability of low-density settlements in the agriculturally rich upland environments. Human presence in the region from 3500 to 2500 cal BP is well documented (Prufer and Kennett, 2020).

Eurasian models of the agricultural demographic transition emphasize the relationship between increasing sedentism and agriculture as potential drivers (Gage and DeWitte, 2009; Betsinger and DeWitte, 2021). The exact mechanisms have not been identified but have been hypothesized as increased fertility, decreased mortality, or increased carrying capacity (Bocquet-Appel, 2011; Smith, 2015). South American studies of demographic change, however, have shown that plant domestication and cultivation likely preceded population growth (Riris and Arroyo-Kalin, 2019; Souza and Riris, 2021). They argue that plant cultivation without full reliance on agriculture may have predominated throughout much of South America from 4800 to 2000 cal BP. Similarly, Rosenswig (2021) argues that mixed-horticultural strategies were very successful for Late Holocene Mesoamericans.

Archaeological and paleoenvironmental reconstructions of human responses to climate change have revealed similar results in other regions globally. People in the northern Arabian Peninsula, for example, invested in water management early on, which mitigated the effects of the shifting climate regime during the Early and Middle Holocene (Petraglia et al., 2020). This was not true for other parts of the peninsula, where the drying climate resulted in depopulation in the interiors and a migration to coastal sites (Petraglia et al., 2020). In Asia, Early Holocene urban communities were also disproportionately affected by climate change compared to more egalitarian communities in the region (Schug et al., 2023). The Maya Lowlands had yet to see the development of urban centers and there is currently no evidence pointing toward the migration of local individuals to other regions of the Maya Lowlands.

6. Conclusions

Our data show both increased maize consumption during the Middle/Late Holocene transition and gradual change in population structure. Although there is variation between individuals, our analysis of $\delta^{15}N_{collagen}$ values across this interval does not indicate significant changes in diet quality across the period from 5600 to 4000 cal BP. Individual's $\delta^{15}N_{collagen}$ values remain higher than those for Classic Maya farmers, suggesting that sufficient sources of protein were available to the population despite slightly decreased precipitation. Unlike many regions in the world where researchers have argued that massive cultural and demographic shifts occurred, including political collapses, or rapid depopulation, we argue that the decrease in precipitation may have been instrumental to the further adoption of maize farming. People in the northern neotropics had already begun to invest in agriculture and maize cultivation well before 5000 cal BP and continued to cultivate and increasingly consumed maize throughout the Middle/Late Holocene transition as populations gradually increased. The transition from the wetter Middle Holocene to the drier Late Holocene provided ideal conditions and adequate precipitation for maize cultivation. Populations appear relatively stable during the Middle Holocene as maize consumption increased. Relatively low initial populations and a lack of evidence for institutionalized social stratification suggest that the people residing in the region may have been more flexible and adaptable to the climate shifts in this humid region.

In the face of our own uncertain climate future, we can look to the past and examine the ways in which people were able to adapt to changing conditions. This research demonstrates how an assessment of continental-scale climate variability suspected of altering human subsistence strategies might instead reveal the resilience of existing dietary pathways and trajectories. We use dietary isotopes and population proxies to explore if climate conditions around 4500-4000 cal BP might have altered the trajectory for the incorporation of maize into the diets of people living in the northern neotropics. By 4500 cal BP the adoption of maize, an important carbohydrate food source, was well underway and maize was also a source of food for some animals that humans were consuming. Maize farming had already been practiced since at least 6000 cal BP and the initial increase in maize consumption appears to predate the onset of drier climate conditions. The trajectory of maize consumption from 4500 to 4000 cal BP is striking with the mean percent of maize in the total diet for the majority of individuals rises from $<25\%$ to $>50\%$ across this interval (Kennett et al., 2020). We see no indications that diet quality was declining prior to or during this period of increased maize consumption which is also a period of gradual population increase. Rapid population growth does not start until centuries later, likely coincident with social institutions increasingly dependent on large-scale surplus production and coincident with emergence of public architecture and institutional inequality. In sum, while climate during the period from 5000 to 4000 cal BP underwent protracted drying, these conditions are isotopically less extreme than contemporary climate over the last century. Our data suggest that because people in this region had already invested in maize cultivation, this drier interval did not cause them to abandon their existing trajectory or pursuits through innovations and experimentation with wetland agriculture and selection of maize varieties resilient to higher levels of soil moisture. Research in other areas of the world has exhibited intra-regional variation in adaptive strategies to deal with drier intervals and the same may be the case for tropical Central America. The people buried at Saki Tzul and Mayahak Cab Pek in the Ek Xux Valley proved to be resilient to this time period. This research shows that climate change does not necessarily limit actions or reactions, but in fact, can facilitate growth, resilience, and innovation.

Data availability

Radiocarbon dates are available from MesoRAD v.1.4 (Hoggarth et al., 2021; https://doi.org/10.5334/joad.83). Stable isotope data are available in Supplementary Table 1 (Kennett et al., 2020; doi: 10.1126/sciadv.aba3245). Full data for the paleoprecipitation proxy from Winter et al. 2020 can be accessed through Paleo Data Search (https://www.ncei.noaa.gov/access/paleo-search).

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Compliance and ethics statement

Permits to conduct field research and for the exportation of charcoal and human remains for radiocarbon dating and stable isotope analysis were issued by the Institute of Archaeology, National Institute of Culture and History, Belize and Belize Forestry Department to KMP. This research was conducted in collaboration with the Ya'axché Conservation Trust. Two of the co-authors (KMP, DJK) as well as other researchers involved in the project have been engaged in ongoing formal consultations and active collaborations with members of descendent communities in the region since 2016. In addition to presenting findings to the local communities, members of the project have also presented research at the Belize Archaeology Symposium, a public forum in 2014, 2016–2019, and 2022.

CRediT authorship contribution statement

Erin E. Ray: Conceptualization, Formal analysis, Investigation, Methodology, Visualization, Writing – original draft, Writing – review & editing. **Nadia C. Neff:** Formal analysis, Methodology, Investigation, Visualization, Writing – original draft, Writing – review & editing. **Paige Lynch:** Methodology, Investigation, Writing – original draft. **Jose Mes:** Methodology, Investigation. **Matthew S. Lachniet:** Investigation, Writing – original draft. **Douglas J. Kennett:** Methodology, Funding acquisition, Writing – original draft, Writing – review & editing. **Keith M. Prufer:** Conceptualization, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Validation, Visualization, Writing – original draft, Writing – review & editing, All authors gave final approval for publication.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

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