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RESEARCH

Hunter-Gatherer Population Expansion and Intensification: Malthusian and Boserupian Dynamics

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Abstract

Despite years of debate, the factors that control the long-term carrying capacity of human populations are not well understood. In this paper, we assess the effect of changes in resource extraction and climate-driven changes in ecosystem productivity on the carrying capacity of hunter-gatherer populations in a terrestrial and coastal ecosystem. To make this assessment, we build time-series estimates of changes in resource extraction using stable isotopes and ecosystem productivity using paleoclimate models and geomorphic records of flood events. These estimates of resource extraction and ecosystem productivity allow us to assess a complex model of population expansion that proposes linked changes between population density, resource extraction, and intensification. We find that changes in resource extraction had a larger effect on carrying capacity in both the terrestrial and coastal ecosystems than climate drivers of ecosystem productivity. Our results are consistent with the idea that both Malthusian limits on resources and Boserupian pressures to reorganize economic systems operate in hunter-gatherer populations over the long term. Our data and analysis contribute to evaluating complex models of population growth and subsistence change across archaeological cases.

Keywords Human population ecology · Hunter-gatherer · Intensification · Population growth

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Introduction

One of the most important debates in human population ecology centers on the processes that control the long-term carrying capacity of human societies (*e.g.*, Anderies, 2003; Bettinger, 2015; Binford, 2001; Boserup, 1981; Cohen, 1995; Freeman *et al.*, 2020, 2021; Hassan, 1981; Kelly, 2013; Kelly *et al.*, 2013; Meyer & Ausubel, 1999; Puleston & Winterhalder, 2019; Puleston *et al.*, 2014; Richerson & Boyd, 1998; Tallavaara *et al.*, 2018; Winterhalder *et al.*, 1988; Wood, 1998, 2020). On one side, many researchers argue that human populations respond mainly to climate-driven changes in the productivity and reliability of ecosystems and, thus, limit on those populations' supply of food (*e.g.*, Bevan *et al.*, 2017; Kelly *et al.*, 2013; Lima *et al.*, 2020; Prentiss *et al.*, 2018; Puleston *et al.*, 2014; Tallavaara & Jørgensen, 2021; Tallavaara & Seppä, 2011). On the opposing side, many researchers acknowledge that climate may impact the supply of food available from ecosystems; however, these researchers emphasize the effects of cultural evolution and/or the adoption of new forms of resource extraction on raising the limits of a population's supply of food (Bettinger, 2015; Boserup, 1981; Cohen, 1995; Freeman *et al.*, 2021; Peralta *et al.*, 2022; Shennan *et al.*, 2013; Smith, 2021; Wood, 1998, 2020). As noted by Kirch *et al.* (2012), moving the above debate forward requires evaluating models of population growth with the many long-term "experiments" of social, technological, and climate changes documented in the past. In this paper, we contribute to this research agenda by developing and analyzing archaeological and environmental data sets to assess a specific model of population expansion and intensification that we call the hunter-gatherer Malthus-Boserup (MaB) Ratchet.

The hunter-gatherer MaB Ratchet is one model drawn from a collection of Malthus-Boserup models of human population expansion, with little cross citation, that integrates three principles: (1) amplifying population feedback, (2) limits, and (3) escapes from limits (*e.g.*, Anderies, 2003; Cohen, 1995; Freeman *et al.*, 2021; Lee, 1986; Meyer & Ausubel, 1999; Richerson *et al.*, 2009; Richerson & Boyd, 1998; Wood, 1998, 2020). (1) Amplifying feedback means that more individuals beget more individuals, thus Malthus' famous statement that human population tends to grow geometrically (Malthus, 1888). (2) However, the supply of food, in a given production system, tends to only increase linearly (Malthus, 1888). In other words, at some point, the amplifying feedback of population growth must be slowed and overcome by a negative feedback in which competition for a limited supply of food creates less and less surplus, decreasing net population growth. These two principles form the foundation of the Verhulst logistic model. In continuous form: $G(p)=pr(1\text{-}p/K)$, where r is the maximum rate of growth controlled by the ability of individuals to convert resources into fitness, and K is the maximum population density of a given area, set by the density of a resource base.

Many researchers realize that K changes over time such that, at minimum, $K_t=(x_{e,t}, L_t, S_t, I_t)$ (*e.g.*, Anderies, 2003; Cohen, 1995; Meyer & Ausubel, 1999; Puleston *et al.*, 2014; Richerson *et al.*, 2009; Richerson & Boyd, 1998; Wood, 1998, 2020); where the maximum density of resources available to a human population (K) depends upon: Ecosystem productivity ($x_{e,t}$), labor (L_t), the social organization of production (S_t), and physical infrastructure (I_t, including tools, roads, etc.) at time t. These four variables interact and change across many scales of space and time, creating a complex theoretical and methodological research problem. The two opposing approaches noted in the opening paragraph simplify the problem by making one of two assumptions: (a) Researchers assume, often implicitly, that the effects of L_t, S_t, and I_t on K are small relative to the effects of changes in climate on ecosystem productivity ($x_{e,t}$) (*e.g.*, Tallavaara & Jørgensen, 2021; Tallavaara & Seppä, 2011; Kelly *et al.*, 2013), or (b) researchers assume that the effects of climate change are small relative to changes in L_t, S_t, and I_t that impact K. Researchers who make assumption (b) often propose that (3) populations escape from limits by substituting human, social, and technological capital for natural capital to improve the productivity of resource extraction (Boserup, 1981).

Although Malthus-Boserup models all integrate the three principles above, there is no consensus model. Significant differences exist regarding how to theorize and model changes in L_t, S_t, and I_t, and this leads to divergent models of population dynamics. For example, Anderies (2003) models a two-sector economy with population and resource dynamics. In Anderies' model, technological changes that both reduce an individual's environmental impact and increase productivity per capita, under most parameter combinations, lead to a population overshoot and collapse. This result resembles the classic *Limits to Growth* simulations in which technological changes that improve efficiency actually amplify global population overshoot and collapse (Meadows *et al.*, 1972). Conversely, Richerson *et al.* (2009) assume that innovations (subsuming all social and technological changes into a parameter) occur very slowly relative to population changes and that this "Boserupian parameter" defines the pool of innovations available to populations. In Richerson and colleagues' model, as long as innovation and diffusion rates are high enough, populations never approach a limit or experience overshoot and collapse. Rather, populations display rapid and then slow and continuous long-term growth.

The Malthus-Boserup Ratchet describes a third approach to Boserupian escapes (Freeman *et al.*, 2021; Meyer & Ausubel, 1999; Wood, 1998, 2020). For example, Freeman *et al.* (2021) propose that as a population approaches the K of any given system (Malthusian limit), competition for resources results in the instability of return rates between habitats in which foragers might reside (Freeman & Anderies, 2012; Freeman *et al.*, 2019). This instability acts as a signal that feeds back onto the decision-making of foragers, creating a selective environment that favors investing in infrastructures that improve the productivity of resource extraction from local habitats and, in an emergent way, hunter-gatherer economies. This change, by definition, occurs at a time scale faster than population change and, due to the basic Malthusian assumption of amplifying feedback, results in population growth (*e.g.*, Wood, 1998, Figs. 8 & 9). Changes in L_t, S_t, and I_t may come from outside (a pool of innovations that a population might learn from others) or inside (modifications to existing infrastructure, etc.) a system; this depends upon the scale of the system under study. A key difference from the above models, however, is the assumption that changes in L_t, S_t, and I_t occur in a punctuated fashion and then also face a limit. Initial changes have a big effect by opening up a new potential niche; however, subsequent changes simply modify how efficiently foragers can exploit the niche, with less and less of an impact on K as many foragers adopt the new social-technological set and make smaller and smaller marginal changes to that set.

Figure 1A summarizes the hunter-gatherer MaB Ratchet. The MaB Ratchet suggests that human societies display waves of density-dependent population growth driven by changes in labor, social organization, and infrastructure that raise a region's carrying capacity over time ($K(t)$). This is captured in Fig. 1A by the red dashed curve. The orange curve illustrates a component of logistic

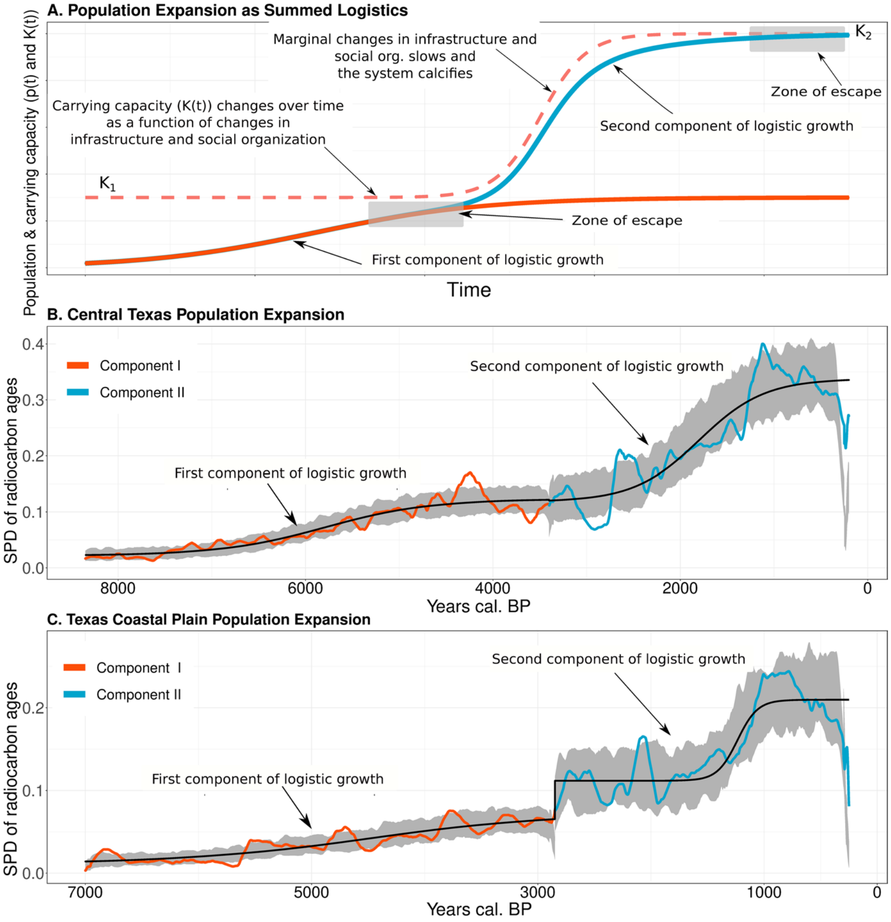


Fig. 1 **A** The proposed population and carrying capacity dynamics of the hunter-gatherer MaB Ratchet. **B** The sum of two logistic models fit to the SPD of Central Texas between 8400 and 250 cal BP. **C** The sum of two logistic models fit to the SPD of the Texas Coastal Plain from 7000 to 250 cal BP. Gray shading indicates a 95% confidence envelope for each respective logistic model using the R package rcarbon (Crema & Bevan, 2021). B and C are redrawn from Freeman *et al*. (2021) using updated data

population growth. As population grows toward the orange curve's carrying capacity, the population enters a "zone of escape." It is in this zone that instability in the return rates from foraging between habitats can act as a selective pressure that favors large changes in S_t and I_t, increasing the productivity of local habitats. Such cultural changes, at first, increase K over time, and the blue curve illustrates how this increase in $K(t)$ drives a population up to a new component of logistic population growth (Freeman *et al.*, 2021; Meyer & Ausubel, 1999). However, notice that the red dashed curve eventually plateaus because foragers eventually fill up a niche, making smaller and smaller marginal improvements to the productivity of this niche, resulting in a new long-term limit in population growth and a new zone of escape.

To evaluate the plausibility of the hunter-gatherer MaB Ratchet, Freeman *et al.* (2021) used 2400 radiocarbon ages from the Coastal Plain and Central ecoregions of Texas to create calibrated summed probability distributions (SPDs) as an estimate of changes in human population (Fig. 1). To assess whether SPDs in Texas display a structure similar to Fig. 1A, Freeman *et al.* (2021) used loglet analysis (Meyer & Ausubel, 1999; Meyer *et al.*, 1999) to fit summed logistic models to the SPDs in Central Texas and the Texas Coastal Plain. Loglet analysis fits a series of summed logistic models and uses a simulated annealing process to find the set of summed logistics, for a given set of initial conditions, that best describe the overall curve. Freeman *et al.* found two potential components of population growth (*i.e.*, two logistic curves) fit the overall curve best in Central and Coastal Texas over the last 8400 and 7000 years, respectively. Figure 1B and C illustrate these logistic curves with 95% confidence envelopes. For example, note the s-shape of the logistic curve in Fig. 1B from 8400 to 3400 cal BP and the ratchet-up to a new s-shaped logistic curve from 3399 to 250 cal BP. Figure 1C displays an analogous pattern. The fit of these component logistic models suggests that hunter-gatherers in these regions of Texas, perhaps, experienced punctuated population expansions consistent with the MaB Ratchet.

However, fitting a population model is suggestive but in no way definitive. As noted, large changes in the productivity of ecosystems driven by climate or geological processes may also lead to expansions in the carrying capacity of hunter-gatherer populations (*e.g.*, Kelly *et al.*, 2013; Lima *et al.*, 2020; Tallavaara & Jørgensen, 2021; Tallavaara & Seppä, 2011). The MaB Ratchet only focuses on social and economic changes, generated in the zone of escape, that increase $K(t)$ and drive a population toward a new, higher, but ultimately limited carrying capacity. Thus, the central question of our paper is whether the structural changes documented in the SPDs of Fig. 1B and C associate with changes in resource extraction that increased the productivity of hunter-gatherer economies, externally driven changes that increased ecosystem productivity, or some combination of both? If the structural changes in the SPDs associate with evidence of intensification and increasing economic productivity rather than evidence of externally driven increases in ecosystem productivity, then this would provide corroborating evidence for the MaB Ratchet process.

Data and Methods

To assess the effects of changes in resource extraction and ecosystem productivity on the expansion of human carrying capacity, we collected data in three steps. *Step One*, we developed time-series of changes in the external drivers of ecosystem productivity and the extraction of resources over the two potential components of logistic population growth displayed in Fig. 1B and C. We developed these time-series at a 200-year resolution from 7500 to 200 years cal BP in Central Texas and 6900 to 200 years cal BP on the Texas Coastal Plain (Fig. 2). This resolution balances the availability of data and the statistical power necessary to detect the effects of resource extraction and ecosystem productivity estimates on human carrying capacity.

To estimate externally driven changes in the terrestrial productivity of ecosystems, we modeled net primary productivity (NPP) in Central Texas from 7500 to 200 cal BP and on the Texas Coastal Plain from 6900 to 200 cal BP. In theory, higher NPP results in more food produced per unit area per unit time, and previous work indicates that as NPP increases, the population density of ethnographically recorded hunter-gatherers increases (though at a diminishing rate at higher levels of NPP) (Allen *et al.*, 2016; Binford, 1983; Codding & Jones, 2013; Freeman *et al.*, 2020; Tallavaara *et al.*, 2018). As a first approach, we used PaleoView (Fordham *et al.*, 2017) to estimate the mean annual temperature and precipitation in our two regions. We then used the Miami model to convert the temperature and precipitation estimates into NPP estimates (Lieth, 1973) at each 200-year time step. Finally, we examined the time-series and, qualitatively, compared these time-series to the best synthesis of paleoclimatic/ecological data in Central and Coastal Texas (Wong *et al.*, 2015, p. 170; see also the Supporting Information, Section I). The fit in Central Texas between the paleoecological records and modeled NPP suggests that the

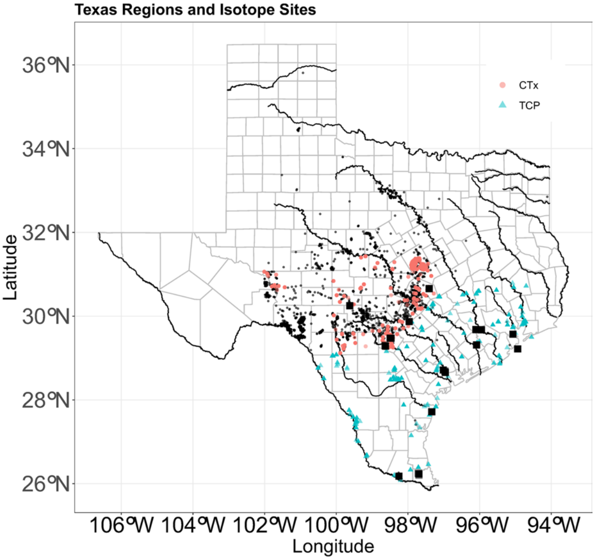


Fig. 2 The Central Texas and Texas Coastal Plain regions. The red dots and blue triangles illustrate the distribution of radiocarbon ages used to construct the population curves of Central Texas and the Texas Coastal Plain, and the black squares indicate mortuary sites in each region with data on human stable isotopes. Small black dots indicated recorded burned rock midden features

modeled data track changes in terrestrial productivity, primarily driven by changes in precipitation.

Hunter-gatherers on the Texas Coastal Plain also had access to estuary ecosystems. We estimate changes in the productivity of these ecosystems by the frequency of estuary flood events recorded for five bays along the Texas Gulf Coast (Anderson & Rodriguez, 2008; Anderson *et al.*, 2014). These data allow us to classify time periods of more vs. less frequent estuary flooding. The idea is that flood events disrupt species distributions and decrease the area of estuaries, and, thus, estuary productivity (Ricklis & Weinstein, 2005). We assume that the more frequent the flood events, the lower the potential productivity of estuary ecosystems.

Step Two, to estimate changes in the extraction of energy-dense resources by hunter-gatherers, we use stable isotopes from human bone from Central and Coastal Texas. In Central Texas, a primarily terrestrial ecosystem, we used changes in $\delta^{13}C$ apatite from 160 individuals buried over the last 7500 years (Fig. 2) to estimate changes in the extraction and consumption of carbohydrate-rich plants. Apatite carbon provides an estimate of the whole diet, while carbon isotopic values from collagen track the consumption of protein, primarily derived from animals. As such, apatite $\delta^{13}C$ includes carbon from both plants and animals, and in our Central Texas sample, $\delta^{13}C$ from apatite and $\delta^{13}C$ collagen strongly correlate ($\varrho = 0.93$, $p < 0.05$). Similarly, as discussed below, δ^{15}N potentially tracks changes in the trophic position of foragers, with less consumption of large animals and carnivores leading to lower values. In our sample, $\delta^{13}C$ from apatite and $\delta^{15}N$ strongly and positively correlate ($\varrho = 0.62$, $p < 0.001$). Thus, lower values of $\delta^{13}C$ from apatite indicate relatively more consumption of resources with a C_3 photosynthetic pathway and less protein consumption from animals. While we cannot rule out increased consumption of C_3-feeding animals from human bone isotope values alone (see below), in terrestrial environments like Central Texas, ethnographically recorded hunter-gatherers increase their extraction and consumption of carbohydrate-rich plants to increase the energy produced from their resource base (*e.g.*, Freeman *et al.*, 2021; Morgan, 2015; Binford, 2001).

To better establish that changes in $\delta^{13}C$ from apatite in Central Texas result from the increased extraction and consumption of plants with a C_3 photosynthetic pathway, we also collected data on the surface area of potential earth oven features, including large burned rock middens (see Supporting Information, Section II). Burned rock midden features, in Central Texas, result from the repeated baking of large quantities of bulbs and hearts in rock-lined earth ovens (*e.g.*, Black & Thorns, 2014; Thoms, 2008, 2009; Black, 2003; Mauldin *et al.*, 2003; Ellis, 1997). In Central Texas, hundreds of burned bulb fragments recovered from feature macrobotanical and flotation samples indicate that these features were used to roast geophytes (all C_3 plants), such as wild onion (*Allium sp.*), eastern camas (*Camassia scilloides*), and dog's tooth violet (*Erythronium mesochoreum*) (*e.g.*, McAuliffe *et al.*, 2023; Acuña, 2006; Dering, 2003). These bulb species are high in carbohydrates and low in protein. Thus, consuming these resources more frequently should lower $\delta^{13}C$ apatite values among foragers. The assumption here is that the larger the surface area of remnant cooking features, the more cooking events occurred, indicating more extraction and consumption of carbohydrate-rich plants low in protein.

On the Texas Coastal Plain, where foragers exploited aquatic ecosystems, we use $\delta\ ^{15}N$ from 267 individuals to estimate the intensification of fishing over time. Increases in $\delta\ ^{15}N$ indicate more protein consumption at higher trophic levels, and consumption from aquatic ecosystems increases these values due to more complex and longer aquatic ecosystem food webs (Hard & Katzenberg, 2011). In coastal environments, hunter-gatherers living at high population densities consume large quantities of fish and shellfish, in part, because such resources provide greater energy and protein returns over carbohydrate-rich plants (Binford, 2001; Morgan, 2015). Thus, we argue that increases in $\delta\ ^{15}N$ signal intensified extraction and consumption of fish, shellfish, and other aquatic taxa, whether from freshwater rivers or coastal estuaries on the Texas Coast (Hard & Katzenberg, 2011; Johnson & Hard, 2008).

Finally, we arrayed all individuals into a time-series and then averaged the stable isotope values of individuals for every 200-year interval from 7500 to 200 cal BP in Central Texas and 6900 to 200 cal BP on the coast. In Central Texas, 6/36 or 16.6% of time-series points contained missing data (*e.g.*, no individuals with isotope data from 5900 to 5700 cal BP). On the Texas Coastal Plain, 2/33 or 6% of time points contained missing data (Supporting Information, Section II). Rather than delete these time points, we used the Missforest R package to impute the missing data (Stekhoven & Stekhoven, 2013). We ran 15,000 random forest regression trees to impute the missing isotope data (Supporting Information, Section II). This conserves the information in the data set and results in more fair statistical analyses. Missing information can bias analyses in favor of preferred results. In this case, the results are the same whether we impute missing data or not.

Step Three, following Freeman *et al.* (2021), we collected 1772 archaeological radiocarbon ages from Central Texas and 995 archaeological radiocarbon ages from the Texas Coastal Plain. We ran the three-component loglet analysis proposed by Freeman *et al.* (2021) for Central Texas and the Texas Coastal Plain (see Supporting Information Section III). Using the R package rcarbon, we constructed unnormalized summed probability distributions (SPDs) for the radiocarbon ages to estimate changes in population over the last 12,500 years in Central Texas and 11,000 years along the coast (Crema & Bevan, 2021). Given that radiocarbon records are subject to several potential biases, such as sampling intensity, preservation, and the non-linear radiocarbon calibration curve (*e.g.*, Crema & Bevan, 2021; Freeman *et al.*, 2018; Crema *et al.*, 2017; Timpson *et al.*, 2014; Shennan, 2013; Williams, 2012; Surovell *et al.*, 2009), we constructed all SPDs using 100-year moving means. We control for the oversampling of particular archaeological sites by clustering dates by site using the h function ($h = 100$) in rcarbon. Both of these procedures smooth the SPD to capture the long-term trend over time, reducing larger fluctuations over shorter time scales. In both cases, we used the Intcal2020 calibration curve (Reimer *et al.*, 2020) in the rcarbon package to calibrate the radiocarbon ages (Crema & Bevan, 2021).

The loglet analysis largely replicates the findings of Freeman *et al.* (2021) (see Supporting Information, Section III). Once we identified potential components of logistic growth in the SPDs of Central and Coastal Texas, we used rcarbon to fit logistic models to the data. In both regions, we fit two separate, four-parameter logistic models (see Fig. 1B and C). We then summed the resulting SPD, fit logistic models, and confidence envelopes up to 200-year bins, beginning at 7500 in Central

Texas and 6900 cal BP along the coast. This allowed us to create the time-series displayed in Figs. 3 and 4.

Time-series and regression models

Figures 3 and 4 provide a visual representation of the data. On each graph, we use color ramps to illustrate how the values of ecosystem productivity and resource extraction change as the values of the SPD change over time. Figure 3A illustrates the relationship between modeled NPP and the SPD in Central Texas. Over

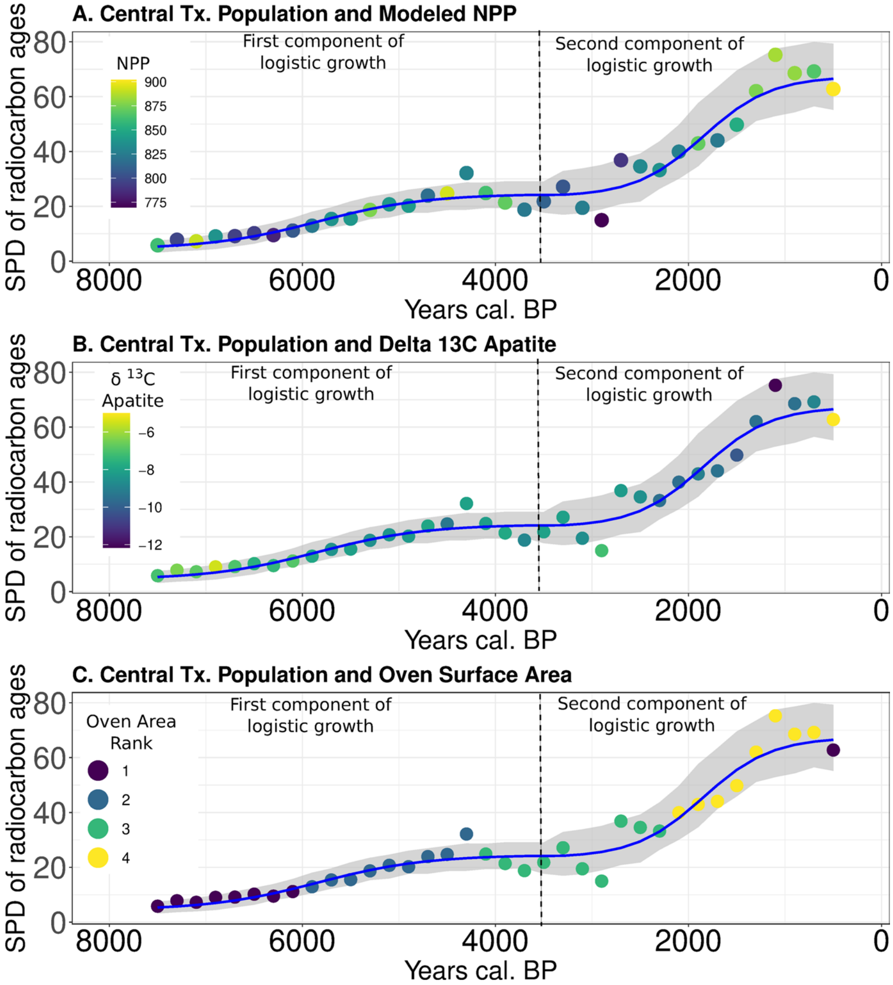
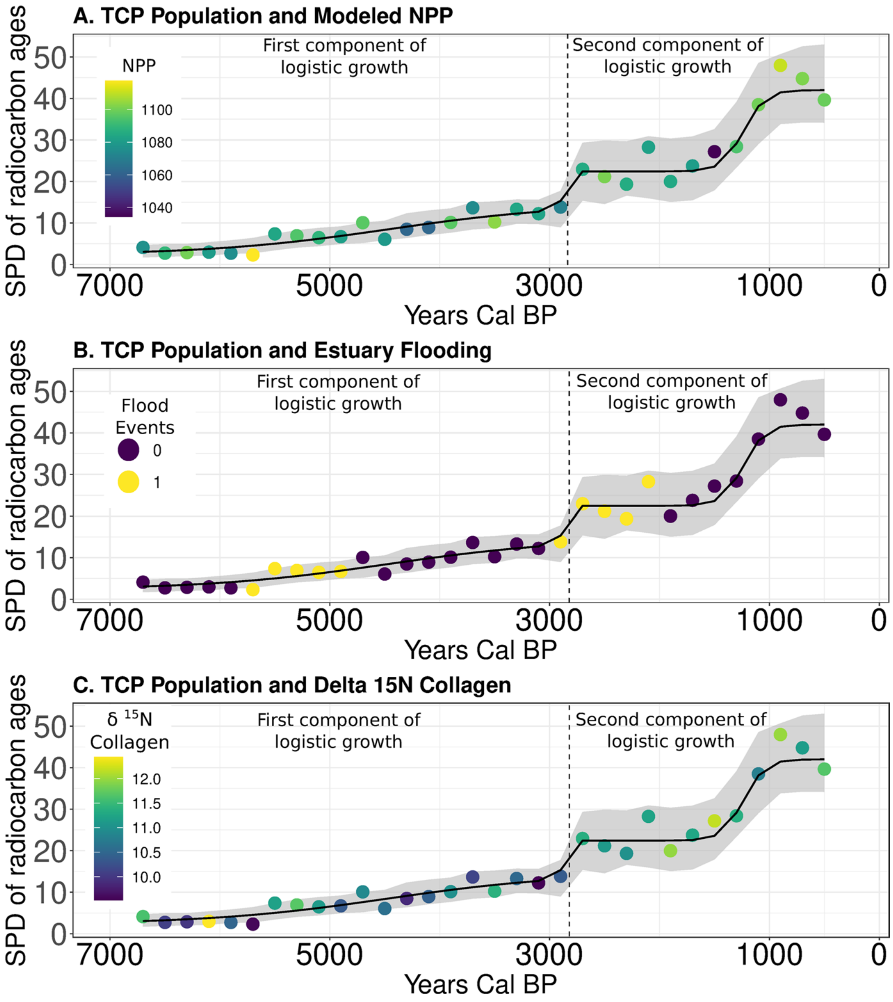


Fig. 3 Summary of the 200-year time-series of data from Central Texas. Each dot is a summed SPD for a given 200-year interval, and the color of each dot indicates an ecosystem productivity or resource extraction estimate. **A** Central Texas population and modeled NPP estimates. **B** Central Texas population and $\delta^{13}C$ apatite data. **C** Central Texas population and rock oven feature surface area ranks


A. TCP Population and Modeled NPP

B. TCP Population and Estuary Flooding

C. TCP Population and Delta 15N Collagen

Fig. 4 Summary of the 200-year time-series of data from Coastal Texas. Each dot is a summed SPD for a given 200-year interval, and the color of each dot indicates an ecosystem productivity or resource extraction estimate. **A** Coastal Texas population and modeled NPP estimates. **B** Coastal Texas population and estuary flood frequency estimates. **C** Coastal Texas population an $\delta\ ^{15}N$ collagen data

the entire 7500 years, modeled NPP ranges from 900 to 775 g/m^2/year and peaks twice, at about 4500 cal BP and, again, at 300 cal BP. There is not a clear difference in the mean of modeled NPP between the first and second components of logistic population growth. Figure 3B demonstrates a trend of decreasing $\delta\ ^{13}C$ apatite values in Central Texas over time, with the lowest values occurring between 2000 and 700 cal BP. Figure 3C illustrates a positive association between earth oven surface area (rank of 4 = largest surface area) and the SPD of Central Texas, until 500 cal BP when earth oven rank declines.

On the Texas Coastal Plain, Fig. 4A illustrates that NPP weakly associates with increasing values of the SPD. As in Central Texas, modeled NPP varies within a well-defined range between 1040 and 1120 g/m^2/year, peaking at 5700 and, again, at 900 cal BP. Figure 4B illustrates that flood events, which degrade the productivity of estuaries and might be expected to limit population growth, occur in two long periods, from 5900 to 4900 cal BP and 3000 to 2000 cal BP. This last period of high flooding frequency occurs when the SPD indicates a large increase in population and shifts to a new component of logistic growth. Finally, Fig. 4C illustrates that $\delta\,^{15}N$ collagen increases slightly on the Texas Coastal Plain as the SPD increases, with more green and yellow dots in the second component of growth than in the first.

Given the time-series above, in order to assess the effects of resource extraction and ecosystem productivity on increases in the carrying capacity of human populations, we ran a binary logistic regression. This regression model evaluates whether the increased carrying capacity suggested by the SPDs in Central and Coastal Texas associates with evidence for the increased extraction of energy-dense resources, external drivers of ecosystem productivity, or a combination of both.

To conduct this analysis, first, we divided the time-series (illustrated in Figs. 3 and 4) into two distinct sets, classifying each time point as either the “first” or “second” component of logistic population growth. The first component of population expansion has a lower carrying capacity, and the second component of population expansion has the higher carrying capacity. This allows us to assess if the characteristics of time points, like modeled NPP and isotope values, can predict the increase to a higher carrying capacity suggested by the SPD.

Second, we checked for associations between the independent variables documented in Figs. 3 and 4 and used a general linear model with a normal distribution to check for the effect of ecosystem productivity on resource extraction. Specifically,

$$Isotope_t = B_0 + \sum\nolimits_i b_i x_{i,t} + b_j Isotope_{t-1} + E_1 \tag{1}$$

where $x_{1t}\ldots x_{it}$ refer to a given set of explanatory variables at time t, B_0 is a constant, and b_i is a coefficient associated with each explanatory variable. $Isotope_{t-1}$ simply posits that the isotope value at a given time point depends on the value at the previous 200-year time step, and b_j is the coefficient associated with this term. The E_1 term stands for the residual error of the model. In prose, Eq. 1 states that the mean value of a stable isotope depends on the ecosystem and technology variables at a given time and on the mean isotope value at the previous time step. This regression model checks the possibility that changes in resource extraction and ecosystem productivity are not independent (see also Supporting Information, Section IV).

Third, we ran the binary logistic regression. In this case, the binary logistic model allows us to assess the effects of ecosystem productivity variables (flood events, NPP) and resource extraction (isotope values) on the correct placement of time-series data points into the first and second components of population expansion. In linear form, we write the binary logistic regression as:

$$ln\left(\frac{p}{p-1}\right) = B_0 + \sum\nolimits_i b_i x_i + E_2 \tag{2}$$

where p is the joint probability that a time point falls within the second component of logistic growth with a higher carrying capacity, given the values of stable isotopes at time t ($\delta\ ^{13}C$ or $\delta\ ^{15}N$) and estimates of ecosystem productivity (Flood events, NPP) at time t. The E_2 term stands for the residual deviance of the model. In short, Eq. 2 assesses whether increases in ecosystem productivity, the extraction and consumption of energy-dense plant or aquatic resources, or some combination of both have an effect on the carrying capacity that limits the growth of population in each respective region.

Regression Results

In summary, changes in ecosystem productivity do not have a significant effect on the consumption of energy-dense plant or aquatic resources. Further, and consistent with the MaB Ratchet, resource extraction variables have a significant effect on carrying capacity.

Table 1 Coefficient estimates, standard errors, and confidence intervals for each of the four regression models. ** indicates that a variable's estimated coefficient is significant at $p < 0.05$

Variable	Coeff. symbol	Coefficient	Std. error	95% C.I.
A. Central Texas: $\delta^{13}C_{\mathrm{t}} = B_0 + b_1 NPP_t + b_2 RockOven_t + b_3 \delta^{13}C_{\mathrm{t-1}}$				
Intercept	B_0	− 2.95	3.63	[− 9.70,4.16]
NPP	b_1	− 0.004	0.005	[− 0.014, 0.006]
*RockOven***	b_2	− 0.97	0.19	[− 1.27, − 0.59.]
$\delta^{13}C_{t-1}$	b_3	− 0.07	0.19	[− 0.44,0.30]
B. Coastal Plain: $\delta^{15}N_{\mathrm{t}} = B_0 + b_1 NPP_t + b_2 FloodEvents_t + b_3 \delta^{15}N_{\mathrm{t-1}}$				
Intercept	B_0	11.73	9.69	[− 7.26, 30.72]
NPP	b_1	− 0.002	0.008	[− 0.017, 0.018]
FloodEvents	b_2	− 0.023	0.30	[− 0.61, 0.56]
$\delta^{15}N_{t-1}$	b_3	0.13	0.19	[− 0.24, 0.50]
C. Central Texas: Logit.: $Component = B_0 + b_1 NPP_t + b_2 \delta^{13}C_{\mathrm{t}}$				
Intercept	B_0	− 2.49	10.03	[− 17.16, 17.69]
NPP	b_1	− 0.007	0.013	[− 0.018, 0.18]
**$\delta^{13}C$	b_2	− 1.02	0.48	[− 1.96, − 0.08]
D. Coastal Plain Logit.: $Component = B_0 + b_1 NPP_t + b_2 Floodevents_t + \delta^{15}N_{\mathrm{t}}$				
Intercept	B_0	− 39.35	32.15	[− 102.36, 23.66]
NPP	b_1	0.017	0.027	[− 0.035, 0.07]
FloodEvents	b_2	0.02	0.86	[− 1.66, 1.7]
**$\delta^{15}N$	b_3	1.74	0.72	[0.32, 3.15]

Table 1 (A and B) illustrates that changes in ecosystem productivity do not have a statistically significant effect on changes in resource extraction. In Central Texas, modeled NPP has a statistically insignificant effect on $\delta\ ^{13}C$ apatite values (Table 1A). Conversely, the rank order surface area of earth ovens has a positive and statistically significant effect on $\delta\ ^{13}C$ apatite values (Table 1A). This suggests that changes in earth oven use drive changes $\delta\ ^{13}C$ apatite values rather than increases in ecosystem productivity. Note here that earth oven surface area and modeled NPP do not correlate ($\varrho = 0.2$, $p = 0.24$, see also Supporting Information, Section IV). On the Coastal Plain, modeled NPP and flood event frequency have weak and statistically insignificant effects on $\delta\ ^{15}N$ values (Table 1B). This indicates, again, that ecosystem productivity and the extraction of aquatic resources, in this data set, are independent.

Table 1 (C and D) illustrates that only resource extraction variables have a significant effect on the increased carrying capacity of human populations. In Central Texas, modeled NPP has a weak and statistically insignificant effect on the log odds that a given point in time falls within the second component of population expansion (Table 1C), and $\delta\ ^{13}C$ apatite values have a statistically significant effect on the log odds that a given point in time falls within the second component of population expansion (Table 1C). These results are consistent with the MaB Ratchet postulate that social and technological changes, independent of changes in modeled NPP, underlay the expansion of carrying capacity in Central Texas.

On the Texas Coastal Plain, modeled NPP and the frequency of estuary flood events have statistically insignificant effects on the log odds that a given point in time falls within the second component of population expansion (Table 1D). However, $\delta\ ^{15}N$ has a significant effect on the log odds that a time point falls within the second component of population expansion (Table 1D). Again, these results suggest that the increased extraction of marine and freshwater fish, as proposed by the MaB Ratchet and previous work (Hard & Katzenberg, 2011; Johnson & Hard, 2008), drove the increase in human carrying capacity on the Texas Coast after 2900 cal BP.

Discussion

A basic question in human population ecology is as follows: What processes control the long-term carrying capacity of human societies (*e.g.*, Anderies, 2003; Bettinger, 2015; Binford, 2001; Boserup, 1981; Cohen, 1995; Freeman *et al.*, 2020, 2021; Hassan, 1981; Kelly, 2013; Kelly *et al.*, 2013; Meyer & Ausubel, 1999; Puleston & Winterhalder, 2019; Puleston *et al.*, 2014; Richerson & Boyd, 1998; Tallavaara *et al.*, 2018; Winterhalder *et al.*, 1988; Wood, 1998, 2020). To help answer this question, in this paper, we built and analyzed time-series that track changes in human bone chemistry, intensive plant processing, and the productivity of terrestrial and estuary ecosystems over time. We used these data to investigate whether expansions in the carrying capacity of hunter-gatherer populations in Texas associate with investments that increase the extraction of energy-dense resources, ecosystem productivity, or some combination of both. Our results suggest that changes in social organization and infrastructure that impact the efficiency and productivity of resource extraction rather than climate-driven shifts in the productivity of ecosystems underlie the expansion of hunter-gatherer carrying capacity in Texas. Our results are consistent with the hunter-gatherer MaB Ratchet model. In Central Texas, foragers invested in large earth ovens to bulk process plant resources, such as geophytes, and intensified on these resources, it appears, generating the shift from one component to the next of population expansion. On the Texas Coastal Plain, foragers invested in exploiting point-specific fisheries along meandering rivers and in coastal estuaries (Hard & Katzenberg, 2011) to increase the productivity of resource extraction. In short, the proposed shifts in population growth components predicted by the hunter-gatherer MaB Ratchet seem to have a basis in real changes in resource extraction and consumption.

Although these results are consistent with the hunter-gatherer MaB Ratchet, two important sets of challenges require future research. We begin with methodological challenges specific to our study area, and then we end with a discussion of the broader issue of how to model and understand the processes by which human populations escape from long-term resource limits in archaeological contexts.

Our analysis does not rule out externally driven changes in ecosystem productivity as key drivers of long-term changes in the carrying capacity of Texas foragers. First, one might argue that modeling the productivity of key resources, such as geophytes, is more important than modeling NPP, which is an aggregate estimate of biomass produced per unit area per unit time. It is possible that geophytes became more productive over time in Central Texas semi-independent of changes in NPP. In general, geophytes do poorly in dry, low NPP settings and should increase in productivity until they are out-competed by dense forests that limit sunlight in moderate to high NPP settings (Freeman, 2007; Mauldin *et al.*, 2003). Central Texas never displays evidence of closed canopy forest cover during the Holocene (Wong *et al.*, 2015), and thus, we suspect that geophytes would have done better with more rainfall and increases in NPP in Central Texas. Future research can and should evaluate this suspicion by developing estimates of geophyte productivity and correlating these estimates with climate and other ecosystem variables.

Second, very few paleo-environmental records useful for estimating changes in terrestrial productivity exist on the Texas Coastal Plain. Thus, it has not been possible to assess the quality of the modeled paleoclimate data, as we do, at least qualitatively, in Central Texas. More work is needed to calibrate paleoecological models with paleoecological data in this region.

Finally, the process of sea-level stabilization after 3,300 cal BP has long been argued to increase the productivity of estuaries on the TCP (Ricklis & Weinstein, 2005). Estuary flooding events do not associate with decreases in $\delta\ ^{15}N$ in our analysis. However, flood events may associate with less vs. more use of marine resources, and this should be an avenue of future research (Supporting Information, Section II). Further, estuary flood events may have larger impacts on deep estuaries than shallow estuaries. Today, Texas coastal estuaries are quite shallow, and it is possible that sedimentation throughout the Holocene led to this shallow condition. Thus, it is possible that sea-level stabilization, along with more shallow estuaries after 3300 cal BP, led to more consistently available marine resources, and this could, in part, underlie the population expansion noted on the

Texas Coastal Plain. More work is needed to link flood events and estuary depth to the productivity of estuary ecosystems in the region.

In terms of theory, although all Malthus-Boserup models of population growth integrate three principles (amplifying population feedback, limits, and escapes from limits), there is no consensus on how to theorize and model escapes from limits. This creates confusion in the theoretical literature and, importantly, potential difficulty in interpreting the results of particular case studies in favor of one model or another. In the extant literature, there are at least three approaches to modeling escapes, which we call: Escape trap, technological diffusion, and ratchet models. Escape trap models fundamentally question whether social and technological changes that increase the productivity of individuals actually result in true Boserupian escapes (*e.g.*, Anderies, 2003; Meadows *et al.*, 1972), and whether endogenous escapes are even possible in food-limited systems (Puleston & Winterhalder, 2019; Puleston *et al.*, 2014). No one has applied such models to hunter-gatherer populations. Technological diffusion models describe long-term population growth as a function of the rate of innovation and the diffusion of these innovations from outside a system. If these rates are high enough, populations experience slow, continuous long-term growth, and if the rates are too low, stagnation (Bettinger, 2015; Richerson *et al.*, 2009). For example, Bettinger (2015) argues that foraging populations in the western US were limited in growth until the compound bow diffused to those populations (Bettinger, 2015). The diffusion of the compound bow then initiated a set of linked changes in group size, sharing behavior, plant resource use, and increased fertility over mortality (Bettinger, 2015), generating population growth (see also Smith, 2021, for an application of this model in prehistoric Wyoming).

Our approach falls into the category of a ratchet model. As with all Malthus-Boserup models, we assume that as populations approach a limit, signals are sent to individuals via the food production system that create incentives for social and technological change. However, we propose that innovations in social organization or infrastructure that improve the productivity of resource extraction may occur inside or outside of a system. Critically, the metaphor of the ratchet assumes that, at first, big changes in social organization and infrastructure systems themselves generate an amplifying feedback in which higher carrying capacity leads to higher carrying capacity through niche filling and the spread of more productive social organization and infrastructure for resource extraction. However, as a landscape fills up, subsequent changes in social organization and infrastructure are small and have declining marginal effects on carrying capacity until an infrastructure system calcifies. One might think of this process as doubling down on what has worked in the past, and this is where James Wood's ratchet metaphor comes from (Wood, 2020). Every turn of the socket wrench gets harder and harder as a population doubles down on their existing infrastructure and sets of norms to increase productivity. The result is a convergence of limits in the social-technological and population systems. Near such convergence of limits, strong signals of instability in the production of resources potentially create incentives for large changes in social organization and infrastructure systems.

Based on our results, we argue that changes in social organization and infrastructure that increased the productivity of resource extraction led to the long-term expansion of human populations in Texas. However, more work is needed to identify whether the ratchet model, the escape trap and technological diffusion models, or some combination of models fits the data best. We suspect that the ratchet model is useful in Texas as critical changes in social organization and infrastructure appear to occur at the boundaries of proposed population growth Components I and II.

For example, previous work suggests that large Burned Rock Middens 10 m or more in diameter and more than 1 m thick began to appear consistently at the boundary of Components I and II (4,200 and 3,400 cal BP) in Central Texas (Black *et al.*, 1997; Mauldin *et al.*, 2003; McAuliffe *et al.*, 2023). It is important to recognize that burned rock middens are the result of people repeatedly using a highly generalized baking technology in the same locations. The earth ovens used were large and certainly required more upfront labor to construct than small hearths and small ovens. More impactful, however, the middens represent a “carbohydrate revolution" (Thoms, 2008) in the sense that foragers reduced their home ranges and began using large ovens to cook food from the same geophyte patches over and over and over. Some middens, indeed, fill whole stream valleys, generating surface measurements of 100 by 100 m. One potential implication of this pattern is that an innovation in land tenure toward more restricted home ranges and intensive carbohydrate production occurred during the critical period of 4200 to 3400 cal BP. The result was a new, carbohydrate-intensive niche that slowly filled between 3400 and 1000 cal BP, population growing as a result and peaking between 1000 and 800 cal BP. However, more lines of evidence are needed to assess this idea. For instance, if a “carbohydrate revolution” (Thoms, 2008) based on earth oven technology and restricted land tenure took hold around 3400 cal BP and this reduced home ranges, then we should also observe increasing evidence of violence as foragers increasingly protected their smaller home ranges.

Interestingly, the hunter-gatherer MaB Ratchet would also predict that a new zone of escape emerged around 1000 cal BP in Central Texas as the geophyte baking niche became filled and more labor investment in large earth ovens could no longer generate consistent returns of surplus food. In this regard, the adoption of the bow from 1250 to 1000 cal BP and pottery around 800 cal BP in Central Texas might have occurred due to the convergence of limits in population and social-technological systems. Near this limit, selection may have favored individual/household production strategies focused on seeds and individual hunting over the communal processing of geophytes and group hunting in restricted territories. Had settler-colonials from Europe not severely shocked the system, perhaps the changes in social organization suggested by Bettinger (2015) for the Great Basin would have occurred, in the long run, in Central Texas. That is, perhaps foragers would have experienced incentives for the individual production and ownership of seed plots, opening up a new seed-based economic niche and leading to another round of long-term population growth fueled by intensification on seeds.

Similarly, on the Texas Coastal Plain, the shift between Components I and II of population growth correlates with an increase in the number of mortuary sites, size of mortuary sites, and the exchange of goods from the coast to inland, potentially signaling reciprocal ties between alternative resource zones (Freeman *et al.*, 2017; Ricklis & Weinstein, 2005; Ricklis *et al.*, 2012). Further, as we note in the Supporting Information, Section II, diet partitioning between marine and freshwater fishing locations becomes more pronounced after 2900 cal BP. One potential implication of these patterns is that an innovation in territoriality led to the more productive extraction of fishing resources after 2900 cal BP. Again, as above, more lines of evidence are needed to assess this idea, such as changes in rates of violence and the ratio of fish bones collected to other fauna to better understand the basis and consistency of such changes.

In our view, a productive way to make progress in understanding the processes that control population escapes from limits in archaeological contexts is through the comparative study of archaeological regions. We especially need to develop time-series across regions that track changes in ecosystem productivity, population density, and resource extraction and consumption. We fully expect that such comparisons will reveal cases where the MaB Ratchet model fits and does not fit, providing an opportunity for learning!

Conclusion

In the end, our results are consistent with the hunter-gatherer MaB Ratchet model. Proposed shifts in components of population expansion associate with increasing land use intensification, both in Central Texas and on the Texas Coastal Plain. Our work contributes to understanding how and why population expansion and intensification co-occur. As noted by Kirch *et al.* (2012), archaeologists have an opportunity to help explain the general processes that control the expansion of human carrying capacity by building time-series to test specific models of human population ecology. Intensification can take multiple pathways (Binford, 2001; Morgan, 2015), and most work focuses on the role of agriculture in raising the carrying capacity of human populations. Yet, our analysis indicates that hunter-gatherers increased the carrying capacity of their local environments by intensifying on different wild resource bases. We argue that escapes from population limits through intensification were a human-wide phenomenon during the Holocene that took many forms, and future research should compare the strategies used by hunter-gatherer and agricultural populations.

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Author contribution JF, RPM, RJH, and JMA designed the research; JF, RPM, RJH, RS, and MW collected the data; JF conducted the analysis and interpretation of data; JF drafted the manuscript; and all authors contributed to manuscript revisions.

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Data Availability The data used in this analysis are available at Freeman *et al*. (2023) and as part of the SI appendix.

Declarations

Competing Interests The authors declare no competing interests.

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