

A stochastic density-dependent model of long-term population dynamics in hunter-gatherer populations

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ABSTRACT

Background: All biological populations exhibit fluctuations in size over time due to stochastic variation in growth rates that result in local extinctions, but these dynamics are poorly understood in traditional human populations. Here, we explore extinction processes over human evolutionary history due to the effects of (i) demographic stochasticity, (ii) environmental stochasticity, and (iii) periodic catastrophes.

Organism: Modern humans, *Homo sapiens*.

Methods: We built a mathematical model of stochastic population dynamics, estimated its parameters using ethnographic data, and simulated probability distributions of extinction outcomes using Monte Carlo methods.

Results: Although expected times to extinction vary under different conditions, hunter-gatherer populations likely experienced local extinction events every few hundred years (or every few generations).

Conclusions: Played out over the evolutionary time scale of the human species (~250,000 years), stochastic variation in growth rates resulted in a near-constant turnover of local populations, contributing to the near-zero growth of human populations over much of our evolutionary history.

Keywords: fission-fusion, forager societies, metapopulation, population growth, stochastic processes.

INTRODUCTION

Human hunter-gatherers derive the majority of their subsistence, technological, medicinal, and infrastructure needs from wild populations of plants and animals available in their local environments (Binford, 2001; Kelly, 2001). Most terrestrial hunter-gatherers form residually mobile, small-scale societies (Hamilton *et al.*, 2016), consisting of spatially discrete socioeconomic bands, made up of a few families, some of which are related, some not (Hill *et al.* 2011), and usually numbering around 15–20 individuals (Binford, 2001; Hamilton *et al.*, 2007a; Hamilton *et al.*, in

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revision). Individual bands are connected to neighbouring bands via regional social networks to form metapopulations through which individuals and families move, sharing both social and biological information through trade, exchange, visiting, reproduction, and marriage (Kelly, 2001; Hamilton *et al.*, 2007a).

The human species, *Homo sapiens*, is on the order of 200,000–250,000 years old (Klein, 2009), and for about 95% of evolutionary history, prior to the initial domestication of plants and animals some 12,000 years ago in the Near East, all humans were hunter-gatherers. Modern humans expanded out of Africa approximately 60,000 years ago, and the flexibility of hunter-gatherer socioeconomies allowed humans to adapt quickly to new environments and colonize the majority of the terrestrial planet by ~15,000 years ago. Prior to the evolution of agriculture at the end of the Pleistocene, the global human population likely numbered between 5 and 10 million (Binford, 2001). Genetic and historical demographic data suggest that, aside from local expansions, over this entire period the human global population experienced near-zero net growth, implying either that local hunter-gatherer populations were constantly at – or near – demographic equilibrium, or that population expansions led to a balance of localized extinctions and replacements (Kelly, 2001).

Over the history of anthropology, some researchers suggested that cultural processes such as infanticide act as group selective mechanisms to regulate hunter-gatherer populations (Birdsell, 1968; see also Kelly, 2001). However, ethnographic research showed that infanticide in hunter-gatherer populations was less common and occurred at lower rates than previously thought (Howell, 1979; Daly and Wilson, 1988; Smith and Smith, 1994). Among hunter-gatherer societies that report infanticide, evidence suggests that rather than group-level regulation, infanticide regulates birth spacing (Morales, 1987; Kelly, 2001). Rather than reducing reproductive fitness, birth spacing maximizes reproductive fitness by reducing infant mortality rates, resulting in higher probabilities of children reaching reproductive age (Blurton Jones and Sibly, 1978).

Although population dynamics are recognized as an important mechanism of spatio-temporal variation in quantitative traits within many species, the statistical effects of population-level mechanisms on human demographic history have not been considered widely in the anthropological literature. The most commonly used population growth models assume infinite population sizes and constant growth rates. A well-known example of non-linear population growth is the logistic model $dN/dt = r_0 N(1 - N/K)$, where the per capita growth rate $r(t) = (1/N)dN/dt$ decreases at a linear rate as N approaches the carrying capacity K . The assumption that the intrinsic rate of population increase r_0 is constant forces K to be an absorbing stable state, such that for any initial population size $N(0)$ (where $N(0) > 0$), $N \rightarrow K$ in the limit $t \rightarrow \infty$. However, if N is not large, either due to low carrying capacities or population sub-structure, this approximation breaks down as stochastic effects are introduced into the model statistically via the sampling effects of the central limit theorem. Consequently, population growth rates are no longer deterministic, but result in probability distributions of population sizes over time, which include the possibility of extinction. Stochastic processes are likely to play an important role in hunter-gatherer population dynamics, as populations are typically small, internally structured, and subject to environmental variability.

The dynamics of a hunter-gatherer population, like any naturally occurring biological population, can be described heuristically by combining a core deterministic growth model with relevant stochastic processes (Lande, 1993; Lande *et al.*, 2003, 2017; Coulson *et al.*, 2004). Here, we examine three sources of stochastic variance in populations: (i) demographic stochasticity, (ii) environmental stochasticity, and (iii) periodic population crashes (Goodman, 1987; Lande, 1993).

Demographic stochasticity is defined as the chance realization of birth and death processes over time due to the sampling effects of variation between reproductive females in offspring production in a finite population (Engen *et al.*, 1998; Lande *et al.*, 2003). The degree of demographic stochasticity depends on two factors: the amount of demographic heterogeneity within a population, and population size (Lande *et al.*, 2003). Environmental stochasticity causes density-independent variation in population growth rates due to slight fluctuations in year-to-year environmental conditions that affect the availability of resources, including seasonality, temperature, or rainfall (Goodman, 1987; Lande, 1993). Periodic population crashes cause infrequent, instantaneous reductions in population numbers resulting from a variety of extrinsic mechanisms beyond the control of the population. These extrinsic mechanisms might include severe reductions in resource availability, earthquakes, landslides, disease outbreaks, natural disasters, and extreme weather events (Lande, 1993; Boone, 2002). Although the frequency and severity of catastrophic events are likely to vary geographically, we assume population crashes occur independently of population size and in all environmental settings.

Predator–prey interactions are another potential source of deterministic fluctuations in hunter-gatherer population sizes over time (Belovsky, 1987, 1988). In mathematical models of predator–prey interactions, increasing time lags between reproduction and resource availability induce fluctuations in population sizes that quickly approach chaotic regimes (Turchin, 2003; Mittleldorf, 2006). This is because time lags in response allow populations to temporarily overshoot carrying capacities, inducing complex dynamics. However, if time lags are small in relation to generation times, such complex dynamics are avoided (Mittleldorf, 2006). Hunter-gatherers have flexible foraging strategies, technologies, and broad diet breadths, long-term reciprocal exchange partnerships between individuals that mitigate fluctuations in foraging returns, and are often highly residually mobile, relocating to new resource patches when resources become scarce and depleted (Kelly, 2001; Hamilton *et al.*, 2016). As such, hunter-gatherers have a broad array of behaviours and technologies that allow them to respond to fluctuating resource availability at time scales of hours to days, much shorter than the lag times required to induce complex dynamics in time-delayed logistic models.

The main thesis of this paper is that stochastic processes have played a central role in human population dynamics over evolutionary history. The paper focuses on the statistical properties of fluctuating populations and consequent effects of stochastic processes on long-term population persistence and spatial patterning by developing a stochastic model of human population growth, parameterized by data from contemporary hunter-gatherer societies.

MODEL AND METHODS

Analysis proceeds in five stages: (1) a stochastic model is developed; (2) a quasi-extinction threshold θ is defined; (3) the model is then iterated using Monte Carlo methods to estimate probability distributions of population sizes, and probabilities of extinction, defined as the number of runs out of 1000 a population of initial size $N(0)$ reaches the quasi-extinction threshold, θ , given the parameters of the model; (4) diffusion approximations are used to calculate the expected population persistence time defined as the number of years for a population of initial size $N(0)$ to reach the quasi-extinction threshold, θ , given the parameters of the model; and (5) sensitivity analyses are conducted to understand how sensitive extinction dynamics are to parameters of the model.

For the purposes of this model, hunter-gatherer populations are non-age-structured, discrete breeding populations. Hunter-gatherer populations are metapopulations of local bands (Binford, 2001; Marlowe, 2005; Hamilton *et al.*, 2007a) and migration occurs primarily between bands. Migration rates from outside metapopulations are considered to be low, so that the demographic effects of external migration can be ignored. The general framework for the model is given by the density-dependent model of population growth,

$$\frac{dN}{dt} = r_0 N - \alpha N^2, \quad (1)$$

where N is population size, r_0 is the intrinsic rate of population growth, $\alpha = r_0/K$, where K is the carrying capacity and t is time. On the natural logarithmic scale, the solution to density-dependent growth is approximated by $x(t+1) = x(t) + r(t) - \alpha N(t)$, where $x(t) = \ln N(t)$.

Stochastic variance is incorporated into the growth model by recognizing that the actual rate of population growth varies over time and is more accurately described by $\lambda(t) = \bar{\lambda} + \varepsilon$, where λ is the multiplicative growth rate, $\lambda = \exp(r)$, ε is a normally distributed random number with mean 0 and variance $\sigma_\lambda^2(t) = \sigma_E^2(t) + \sigma_D^2/N(t)$, where σ_E^2 is environmental variance and σ_D^2 is demographic variance. Following Lande *et al.* (2003), the mean and variance of the intrinsic rate of increase are then:

$$\bar{r} = \ln \bar{\lambda} - \frac{\sigma_r^2}{2} \text{ and } \sigma_r^2 = \frac{\sigma_\lambda^2}{\bar{\lambda}^2}. \quad (2a, 2b)$$

Populations experience catastrophic crash events at a frequency f , or probability $P(f) = 1/f$, and with severity s , where s is an independent identically distributed (iid) random number, such that $1-s$ is the proportion of the population surviving a crash event (Boone and Kesler, 1999). By modelling crash severity as an iid random number, crash events are independent. Therefore, the growth trajectory of a population on the logarithmic scale is given by

$$x(t+1) = x(t) + r(t) - \alpha N(t) - [(1/f)\ln(1-s)](t), \quad (3)$$

where $r(t)$ is a normally distributed random number with mean and variance given by equation (2).

We define θ as the minimum critical population size below which populations are deemed extinct, and set this value to be the average size of a single hunter-gatherer band of 20 individuals. The upper limit K to population size N means that there is a finite distance a population can achieve from the critical threshold, θ , unlike exponential growth where there is no limit to population size. Inevitably, due to the combination of stochastic processes in the model, a density-dependent population will experience a long enough run of bad years to fall below θ . Example trajectories of the model are shown in Fig. 1. Figure 2 shows example probability distributions of population sizes that result from the model, where, over time, an increasing number of sample trajectories fall below the critical threshold, θ , resulting in population extinction.

Long-term growth rates and extinction dynamics are then examined using diffusion approximations (Lande *et al.*, 2003). The infinitesimal means μ_r and variances σ_r^2 of the model describe the diffusion process of population trajectories from equation (3), and are given by

$$\mu_r = \frac{1}{q} \sum_{i=0}^{q-1} \ln(N_{i+1}/N_i) \text{ and } \sigma_r^2 = \frac{1}{q-1} \sum_{i=0}^{q-1} [\ln(N_{i+1}/N_i) - \mu_r]^2, \quad (4a, 4b)$$

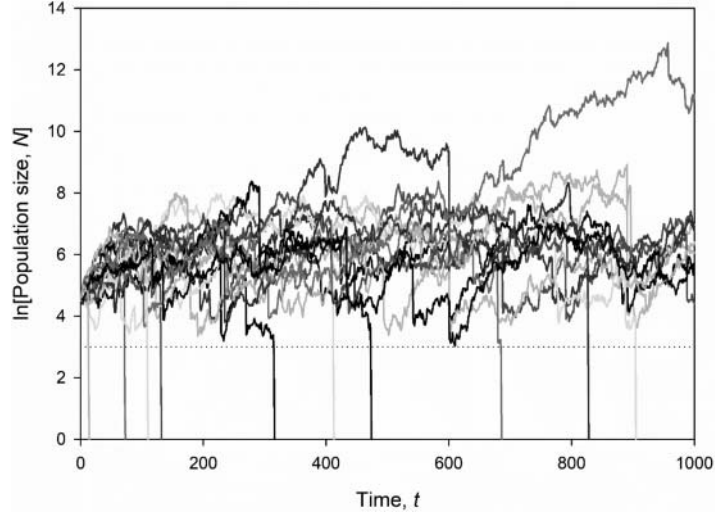


Fig. 1. Twenty sample runs of the stochastic density-dependent model ($N_0 = 100$, $r_0 = 0.04$, $\sigma_E^2 = 0.01$, $P(f) = 1/100$, $K = 600$ shown). Dotted line is the extinction threshold $\theta = 20$ ($\ln \theta = 3.0$).

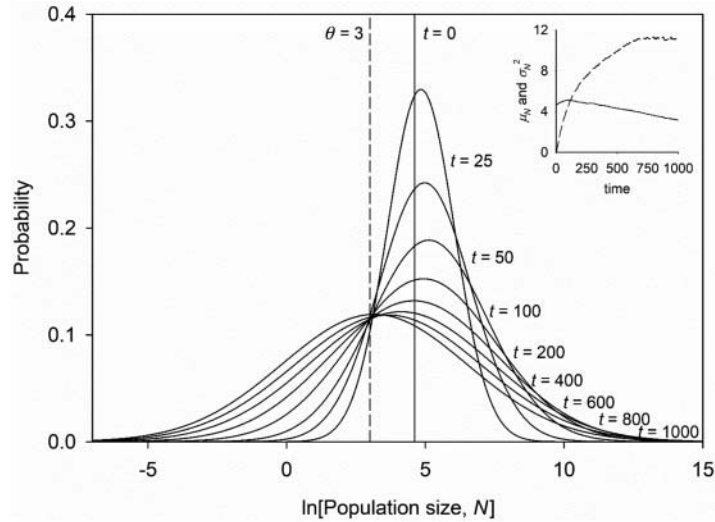


Fig. 2. Example diffusion approximation of the model for $\bar{\lambda} = 1.04$ and $K = 600$. Over time the variance of population size σ_N^2 (inset, dotted line) increases faster than mean population size μ_N (inset, solid line) indicating that even though the mean growth rate $\bar{\lambda}$ is positive, the probability of extinction, $P(\theta)$, increases.

where q is the length of the simulation (Morris and Doak, 2002). In equation (4), μ_r is the expected mean long-term growth rate, and σ_r^2 is the variance in the expected long-term growth rate. These parameters then allow the calculation of the expected mean time to extinction $\bar{T}(\theta)$ for any combination of population parameters, given by

$$\bar{T}(t | \theta, \mu_r, \sigma_r^2) = \frac{1}{2\mu_r c} [e^{2ck}(1 - e^{-2c \ln(\theta)}) - 2c \ln(\theta)], \quad (5)$$

where $c = \mu_r / \sigma_r^2$ and $k = \ln(K/\theta)$ (Morris and Doak, 2002).

Owing to the non-linearity of the model, we use Monte Carlo simulations [in PopTools (Hood, 2010)] (1000 iterations) to estimate the probability and mean time to extinction for combinations of ranges of parameter values. Initial population sizes $N(0) = 100$ for all simulations, and all simulations were run for 1000 years. In order to relate the results of this model to empirical biogeographic patterns of hunter-gatherer diversity, Type I linear regressions were conducted on data from ethnohistoric hunter-gatherer population sizes N , territory sizes A , and densities D as a function of net primary production, NPP .

PARAMETER ESTIMATION

Data were compiled from various published sources of information relating to contemporary hunter-gatherer populations (Binford, 2001; Kelly, 2001; Pennington, 2001). We restricted data on hunter-gatherer population sizes to residually mobile populations ($n = 235$). To estimate the intrinsic rate of population growth for humans, we first estimate the average generation time of hunter-gatherers, G , from the mean age at reproduction, M . In our data $M = 28$ ($n = 10$). The expected rate of population increase is the inverse generation time, $r_0 = 1/G = 1/M = 0.04$.

Demographic variance σ_D^2 is the variability in the net reproductive rates R within a population (Engen *et al.*, 1998; Lande *et al.*, 2003), a measure of heterogeneity in female fitness within natural fertility populations. Calculations of σ_D^2 within hunter-gatherer populations are not possible from published data due to sample size, but can be estimated by considering the variance in reproductive rates between populations. An unbiased estimator of σ_D^2 is given by the standard sum of squares statistic (Engen *et al.*, 1998):

$$\sigma_D^2 = \frac{1}{n-1} \sum_{i=1}^{i=n} (R_i - \bar{R})^2, \quad (6)$$

where R is the net reproductive rate of females of reproductive age given by $R = \int_a^\infty L(x)b(x)dx$, and $L(x)$ is the probability of survival to age x , $b(x)$ is the birth rate in daughters at age x , and a is age at maturity (Charnov, 1993), commonly assumed to be 15 years in human females.

In the forager data, R ranges from 0.25 to 2.63 ($\bar{R} = 1.66$, $\sigma_r^2 = 0.49$, $n = 38$), such that $\sigma_D^2 = 0.24 \pm 0.02$ 95% CL. These values of σ_D^2 likely underestimate within-population demographic heterogeneity, as there is likely to be more variation in female fitness within than between populations. After accounting for the sampling effects of population size, the overall effect of demographic stochasticity on the growth rate is given by $\sigma_D^2(t) = \sigma_D^2/N(t)$.

As there are no estimates for environmental stochasticity in contemporary human forager societies, we examine a range of environmental stochasticity in the model. Lande and colleagues (2003) note that in the few cases where environmental stochasticity has been

quantified, environmental variance is consistently less than demographic variance, often by over an order of magnitude. In the model, we examine $\sigma_E^2(t) \in (0.005, 0.04)$. Although this is an estimate, it is unlikely to overestimate the effects of environmental stochasticity on the population growth rate, because in this case $\sigma_E^2(t)$ is over an order of magnitude less than σ_D^2 , while still providing a non-trivial source of stochasticity for large populations.

The frequency f of crash events is varied between 50 and 400 years such that the probability P of a crash event occurring per year is $P = 1/f \in (0.02, 0.0025)$. As stated above, the severity s of the crash event is an iid random number between 0 and 1 with the result that a single crash event cannot produce population extinction in the absence of stochasticity in population growth. Data relating to population crash events impacting indigenous societies in the Amazon Basin following disease epidemics show crash severities are iid (Hamilton *et al.*, 2014), though time series are not long enough to estimate frequencies, $1/f$.

In the model, K is defined as an estimate of the maximum population size N a given territory size A can support (Hamilton *et al.*, 2007b, 2009). In a stochastic density-dependent model when the population N is at carrying capacity K , $\bar{r} = 0$, but the effects of demographic and environmental stochasticity can cause N to be greater than K , in which case N will decrease to K at a rate determined by the magnitude of the stochastic effects. The model considers a range of carrying capacities K for foraging populations defined by the sample distribution of foraging population sizes. Figure 1 shows that average population sizes of hunter-gatherer populations in our sample are lognormally distributed, $\ln \bar{N} = 6.48$ ($N = 6.55$), $\sigma_{\ln N}^2 = 1.42$ ($\sigma_N^2 = 4.13$). The mean carrying capacity K is approximated by N and so we allow K to vary from 200 to 1600 to explore the effects of carrying capacity on model outcomes (Fig. 3).

RESULTS

Figure 4 is the probability distribution of times to extinction, $T(\theta)$, for hunter-gatherer populations parameterized by ethnographic data ($K = 650$, $r_0 = 0.04$). The distribution is lognormal, and the average time to extinction is 533 years, or about 18 generations, although extinction times range from a minimum of 100 years to a maximum of 10,000 years over 1000 sample runs. Therefore, if we generalize and say that the expected persistence time for an average hunter-gatherer population is on the order of ~ 500 years, over the course of 10,000 years (i.e. the majority of the Holocene), a local population will go

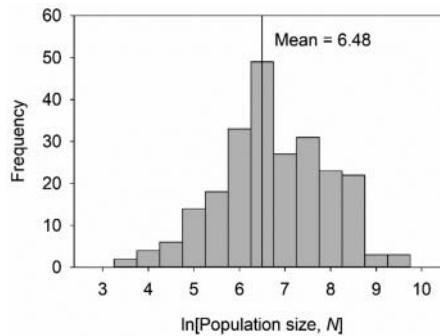


Fig. 3. Frequency distribution of hunter-gatherer sample populations ($\ln \bar{N} = 6.48$, $\sigma_{\ln N}^2 = 1.41$, $n = 242$).

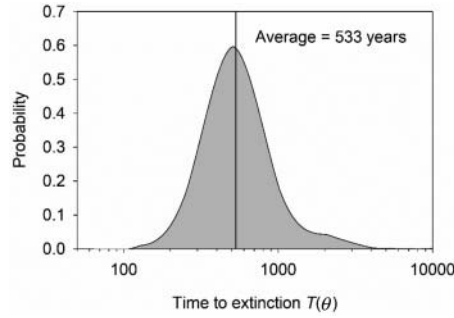


Fig. 4. Probability distribution of the time to extinction for 1000 model runs with average ethnographic parameters ($K = 650$, $r_0 = 0.04$, $\sigma_E^2 = 0.01$, $P(f) = 1/100$).

through about 20 extinction–expansion cycles. Interestingly, Eller *et al.* (2004) estimate extinction rates per generation for hunter-gatherers over evolutionary history to be between 0.06 and 0.12 (see also Soltis *et al.*, 1995), which is consistent with our results, where the expected extinction rate per generation would be $1/18 = 0.06$.

An expected extinction time of ~ 500 years holds only for the model parameterized by average values from the ethnographic record. To understand the sensitivity of extinction dynamics (i.e. probabilities and times), we ran the model under a range of conditions, systematically varying carrying capacity, K , environmental stochasticity, σ_E^2 , and the frequency of crash events, $P(f)$. Figure 5 and Tables 1 and 2 show the results of varying K , and σ_E^2 , on the probability of extinction, $P(\theta)$ (within 1000 years), and diffusion approximations of the eventual time to extinction, $T(\theta)$. The probability of extinction decreases and the time to extinction increases with increasing carrying capacity, across the parameter

Table 1. Model parameters of the probability of extinction and carrying capacity by environmental stochasticity (Fig. 5A)

σ_E^2	c_0	$\pm$ SE	β	$\pm$ SE	r^2	P
0.005	1.55	0.06	−0.09	0.01	0.98	< 0.001
0.01	2.05	0.12	−0.15	0.01	0.98	< 0.001
0.02	3.16	0.27	−0.25	0.01	0.98	< 0.001
0.03	5.47	0.20	−0.37	0.01	0.99	< 0.001
0.04	6.48	0.77	−0.41	0.02	0.99	< 0.001

Table 2. Model parameters of time to extinction and carrying capacity by environmental stochasticity (Fig. 5C)

σ_E^2	c_0	$\pm$ SE	β	$\pm$ SE	r^2	P
0.005	0.14	0.06	1.39	0.06	0.99	< 0.001
0.01	1.19	0.53	0.97	0.06	0.99	< 0.001
0.02	8.39	0.41	0.61	0.01	0.99	< 0.001
0.03	16.55	1.00	0.49	0.01	0.99	< 0.001
0.04	24.14	3.05	0.43	0.02	0.99	< 0.001

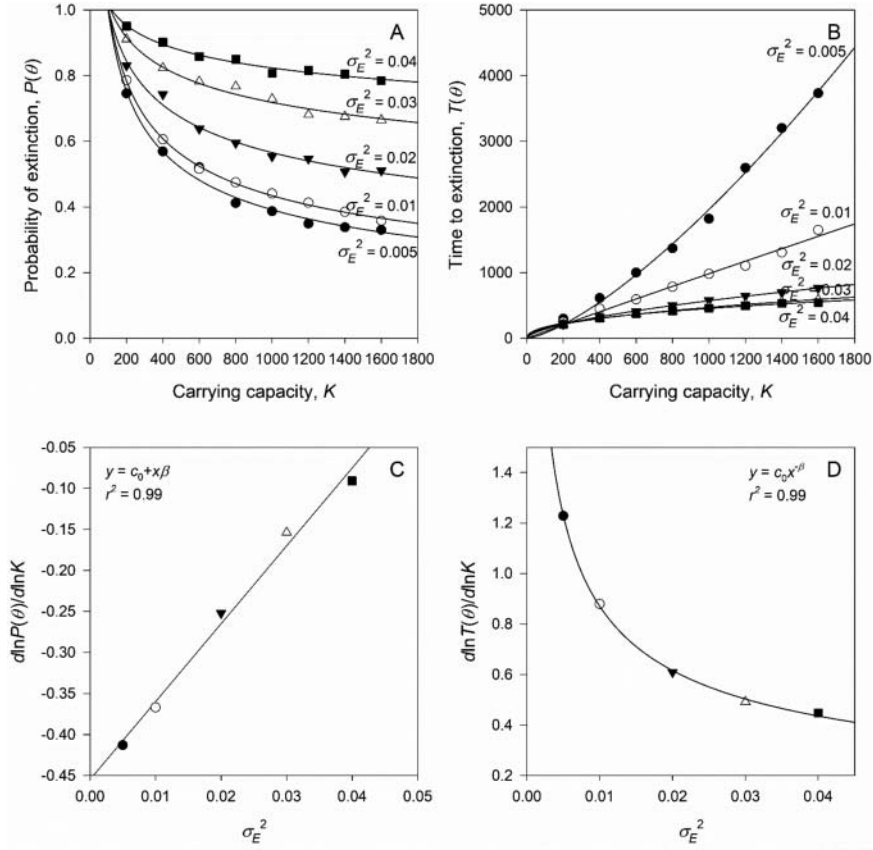


Fig. 5. Plots (A) and (C) are the probabilities of extinction $P(\theta)$ and mean times to extinction $\bar{T}(\theta)$ by carrying capacity K and environmental variance σ_E^2 resulting from Monte Carlo simulations. Plots (B) and (D) are the elasticities $d \ln P(\theta) / d \ln K$ by σ_E^2 . For all simulations, demographic variance $\sigma_D^2 = 0.236$, $f = 100$, and $N(0) = 100$.

range of environmental stochasticity. This is because, regardless of the fluctuations in population size, the higher the carrying capacity, the greater the average time before populations fall below the extinction threshold. However, Fig. 5B shows that increasing carrying capacity has a faster effect on decreasing the probability of extinction the higher the environmental stochasticity, at approximately a linear rate. Similarly, Fig. 5D shows that the gradient at which the predicted time to extinction increases with carrying capacity decreases rapidly (as a power function) with environmental stochasticity. As such, increasing stochastic fluctuations in population size consistently lead to higher probabilities of extinction, and shorter predicted times to extinction.

Figure 6 and Tables 3 and 4 show the results of varying K , and $P(f)$, on the probability of extinction, $P(\theta)$, and time to extinction, $T(\theta)$. The probability of extinction decreases and the time to extinction increases with increasing carrying capacity, across the range of crash events. This is because, regardless of the fluctuations in population size, the higher the carrying capacity, the greater the average time before stochastic fluctuations in population sizes due to external crash events drive populations below the extinction threshold.

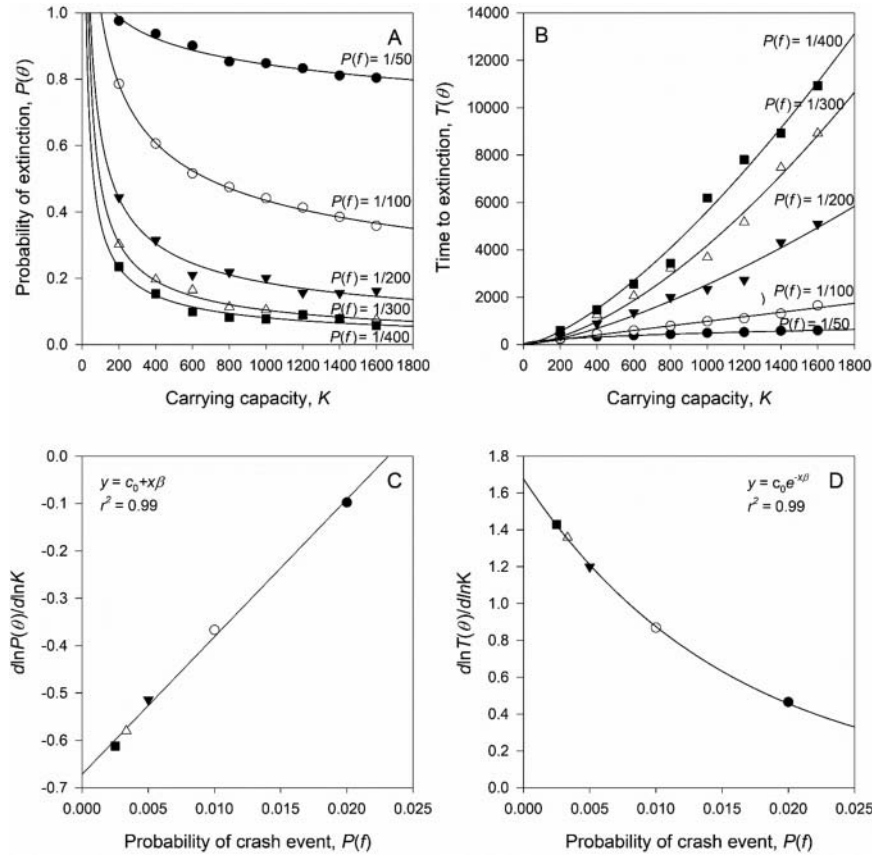


Fig. 6. Plots (A) and (C) are the probabilities of extinction $P(\theta)$ and mean times to extinction $\bar{T}(\theta)$ by carrying capacity K and crash frequency, f , resulting from Monte Carlo simulations. Plots (B) and (D) are the elasticities $d \ln P(\theta) / d \ln K$ by f . For all simulations, demographic variance $\sigma_D^2 = 0.236$, $\sigma_E^2 = 0.01$, and $N(0) = 100$.

Table 3. Model parameters of the probability of extinction and carrying capacity by crash frequency (Fig. 6A)

$P(f)$	c_0	$\pm$ SE	β	$\pm$ SE	r^2	P
1/50	1.65	0.07	-0.10	0.01	0.97	< 0.001
1/100	5.47	0.20	-0.37	0.01	0.99	< 0.001
1/200	7.50	1.67	-0.53	0.04	0.97	< 0.001
1/300	7.45	2.28	-0.65	0.05	0.99	< 0.001
1/400	10.68	1.80	-0.67	0.03	0.99	< 0.001

Figure 6C shows that increasing carrying capacity has a faster effect on decreasing the probability of extinction the more frequent the crash event, at approximately a linear rate. Figure 6D shows that the gradient at which the predicted time to extinction increases with carrying capacity decreases rapidly (exponentially) with the increasing frequency of crash

Table 4. Model parameters of time to extinction and carrying capacity by crash frequency (Fig. 6C)

$P(f)$	c_0	$\pm$ SE	β	$\pm$ SE	r^2	P
1/50	20.18	1.63	0.46	0.01	0.99	< 0.001
1/100	1.20	0.53	0.97	0.06	0.99	< 0.001
1/200	0.14	0.14	1.42	0.14	0.97	< 0.001
1/300	0.27	0.18	1.44	0.10	0.99	< 0.001
1/400	0.07	0.06	1.59	0.11	0.98	< 0.001

events. As such, increasing the frequency of crash events to which populations are subject consistently leads to higher probabilities of extinction, and shorter predicted times to extinction.

The sensitivity analyses indicate that the extinction dynamics of hunter-gatherer populations are sensitive to the range of parameter values. Expected extinction times for the most extreme parameter values of the highest carrying capacities and lowest frequencies of crashes and environmental variance have a maximum of between ~4000 and 10,000 years. In general, the results of the sensitivity analyses suggest that technological or behavioural adaptations that effectively increase local carrying capacities, lower environmental stochasticity, or decrease the frequency of external crash events will increase population persistence times at different rates. As such, behavioural or technological innovations that occur at the individual level may have group-level impacts. Furthermore, if the model were extended to include the probability of extinction resulting from competition (i.e. warfare or raiding) from neighbouring populations, for example by effectively increasing $P(f)$ as a function of N , then group-level competition could have important effects on population persistence times. However, the extent to which hunter-gatherer populations in the ethnohistoric record engaged in group-level warfare, resulting in mass casualties and population replacement, is a matter of anthropological debate (Gat, 2000, 2008; Bowles, 2009; Wrangham and Glowacki, 2012; Allen and Jones, 2014).

Figure 6 demonstrates that while hunter-gatherer territory sizes A decrease with NPP (Fig. 3A), population size N shows no statistical trend with NPP (Fig. 3B). Consequently, population densities D increase with NPP (Fig. 3C) as populations living in energy-rich environments require proportionally smaller home ranges than populations living in energy-limited environments. As NPP explains essentially none of the variation in N ($r^2 = 0.01$, $P > 0.05$; Fig. 3B), and N is an estimate of K , importantly, hunter-gatherer carrying capacities K seems to be independent of NPP .

DISCUSSION

The model developed in this paper has three important implications for population-level mechanisms in human demographic history: (i) population extinction events were common throughout human prehistory due to finite persistence times caused by stochastic variance in small populations; (ii) the near-zero growth rates over much of human evolutionary history were due to the complex interplay of density dependence, naturally occurring variation in reproductive rates, the statistics of sampling effects in small-scale populations, and sources of stochastic heterogeneity in local environments; and (iii) extinction dynamics

should vary predictably through time and space with changing environmental conditions and energetic availability, as population persistence times are ultimately a function of the degree of environmental heterogeneity faced by a population over time.

First, the model suggests that individual hunter-gatherer populations persist on average for a few hundred years, but given the lognormal skew of the actual times to extinction, often much less. These results indicate that stochastic variance in long-term population growth results in population instability and inevitable extinction due to the interplay of low carrying capacities typical of small-scale hunter-gatherer populations, and density-dependent growth. Importantly, irrespective of the severity of catastrophic events, even large populations well above extinction thresholds will eventually drift to extinction due to the inherent stochasticity of population dynamics. Finite persistence times imply that the regional dynamics of hunter-gatherer populations over time followed a cycle of extinction, replacement, and expansion, in a dynamic typical of spatially structured discrete metapopulations, as proposed by Eller (2002; Eller *et al.*, 2004). Played out over evolutionary time, this dynamic would have resulted in a significant source of genetic drift through founder effects, both within and among populations, as genetic variation is continually depleted at both levels (Falconer and Mackay, 1996). Similarly, the cycle of population extinction, replacement, and expansion would be a major source of cultural drift, as the extinction of hunter-gatherer populations characterized by unique sets of cultural traits would result in a net decrease in regional cultural variation over time, as recently argued by several researchers (see, for example, Neiman, 1995; Shennan, 2000, 2001; Bentley *et al.*, 2004).

Second, the stochastic processes outlined in this paper suggest that the near-zero global population growth rates maintained over much of human evolutionary history were due to the combined statistical effects of finite population sizes, naturally occurring demographic heterogeneity, local variation in resource availability, and the frequency and severity of externally driven, climatically or environmentally induced population crashes. While population growth rates were likely positive in most prehistoric hunter-gatherer populations, or at least highly variable, as suggested theoretically by life-history theory (Hill and Hurtado, 1996; Pennington, 2001; Boone, 2002) and empirically by the majority of contemporary hunter-gatherer groups (Hill and Hurtado, 1996), the combined effects of demographic and environmental stochasticity, and catastrophic events ensure $\mu_r < r < \ln \lambda$. Stochastic variation σ_r^2 reduces the growth rate r over time (equation 4a), and as μ_r is simply the long-term mean growth rate of the population (equation 5a), $\mu_r < r$ if the frequency of crashes is greater than zero, which is almost certainly true. Consequently, even those populations in which rates of per capita population growth are positive will decline to extinction eventually due to the statistics of stochastic processes. The sampling effects of demographic heterogeneity indicate that demographic stochasticity is of primary importance in small populations, whereas above a certain threshold environmental stochasticity becomes the major source of instability. In effect, the density-independent mechanisms of environmental stochasticity and catastrophes result in population instability by causing populations to fluctuate around their carrying capacities, eventually driving them below an extinction threshold determined by the statistical properties of demographic heterogeneity. Averaged over many populations through time and space, this cyclic pattern of extinction and replacement results in near-zero global population growth.

While the effects of demographic and environmental stochasticity are internal sources of population fluctuations, the frequency of population crash events is an external, group-level phenomenon. As such, population persistence times are a function of both individual-

and group-level mechanisms. In this model, we assume that the non-zero frequency (and severity) of population crashes is caused by environmental effects (such as earthquakes, floods, forest fires, extreme weather events, etc.), which are neither predictable nor impacted by the internal dynamics of populations. However, another potential external source of population reduction, independent of local population dynamics, is competition with neighbouring groups through mechanisms such as warfare, raiding, or population expansions. A complex way of incorporating group-level competition into this kind of modelling framework would be to use a spatially explicit model, where the degree of inter-group competition is a function of the number of neighbouring populations and local differentials in population size, for example. But a simpler way would be to assume that the frequency of external crash events $P(f)$ includes not only climatic or environmental events, but the frequency of conflict with neighbouring populations. Because the sensitivity analyses show that the frequency of crash events has a large impact on population persistence times, then inter-group competition could potentially be an important group-level mechanism impacting cycles of population extinction, replacement, and expansion.

Third, extinction dynamics are ultimately a function of environmental and climatic stochasticity, and the model predicts that hunter-gatherer population dynamics should vary predictably with environmental stability and energy availability. However, Fig. 7 shows that the empirical relationship between hunter-gatherer populations and energy availability is not straightforward (see Hamilton *et al.*, 2007b, 2009, 2016). Population density increases with energy availability, as might be expected (Fig. 7C), but only as a function of decreasing territory size (Fig. 7B), while variation in population size is independent of energy availability (Fig. 7A). The metapopulation dynamic described above suggests an explanation for these relationships. The stochastic nature of population growth ensures that populations will not remain at their carrying capacities indefinitely, resulting in a synchronic distribution of population sizes, as at any one time some populations will be above their carrying capacities, while others are below theirs as they either drift to extinction or are experiencing growth. In particular, if fitness values are lognormally distributed within a population, population growth rates will also be lognormally probability distributed, resulting in a lognormal distribution of population sizes over time and space (Lande *et al.*, 2003). Indeed, this is the empirical distribution of hunter-gatherer population sizes we see in Fig. 1.

As population density increases with energy availability, while the variation in population size remains approximately constant, we expect a greater number of increasingly dense populations per unit area in the tropics than at the poles (see Hamilton and Walker, in review). Furthermore, as the mean time to extinction is a function of population size, the model predicts a higher population extinction rate per unit area in the tropics than at the poles. More precisely, the model predicts an energy gradient of population turnover rates decreasing with energy availability in a pattern consistent with robust biogeographical trends of increasing species richness and biodiversity along latitudinal gradients (Jablonski *et al.*, 1985; Jablonski, 1993; Brown and Lomolino, 1998; Gaston, 2000; Crame, 2001; Allen *et al.*, 2002; Hamilton and Walker, in review). Energy gradients in species diversity are correlated to within-species genetic diversity in a wide range of taxa [e.g. plants (Vellend, 2005) and vertebrates (Martin and McKay, 2004)], but whether such latitudinal trends exist in human genetic diversity is unclear. It is interesting to note, however, that several independent studies have demonstrated that human cultural and linguistic diversity follows latitudinal trends (Mace and Pagel, 1995; Nettle, 1998; Collard and Foley, 2002; Pagel and Mace, 2004; Maffi, 2005; Hamilton and Walker, in review). The results presented here imply similar relationships for hunter-gatherer cultural diversity.

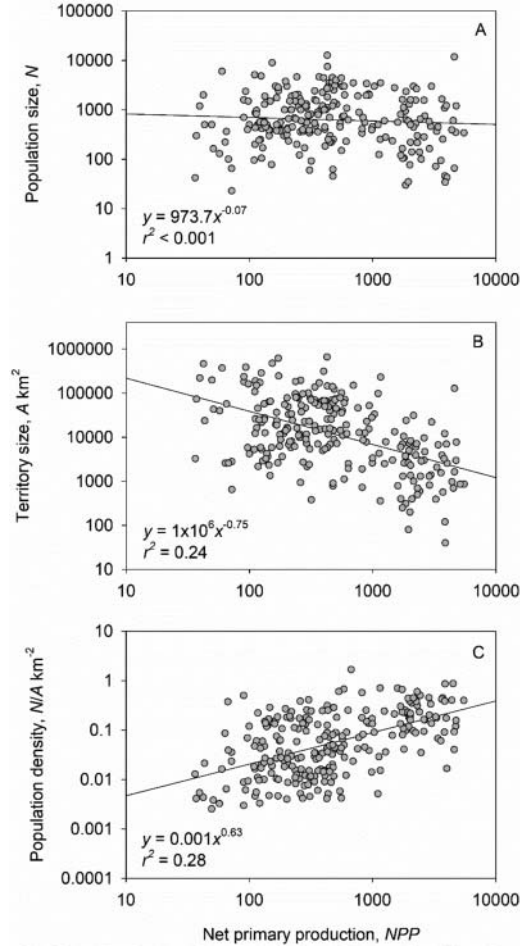


Fig. 7. Log-log plots of hunter-gatherer population sizes, N (A), territory sizes, A (B), and population density, N/A (C) as a function of net primary production, NPP . Best-fit lines are OLS regression models.

Finally, this model has implications for understanding the effects of biological adaptation and cultural innovation on population persistence times. A modification of any of the parameters in the model will necessarily affect persistence times. However, it is important to note that μ_r is a function of both fitness-enhancing and fitness-neutral processes. Persistence times could be increased by: (i) increasing individual fitness (by either raising birth rates or the probability of survival to sexual maturity), (ii) reducing sources of environmental variance, (iii) reducing the frequency or severity of catastrophic events, or (iv) increasing carrying capacities. For example, σ_E^2 can be decreased either by reallocating resources in the life-history budget, which might be expected over time as individuals should invest in lowering exogenous mortality in varying environments (Kaplan and Robson, 2002), or through technological innovations that increase the predictability of heterogeneously distributed resources. Similarly, innovations that either decrease the frequency, or perhaps more likely,

reduce the severity of crash events will necessarily increase persistence times by increasing μ_r (Boone and Kessler, 1999; Boone, 2002). It is also important to consider the effects of population size on persistence times. As the predicted time to extinction scales as a power function of carrying capacity, increasing population sizes will have large effects on persistence time. Consequently, technological innovations or behavioural adaptations over prehistory that resulted in increased mean population sizes by increasing group size or carrying capacity would affect persistence times. As such, population persistence time would increase regardless of effects on individual fitness. For example, while recent studies have shown that increased dependence on agriculture correlates with a gradual increase in both total fertility rates (Sellen and Mace, 1997) and childhood survival (Sellen and Mace, 1999), this model suggests that post-agricultural population growth would have resulted in longer population persistence times due to the simultaneous increase of carrying capacities and buffering against environmental variance and catastrophes through food storage.

There is an emerging consensus that stochastic population dynamics play an important role in all areas of evolutionary anthropology (Neiman, 1995; Hill and Hurtado, 1996; Excoffier and Schneider, 1999; Shennan, 2000, 2001; Pennington, 2001; Boone, 2002; Eller, 2002; Bentley *et al.*, 2004; Eller *et al.*, 2004). This paper shows that stochastic dynamics in hunter-gatherer populations are an inevitable statistical result of finite population sizes, naturally occurring variation in reproductive rates, and the combined long-term effects of environmental stochastic variance and group-level population crashes. Over human evolutionary history, cyclical patterns of local population extinction, replacement, and expansion would have been common, occurring at scales of hundreds of years. Such cyclical population dynamics would have been an important source of genetic and cultural drift. Furthermore, understanding how the sensitivity of extinction dynamics responds to a range of environmental effects provides a quantitative insight into the impact of technological and behavioural innovations on human population dynamics through time and space.

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