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Population and prehistory III: Food-dependent demography in variable environments

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ABSTRACT

The population dynamics of preindustrial societies depend intimately on their surroundings, and food is a primary means through which environment influences population size and individual well-being. Food production requires labor; thus, dependence of survival and fertility on food involves dependence of a population's future on its current state. We use a perturbation approach to analyze the effects of random environmental variation on this nonlinear, age-structured system. We show that in expanding populations, direct environmental effects dominate induced population fluctuations, so environmental variability has little effect on mean hunger levels, although it does decrease population growth. The growth rate determines the time until population is limited by space. This limitation introduces a tradeoff between population density and well-being, so population effects become more important than the direct effects of the environment: environmental fluctuation increases mortality, releasing density dependence and disproportionately raising average well-being for survivors. We discuss the social implications of these findings for the long-term fate of populations as they transition from expansion into limitation, given that conditions leading to high well-being during growth depress well-being during limitation.

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1. Introduction

History and prehistory provide abundant evidence that human populations shape and are shaped by their environment (e.g. Kirch, 1994; Vitousek et al., 2004). The environment plays a role in the demographic and cultural fates of many societies, including whether they are in some sense sustainable (see Kirch, 2007 for a comparison of four cases). This paper completes a quantitative framework for examining how environment, demography, and society jointly affect human population dynamics. Our framework (Lee and Tuljapurkar, 2008; Puleston and Tuljapurkar, 2008) explicitly links population and environment by describing the nonlinear feedbacks between food supply, human mortality, fertility, population density, growth and age structure. This theory of food-dependent demography is an essential first step in linking the biological and social mechanisms that drive macro-demographic change, and advances the development of a quantitative foundation for the study of the joint evolution of human biology and culture (Weiss, 1976). Here we examine the demographic consequences of an environmentally driven, stochastic, year-to-year variation in food supply.

Previously we analyzed two demographic regimes that describe preindustrial populations. In one, population is not limited by space and eventually grows at an asymptotic rate determined by food availability (Lee and Tuljapurkar, 2008). Food availability relative to need depends on environment and on population demography and social factors, loosely defined to include such factors as labor and technology. Food-dependent growth eventually leads to a regime in which space limits food production, and the population reaches an equilibrium density likewise determined by the environment (including available space), demography, and society (Puleston and Tuljapurkar, 2008). The former regime describes populations colonizing or expanding into a new area. The latter describes populations that are constrained within some spatial region, e.g., by physical or climatic factors. In both, we quantify relative food availability using the *food ratio*, which is the number of calories available to consume in a given year relative to the number of calories needed to maximize survival and fertility. The food ratio is a measure of food consumption relative to ideal levels, and thus describes hunger and its effects on population well-being as reflected in age-specific mortality and fertility rates. Our theory of food-dependent demography allows us to ask how environmental factors (such as climate and soil properties) and human factors (such as crop choice, labor organization and harvest efficiency) act via food to influence populations' fates. Thus, it is a foundation for the quantitative study of human-environment interactions in preindustrial societies.

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Our previous work **was** on food-dependent demography analyzed population dynamics in a constant environment. Clearly **however**, every population experiences year-to-year variability. The various species that provide resources to hunter-gatherer societies fluctuate in response to their own population dynamics and to harvest by humans. **Agricultural yields** can vary substantially in response to climate, nutrient cycling dynamics, and cultivation procedures (e.g., Lee et al., 2006; Holopainen and Helama, 2009). Such **fluctuations are likely to be** an important factor in the growth and welfare of human societies (Jorde and Harpending, 1976; Lee, 1993). One might intuit that a constant food supply is better than a variable one in the absence of storage or other explicit mechanisms for coping with or exploiting fluctuations. A long tradition of quantitative population analysis moves beyond intuition, showing how environmental variability and other random fluctuations affect populations in both the growth and limitation regimes (e.g. Lewontin and Cohen, 1969; Tuljapurkar, 1990; Lande, 1993). Here we provide a quantitative analysis of food-dependent demography in varying environments, including the novel nonlinear population feedbacks embodied in the food ratio (Lee and Tuljapurkar, 2008; Puleston and Tuljapurkar, 2008). We show that the effects of fluctuations can be counterintuitive, which illuminates possible human responses to the effects of variability.

In the next section, we briefly summarize the constant-environment dynamics for both expanding and space-limited food-dependent populations, and then provide an overview of our analysis of food and population dynamics in varying environments. In the next two sections, we examine the mean and variance of the food ratio and population dynamics in the expansion and limitation phases, drawing on insight from the previous section regarding the slope and curvature of population and food ratio to interpret our results. We show that in expanding populations, environmental variability has little effect on the mean food ratio, but nevertheless decreases the population growth rate. Slower growth can have negative consequences such as increasing the likelihood of extinction, but it does also delay the onset of space limitation and its depression of the food ratio. In limited populations, yield fluctuation decreases mean population size through reduced fertility and increased mortality. The resulting release from density dependence raises the mean food ratio for the survivors. We discuss the implications of these findings for the long-term fate of populations as they transition from the expansion regime to the limitation regime, and interpret their concrete consequences for populations in differentially productive environments.

2. Variability and food-dependent dynamics

In any food-dependent population, the food ratio determines vital rates; through them, it determines population dynamics and individual well-being. The food ratio depends upon the current state of the population and the environment. When the food ratio is equal to or greater than 1, population survival and fertility rates are maximal. As the food ratio falls below 1, survival and fertility rates decrease. We detail additional assumptions and data sources for parameter values elsewhere (Lee and Tuljapurkar, 2008; Puleston and Tuljapurkar, 2008). Two of these points will play important roles in the current work. First, we assume that the increasing relationship between the food ratio and vital rates is concave, which is reasonable if physiological limitations prevent survival and fertility from rising beyond their maximum values even as food becomes very abundant (we neglect any decreases due to obesity or related ailments). Second, data from historical demography indicate that mortality is most responsive to food **shortages** at very young and at old ages (Bengtsson et al., 2004). To clarify our objectives for analyzing the dynamics of the food ratio in a varying

environment, we briefly summarize our main previous findings for constant environments, focusing for illustration on agricultural societies.

When arable land is abundant, as a population grows, additional workers can claim new, previously unfarmed plots as needed. In a constant environment, the population achieves an equilibrium where the food ratio, growth rate and population age composition are unchanging. One consequence of these dynamics is that a growing population's most effective route to increasing the food ratio is to raise crop yield, or if possible to work harder or recruit non-workers to agricultural labor. By contrast, though fertility control does affect the food ratio, its effects depend on the population's growth rate (Lee and Tuljapurkar, 2008). In a variable environment, the food ratio fluctuates persistently over time. Our analysis of the population equilibrium therefore involves the mean and variance of the food ratio and the long-term average change in population or stochastic growth rate. More importantly, social choices (such as those regarding labor contributions or fertility) now affect the mean and the variance of the food ratio and the stochastic growth rate, and these different quantities may respond to a given choice in differing ways.

As a population approaches the point where all available farmland is under cultivation, additional workers cannot claim new land, so every worker must farm a smaller plot. Alternatively, additional workers can go idle, but the population effect is the same: as population numbers increase, the food produced relative to food demand falls until the food ratio and population numbers stabilize. Consequently, in a constant environment, increases in crop yield do not increase the equilibrium food ratio because an increase in food ratio spurs population growth, which in turn eventually brings the food ratio back down to its previous value. Thus, yield and labor affect equilibrium density but not equilibrium food ratio; instead, maximal life expectancy and fertility rates are primary controls, and an effective way for a society to increase the food ratio when space is limiting is fertility control (Puleston and Tuljapurkar, 2008). In a variable environment, the steady state is again characterized by persistent fluctuations over time, and we must examine the means and variances of the food ratio and population size and the ways in which societies might intentionally or unintentionally manipulate these quantities.

In each year t , a population realizes a food ratio that depends on labor and food demand, which are both functions of population age composition, and on the yield Y_t per unit cultivated area, which is a function of the environment. We can write the food ratio E_t as proportional to the yield per unit area,

$$E_t = Y_t f(\mathbf{n}_t), \quad (1)$$

where $\mathbf{n}_t = \{n_{x,t}\}$ is a vector of the numbers of individuals aged x at time t ; we will specify how the food ratio depends on population ($f(\mathbf{n}_t)$) in the following sections. The population's vital rates depend on E_t and constitute a population projection matrix $\mathbf{A}_t = \mathbf{A}(E_t)$. Later, we will take the logarithm of both sides of (1) in order to work with an additive function of log yield and log population: $\log E_t = \log Y_t + \log f(\mathbf{n}_t)$.

To introduce environmental variability, we suppose that Y_t varies around a mean yield \bar{Y} with a coefficient of variation C (the ratio of the standard deviation to the mean of yield). Formally,

$$Y_t = \bar{Y}(1 + W_t),$$

where the random variable W_t has mean 0 and variance $\overline{W_t^2} = C^2$, where a bar denotes an expectation. This does not necessarily imply that the variation around \bar{Y} is symmetrical, although we do assume independence and identical distribution between years; in our numerical work, we use a gamma random variable for yield because the gamma distribution is continuous and nonnegative. Finally, we assume that the magnitude of annual variation $C^2 \ll 1$,

so that C is less than about 0.5. We do not consider here other potential consequences of environmental variability, such as fluctuations in maximal vital rates or other parameters, but in the Discussion we briefly describe how the insights we gain from analyzing variation in food availability help us to infer their effects.

Associated with constant yield \bar{Y} is a constant food ratio \hat{E} , where a hat denotes an equilibrium quantity. In addition, there is a stable equilibrium population age structure $\hat{\mathbf{u}}$, and in the limitation regime, the population vector is also constant at $\hat{\mathbf{n}} = \hat{N}\hat{\mathbf{u}}$, where \hat{N} is the stable equilibrium population size. When yield fluctuates around its mean, the food ratio differs from \hat{E} . As a result the projection matrix \mathbf{A}_t differs from $\mathbf{A}(\hat{E})$, and the population fluctuates around its stable equilibrium. In each year the food ratio is affected by current variation in yield and the population deviation generated in the preceding year. To follow these fluctuations we analyze together the dynamics of the food ratio and the population vector, focusing on how the mean values of food ratio and population differ from their deterministic equilibrium values, and on the variance in these quantities over time.

The log food ratio is a nonlinear function of yield and of population. The population vector, via the projection matrix, is a nonlinear function of the food ratio. To illustrate the effect of fluctuation on such a system, we begin with a simpler nonlinear example. Let X_t be a nonlinear function $g(D_t)$ of some stochastically varying quantity D_t . When D_t is fixed at D_0 , the value of X_t is X_0 . Letting D_t fluctuate around a mean of D_0 with a coefficient of variation C , then $\text{Var}[D] = C^2 D_0^2$. We expand X_t around X_0 and take expectations to find that, to second order, the mean value of X_t is

$$\bar{X} = X_0 + \frac{1}{2} C^2 D_0^2 g_2,$$

where g_2 is the second derivative of the function g with respect to D computed at D_0 . The variance in X_t is

$$\text{Var}[X_t] = C^2 D_0^2 g_1^2,$$

where g_1 is the first derivative of the function g computed at D_0 . Both the shift in the average of X_t and the variance of X_t are proportional to C^2 , which is intuitively reasonable. The shift in the mean depends on the curvature of the nonlinear function g at D_0 : a concave g lowers \bar{X} relative to X_0 , whereas a convex g yields the converse (Jensen, 1906). The variance of X_t depends on the square of the slope of g at D_0 : steep slopes mean a larger range of X_t deviations around X_0 , leading to higher variances when these deviations are squared. The equations for the means and the variances of the food ratio and population vector, both nonlinear functions of fluctuating quantities, are analogous to the equations for our example function X_t , and we can interpret the effects of variation in yield and in population precisely as we have interpreted the effect of variation in D_t .

Yield fluctuations affect population through fluctuations in the food ratio. As in the simple example above, we find that to the second order, the average population vector is

$$\bar{\mathbf{n}} = \hat{\mathbf{n}} + C^2 \mathbf{h}^{(2)}, \quad (2)$$

where $\mathbf{h}^{(2)}$ is a vector that depends on the curvature of population at each age as a function of the food ratio (though it is not itself a derivative, as we indicate by the superscript notation). We will see that $\mathbf{h}^{(2)}$ involves the relationship between the projection matrix and the food ratio (indeed, to derive Eq. (2) requires expanding the projection matrix to the second order and solving together with expansions for population and for the food ratio). Instead of the scalar variance in our example above, we have a vector containing

the population variances at each age and the covariances between pairs of ages,

$$\sigma_n = C^2 \mathbf{h}^{(1)}, \quad (3)$$

where $\mathbf{h}^{(1)}$ depends on the square of the slope of the relationship between population at each age and the food ratio. We can rearrange σ_n into the square variance-covariance matrix of population, Σ_n .

Returning to the food ratio, we use (2) and (3) in a second-order expansion of the log food ratio and equate terms of the same order to find that

$$\overline{\log E} = \log \hat{E} + C^2 \left[-\frac{1}{2} + \langle \psi^{(1)}, \mathbf{h}^{(1)} \rangle + \langle \psi^{(2)}, \mathbf{h}^{(2)} \rangle \right] \quad (4)$$

where angle brackets denote a scalar product. The terms $\psi^{(1)}$ and $\psi^{(2)}$ involve the food production net of consumption, and thus convert population into food. Eq. (4) separates the direct effect of variance in yield (given by the first term in square brackets), the difference between the average population and the deterministic equilibrium (the third term in square brackets, compare (2)), and the effect of the variance in population (the middle term in square brackets, compare (3)). Because the log function is concave, the effects of variance in yield or in population are negative, as shown above for the yield and as we will see below for the population variance.

If yield fluctuation is independent between years, the variance of the log food ratio is the sum of the variance in its two parts,

$$\text{Var}[\log E_t] = C^2 [1 + \langle \psi^{(3)}, \mathbf{h}^{(1)} \rangle], \quad (5)$$

where we can show that (to second order) C^2 is the variance of the log of yield, and the second term is the variance in the log of $f(\mathbf{n}_t)$.

The specific forms of the $\mathbf{h}^{(i)}$ and the $\psi^{(i)}$ depend on the forms of E and the population projection equation, which differ depending on whether a population is in the expansion regime or the limitation regime. In the next sections we discuss the differences between the regimes in their response to fluctuation. We will show that in an expanding population, the variable-environment mean food ratio is not much different from its constant-environment equilibrium value, but the stochastic population growth rate is lower than the constant-environment rate. Just as in constant environments, the direct and linear effects of yield on the food ratio dominate the nonlinear effects of age structure dynamics, so that the mean and variance of the food ratio are essentially straightforward functions of the mean and variance in crop yield. Because survival and fertility rates are concave functions of food consumption, however, years of high food ratio cannot compensate for bad years: survival and fertility cannot increase beyond a maximum. Variations in the food ratio therefore depresses long-term average growth. We discuss the concrete implications of lower growth rates, including potentially increasing extinction probability and lengthening the time before transition to the space-limited regime.

In the limitation regime, yield variation decreases the mean population size and increases the mean food ratio. Because single bad years can decrease a population more quickly through mortality than single good years can increase it through population growth, yearly fluctuation reduces mean size, thereby releasing density dependence and increasing per capita food availability. Nevertheless, the transition from the relatively high food ratios enjoyed during population growth to lower levels under space limitation is dramatic except in unproductive environments. Just as in constant environments, environmental and demographic factors that encourage fast population growth eventually lead to large mean population sizes, with associated high levels of hunger and food dependency. These relationships have potential economic and social consequences in addition to their implications for population health.

3. Expansion regime

The core equations of a growing food-dependent population are given in Lee and Tuljapurkar (2008). The dynamics of the age-structure vector follow

$$\mathbf{u}_{t+1} = \frac{\mathbf{A}(E_t)}{\lambda_t} \mathbf{u}_t, \quad (6)$$

and the per capita change in population size N_t over one time step is

$$\lambda_t = \frac{N_{t+1}}{N_t} = |\mathbf{A}(E_t) \mathbf{u}_t|. \quad (7)$$

Here the age-structure vector \mathbf{u} describes relative population numbers, and substitutes directly for the absolute population vector \mathbf{n} in the general analysis of the previous section.

Given abundant space, the food ratio is

$$E_t = \frac{Y_t H k \langle \phi, \mathbf{u}_t \rangle}{J \langle \rho, \mathbf{u}_t \rangle}. \quad (8)$$

The numerator of this expression is the per capita amount of food produced in a population where each effective worker cultivates a plot of land of size k , so that the area cultivated increases linearly with the population effective work force. The hours of labor contributed by a worker of age x are $H\phi_x$, and Y_t is the crop yield per unit area in year t . The denominator of expression (8) similarly describes the amount of food needed per capita to maximize vital rates, as an individual of age x requires $J\rho_x$ calories.

Details of the analytical approach we outlined in the previous section appear in the Appendix. In this and the following section, we simply present and interpret the terms in Eqs. (4) and (5). Recall that in (4), the deviation between the mean age structure vector and its deterministic equilibrium depends on $\mathbf{h}^{(2)}$ and on $\mathbf{h}^{(1)}$, whereas the variance in age structure depends only on $\mathbf{h}^{(1)}$.

The $\mathbf{h}^{(1)}$ term describes the variance–covariance structure of fluctuations in age structure, given that its dependence on the variance of yield fluctuations C^2 has been factored out (see Eq. (3)):

$$\mathbf{h}^{(1)} = (\mathbf{I} - \mathbf{S}_X \otimes \mathbf{S}_X)^{-1} \left[(\mathbf{I} - \hat{\mathbf{u}} \mathbf{e}^T) \frac{\mathcal{A}_1 \hat{\mathbf{u}}}{\hat{\lambda}} \otimes (\mathbf{I} - \hat{\mathbf{u}} \mathbf{e}^T) \frac{\mathcal{A}_1 \hat{\mathbf{u}}}{\hat{\lambda}} \right]. \quad (9)$$

Here the symbol \otimes indicates a Kronecker product, a superscript -1 a matrix inverse, and a superscript T a matrix transpose, while \mathbf{I} is the identity matrix, and \mathbf{e} is a column vector of ones. The \mathbf{S}_X matrix is the stability matrix of the deterministic equilibrium, where the subscript X denotes the expansion regime (see Appendix for details). Generally speaking, the larger the values making up the stability matrix, the greater the tendency of deviations from equilibrium age structure to grow due to intrinsic dynamics; thus it is intuitively reasonable that larger \mathbf{S} should increase the magnitude of age-structure fluctuations. We define \mathcal{A}_1 as the first derivative of the projection matrix \mathbf{A} with respect to the log food ratio, evaluated at equilibrium:

$$\mathcal{A}_1 = \left(\frac{\partial \mathbf{A}}{\partial \log E} \right)_{\hat{E}}. \quad (10)$$

Thus, $\mathcal{A}_1 \hat{\mathbf{u}} / \hat{\lambda}$ describes population changes due to food ratio fluctuations near equilibrium, and its square (given by the Kronecker product in (9), scaled by the age-structure vector via $\mathbf{I} - \hat{\mathbf{u}} \mathbf{e}^T$) describes the variance of direct population response to extrinsic variation.

The $\mathbf{h}^{(2)}$ term is complex and appears in the Appendix; here we note only that it involves the second derivative of the projection matrix to food ratio \mathcal{A}_2 in addition to the first derivative. Curvature in the response of population to changes in yield has two sources. The first is the physiological cap on survival and fertility rates,

which prevents linear responses to very abundant food. The second is a disproportionate age-structure response to large, negative perturbations: in particularly bad years, food shortage results in not only fertility reductions but also significant mortality at young and old ages. Since younger and older people are less likely to participate in agricultural labor, this change in the age structure decreases the population ratio of dependents to laborers, increasing the average log E_t and helping to buffer the effect of bad years for those who survive.

In Eqs. (4) and (5), both the deviation in the mean log food ratio from deterministic equilibrium and the variance in food ratio depend on $\mathbf{h}^{(1)}$ through the vectors $\psi^{(1)}$ and $\psi^{(3)}$, whereas only the deviation from the mean depends on the shift in mean age structure via $\psi^{(2)}$:

$$\begin{aligned} \psi^{(2)} &= \frac{\phi}{\langle \phi, \hat{\mathbf{u}} \rangle} - \frac{\rho}{\langle \rho, \hat{\mathbf{u}} \rangle} \\ \psi^{(1)} &= -\frac{1}{2} \left[\frac{\phi \otimes \phi}{\langle \phi, \hat{\mathbf{u}} \rangle^2} - \frac{\rho \otimes \rho}{\langle \rho, \hat{\mathbf{u}} \rangle^2} \right], \\ \psi^{(3)} &= \psi^{(2)} \otimes \psi^{(2)}. \end{aligned} \quad (11)$$

These terms translate fluctuations in age structure into excesses or deficits of calories relative to the deterministic equilibrium. The contribution of deviations in mean log age structure to mean log food ratio is most straightforward, as the scalar product between $\psi^{(2)}$ and an age structure deviation clearly yields a net relative calorie gain. The contributions of the variance of age structure involve squares of $\psi^{(2)}$ or of its components. Note that $\psi^{(1)}$ is negative, indicating that a variance in age structure has a negative influence on mean log food ratio through the concavity of the log function.

For most reasonable combinations of mean yield, yield variation, and other parameters affecting the population's demography and environment, both $\mathbf{h}^{(1)}$ terms are negligible and the $\mathbf{h}^{(2)}$ term is in the order of 10^{-2} . These are small relative to the yield terms in (4) and (5), indicating that the dynamics of the food ratio essentially reflect direct responses to yield variation, which mirrors our findings in a constant environment (Lee and Tuljapurkar, 2008). Under conditions that are very unfavorable to population growth, however (e.g. medium to low life expectancy and total fertility rate when food is abundant, small labor force, high sensitivity of vital rates to food shortage and low mean yield and/or high yield variability), the $\mathbf{h}^{(1)}$ terms are larger, on the order of 10^{-3} in magnitude, while the $\mathbf{h}^{(2)}$ term can reach as high as 0.4. While still smaller than the direct effects of yield, age-structure fluctuations do affect food ratio dynamics under unfavorable conditions. This is because an unfavorable combination of environmental and population factors makes it more likely for bad years to trigger widespread mortality, where decreases in the ratio of dependents to laborers buffer the food ratio during bad years and for some years following.

We conclude that during population expansion, environmental variation does not generally have negative indirect consequences for the mean or variance of the food ratio. On the contrary, age-structure feedbacks can sometimes slightly mitigate large, negative yield fluctuations. Thus, in a varying environment, individuals in a growing population are on average as well off or even slightly better fed than in a constant one. (As a reminder, though we have worked with the log food ratio, the mean of which is depressed by fluctuations due to the concavity of the log function, the food ratio itself is the quantity that matters from the point of view of the population.)

How do fluctuations in the food ratio and in age structure affect the long-term population growth rate? Population size is a function of the fluctuating food ratio via the projection matrix. Unlike age structure, however, population size in the expansion regime does not fluctuate around an attractor. The growth rate in

a given year depends on the projection matrix in that year and also on the current state of the population, which depends on previous matrix perturbations. As a result, the average long-run growth rate depends not only on the variance–covariance structure of the matrix fluctuations (analogous to the way in which the average food ratio depends on the variance–covariance structure of population in Eq. (4)) but also on the lagged variance–covariance structure of the fluctuations, which describes how the variation in each matrix element at time t relates to the variation in each other matrix element at time $t - \tau$ for every lag τ . If variation in the projection matrix were independent and identically distributed, then the lag terms would be zero in expectation, but because the matrix fluctuations depend on food ratio dynamics, they are nonzero.

The full expression for the stochastic growth rate appears in the Appendix. We focus here on its leading term, which is the dominant eigenvalue of the mean projection matrix. This eigenvalue is a monotonic increasing function of the elements of the mean matrix, so its deviation from the deterministic equilibrium growth rate depends upon the deviation of the mean projection matrix from its deterministic equilibrium, $\mathbf{A}(\hat{E})$. As shown in the Appendix, this deviation has two parts. The first term converts the deviation in mean log food ratio into a deviation in mean matrix elements via \mathcal{A}_1 , the derivative of \mathbf{A}_t with respect to $\log E_t$. Because both survival and fecundity increase with the log food ratio, this derivative is positive; because the shift in mean log E_t is negative, the contribution to the matrix deviation is also negative. The second term translates variance in $\log E_t$ into a shift in the mean matrix via \mathcal{A}_2 , which describes curvature in the matrix elements as a function of $\log E_t$. This function is concave at medium to high $\log \hat{E}$ (up to a point where \hat{E} sufficiently exceeds 1) because vital rates increase toward their maxima. The overall result is a negative deviation in the mean matrix from the deterministic equilibrium. The stochastic growth rate is thus lower than the equilibrium growth rate because in general, the population is unable to capitalize on good years enough to compensate for bad. While the functions relating vital rates to food could be convex under severe food shortages, this would affect only dramatically shrinking populations with little relevance for ones that persist.

Fig. 1 illustrates the influence of mean yield and yield variation on the stochastic growth rate as given by the full approximation, Eq. (36) in the Appendix. Increases in mean yield increase the stochastic growth rate through increases in the deterministic equilibrium and decreases in the deviation from equilibrium, while increasing yield variation decreases it through the mechanisms we have discussed.

Except in very productive environments, the long-term average population growth rate decreases due to fluctuations. This response to environmental variation is a likely factor suppressing long-term growth rates for early societies. Slow growth has many demographic and social consequences. For instance, longer times spent at smaller population sizes can increase the probability of extinction, whether due to food shortage or other random events. Also, slower growth and spatial spread could delay the development of social, economic, and political infrastructure, potentially affecting relations between distinct populations in addition to conditions within a given population. On finer temporal scales, a slower growth trajectory likely includes more frequent periods of short-term population decrease, during which the population would suffer all the adverse social consequences of a decline. On the other hand, slower growth delays the onset of space limitation and its associated depression of the food ratio. A lengthening of the growth period also increases the time during which, for example, potential exists to increase the food ratio over the long term through advances in labor efficiency or crop yield. If such advances proved successful, however, they would also have the unintended consequence of increasing the stochastic growth rate and bringing on space limitation more rapidly.

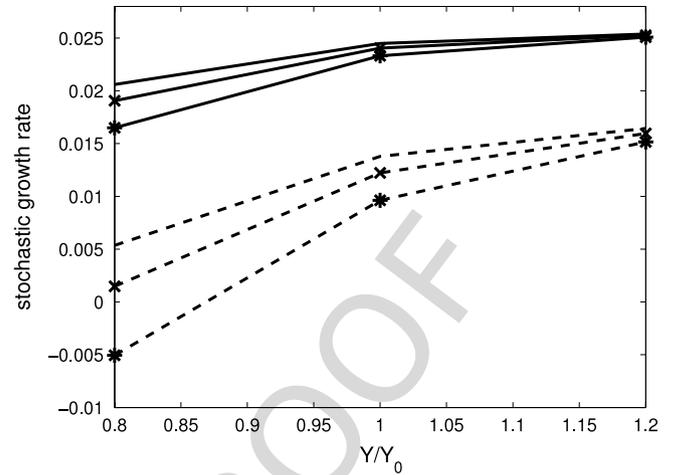


Fig. 1. Stochastic growth rate (Eq. (36)) as a function of mean yield. The x axis is the ratio of mean yield to yield needed to maximize vital rates. Solid lines: demography favorable to population growth (maximal life expectancy is high (60 years), individuals work productively from age 10 to age 65, and elasticities describing the response of vital rates to food consumption are based on data from historical demography (Lee and Tuljapurkar, 2008)). Dotted lines: unfavorable demography (maximal life expectancy is 45 years, individuals work from age 15 to age 55, and vital rate elasticities are doubled). Shown are three levels of yield variation: CV = 0.1 (no symbol), 0.2 (cross), and 0.3 (asterisk).

4. Limitation regime

When cultivable land becomes limiting, populations cannot continue to expand onto new farmland. The population vector is

$$\mathbf{n}_{t+1} = \mathbf{A}(E_t) \mathbf{n}_t \quad (12)$$

with

$$E_t = \frac{Y_t A_m F(Hk(\rho, \mathbf{n}_t)/A_m)}{J(\rho, \mathbf{n}_t)}, \quad (13)$$

where R is the area of available arable land, and $F(\mathbf{n}_t) = F(Hk(\rho, \mathbf{n}_t)/A_m)$ is the fraction of that area actually cultivated (Puleston and Tuljapurkar, 2008). It is a concave increasing function of \mathbf{n}_t , bounded between 0 and 1. This does not impose a ceiling on population numbers, but rather introduces a tradeoff between population size and per capita food production: when all land is under cultivation, population size may increase, but food production remains constant. As a result, the food ratio decreases as the population density increases.

Using (12) and (13), the term describing the variance–covariance structure of population is

$$\mathbf{h}^{(1)} = (\mathbf{I} - \mathbf{S}_t \otimes \mathbf{S}_t)^{-1} [\mathcal{A}_1 \hat{\mathbf{n}} \otimes \mathcal{A}_1 \hat{\mathbf{n}}], \quad (14)$$

where \mathbf{S}_t is the stability matrix of population equilibrium in the limitation regime (details appear in the Appendix). Again it is intuitively reasonable for the magnitude of population fluctuations to increase with the stability matrix, and $\mathcal{A}_1 \hat{\mathbf{n}}$ describes the population response to changes in the projection matrix. The $\mathbf{h}^{(2)}$ term describing the shift in the mean population vector due to food ratio fluctuation appears in the Appendix.

The vectors describing the effects of the shift in mean population and population variance–covariance on the deviation in mean log food ratio (Eq. (4)) are

$$\begin{aligned} \psi^{(2)} &= \phi \frac{\hat{F}_1}{\hat{F}} - \frac{\rho}{\langle \rho, \hat{\mathbf{n}} \rangle}, \\ \psi^{(1)} &= -\frac{1}{2} \left[\phi \otimes \phi \left(\frac{\hat{F}_1^2}{\hat{F}^2} - \frac{\hat{F}_2}{\hat{F}} \right) - \frac{\rho \otimes \rho}{\langle \rho, \hat{\mathbf{n}} \rangle^2} \right], \end{aligned} \quad (15)$$

where $\hat{F} = F(\hat{\mathbf{n}})$, and \hat{F}_1 and \hat{F}_2 are the first and second derivatives, respectively, of F with respect to \mathbf{n} , evaluated at $\hat{\mathbf{n}}$. The $\psi^{(i)}$ vectors convert population perturbations into net food production, the F terms accounting for changes in area cultivated near equilibrium as the population fluctuates. We note that \hat{F}_1 is small compared to \hat{F} , with the result that $\psi^{(2)}$ is negative. The term in Eq. (5) converting population variance into food-ratio variance is again $\psi^{(3)} = \psi^{(2)} \otimes \psi^{(2)}$. The magnitude of the $\psi^{(i)}$ decreases as equilibrium population $\hat{\mathbf{n}}$ increases; as a result, although factors that affect $\hat{\mathbf{n}}$ (such as average environmental productivity) also affect population mean and variance, for reasonable parameter ranges they have essentially no effect on the mean or variance of the food ratio.

The $\mathbf{h}^{(2)}$ term in (4) is an order of magnitude larger than $1/2$ under reasonable parameter ranges, while the $\mathbf{h}^{(1)}$ term is on the order of 10^{-2} and is therefore essentially negligible. The $\mathbf{h}^{(2)}$ term describes disproportionate population responses to large changes in yield, and its leading term is the last one in Eq. (29) in the Appendix. This term depends on the shape of the relationship between vital rates and log food ratio through the matrix derivatives $\mathcal{A}_2 - \mathcal{A}_1$. As \mathcal{A}_1 is positive and \mathcal{A}_2 is negative, the mean population deviation from equilibrium is negative. In concrete terms, during severe food shortages, people die and birth rates drop. The concavity in population response indicated by \mathcal{A}_2 means that in years of plenty the population increase is slower, so that good years do not compensate for mortality during bad ones.

The effect of the large, negative deviation from equilibrium population is to increase the mean log food ratio, due to large decreases in food consumption caused by decreases in older and particularly younger dependents. Reducing the absolute number of mouths to feed releases the population from the density dependence imposed by the space limitation of equilibrium food resources, as reflected in $\psi^{(2)}$. This mechanism accords with the previous finding that sustained fertility control is an effective means of improving the equilibrium food ratio in constant environments (Puleston and Tuljapurkar, 2008). Here, each crop failure triggers mortality which increases $\log E_t$ for the survivors. Isolated increases in the food ratio would be followed by decrease as population numbers recovered, but repeated fluctuations decrease the average population size and increase the average food ratio.

Thus in the limitation regime, direct responses of mean $\log E_t$ to yield fluctuations are dwarfed by opposing population-mediated responses, which result from concavity of the functions relating population to yield. As a result, yield fluctuations increase the mean food ratio over its constant steady-state value, due to release of the population from density dependence. In contrast with the food ratio, population size responds comparably to environment and to demography, largely because it is sensitive to mean crop yield. Figs. 2 and 3 illustrate the mean and variance of population size for the conditions shown in Fig. 1, showing the relative effects of mean yield, yield variation, and favorable vs. unfavorable demography. We calculate mean size as the sum of $\hat{\mathbf{n}}$ (Eq. (2)), and the variance as the sum of the elements of the variance-covariance matrix (the sum of σ_n , Eq. (3)). The yield values on the x axis, yield CVs, and other aspects of population demography are as in the previous figure, and the area of farmland A_m is the same for all cases. As expected, the figures show that as yield variation increases, mean population falls and variation increases. The effects of mean crop yield and of favorable vs. unfavorable demography on mean population in Fig. 2 are comparable in magnitude, largely due to their influence on equilibrium population size (Puleston and Tuljapurkar, 2008). High mean yields and favorable demography also raise population variance in Fig. 3, largely through the same mechanism (see (12)); the effect of demography is smaller than that of environment.

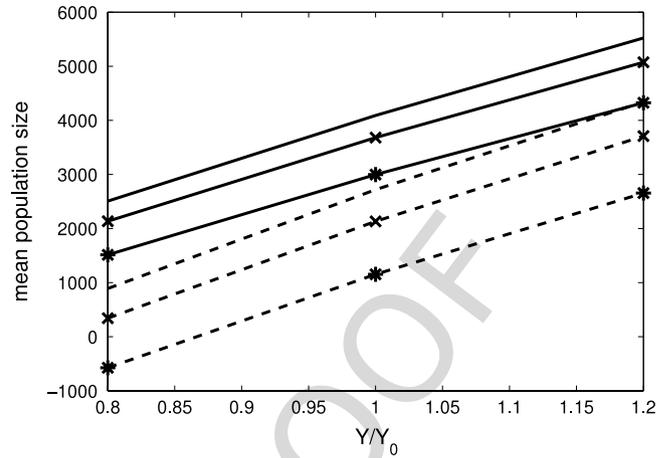


Fig. 2. Mean population size under space limitation for the populations shown expanding in Fig. 1, illustrating the relative effects of mean crop yield, yield variation, and other aspects of demography. Size is the sum of Eq. (2) in the text, where we find $\hat{\mathbf{n}}$ numerically (Puleston and Tuljapurkar, 2008). All lines and symbols are as in Fig. 1.

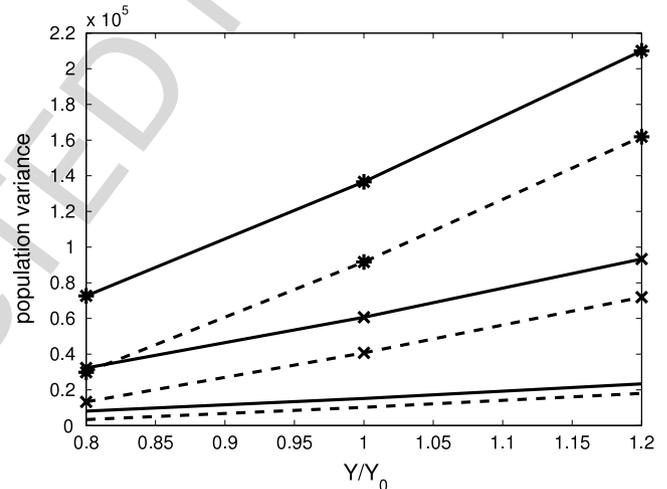


Fig. 3. Variance in population size in the limitation regime for populations shown in Fig. 1. Variance is the sum of the terms of the population variance-covariance matrix Σ_n , given in Eq. (3) in the text.

Figs. 2 and 3 display the eventual fates of each growing population in Fig. 1 (populations with unfavorable demography, extremely low mean yield, and high yield variation, which previously had negative stochastic growth rates, here are extinct as evidenced by small or negative mean population sizes). Putting the three figures together, we see that factors encouraging fast population growth also favor large average populations under space limitation. In the previous section we considered several reasons why faster growth to large population sizes might be socially advantageous, but when space becomes limiting, a clear tradeoff between population size and per capita food availability emerges and intensifies. This transition to greater levels of hunger would presumably require some measure of social adaptation, even if it took place over many generations. In productive environments the necessary transition from a high average food ratio during growth to a low one at stasis is particularly dramatic, because as we have discussed, in terms of the mean and variance of food ratio, societies in productive environments fare the same as ones in unproductive locations at the limitation equilibrium. The drop in mean well-being during transition would be somewhat offset by the increasingly positive effect of variability, but given that mortality is the mechanism by which fluctuations increase the

1 food ratio, emigration or other solutions would likely be preferable.
 2 In larger areas A_m , the transition would be delayed, but its eventual
 3 impact would not be mitigated.

4 Although space limitation in productive environments lowers
 5 per capita food availability, it also results in large numbers
 6 of working-age individuals who cannot productively farm. In
 7 growing populations, people can certainly choose not to farm, and
 8 we have previously considered the resulting effects on the food
 9 ratio (Lee and Tuljapurkar, 2008). Here, however, the shortage of
 10 land enforces high degrees of “food dependency”. Whereas the
 11 concept of dependency in modern contexts involves individuals
 12 who are too young or too old to contribute effectively to the
 13 economy, food dependents can contribute economically or socially
 14 depending on their specific non-agricultural activities, but they
 15 cannot contribute positively to food supply in a closed system.
 16 Thus, voluntary or enforced food dependency is a potential engine
 17 of economic specialization, but one that comes with individual
 18 and population nutritional costs. Its conflicting roles provide a
 19 promising direction for future research.

20 Upon reaching space limitation, slower-growing populations
 21 suffer a more modest decrease in food ratio due to smaller mean
 22 population sizes. They may incur problems associated with smaller
 23 populations, discussed above, but may also avoid some non-food
 24 consequences of crowding, such as sanitation issues. In addition, if
 25 the slow growth is due at least in part to demographic factors such
 26 as low maximal life expectancy or fertility rates and/or high vital
 27 rate sensitivity to food, the mean $\log E_t$ is higher than it would be
 28 if the population had a demography more favorable to fast growth
 29 and large size. Whether lower mean levels of hunger outweigh the
 30 penalties of small population size and lower maximal vital rates
 31 (due to harsh climate, disease, or other adverse food-independent
 32 factors) is unclear. In the next section we consider the mean and
 33 variance of lifetime measures of well-being such as life expectancy
 34 and total fertility, which involve the combined effects of food and
 35 other factors affecting quality of life.

36 We note one final potential drawback associated with small
 37 mean population size: the mean sizes and variances in Figs. 2
 38 and 3 combine to increase the CV of population size at low levels
 39 of yield, provided that yield variation is high and demography is
 40 also unfavorable. Though the absolute magnitude of population
 41 variation is less, the proportional changes are greater, possibly
 42 placing larger stress on survivors. Without being more specific
 43 about the structure of a given society, it is difficult to assess
 44 whether high population CV or high population variance would
 45 be more important, but this analysis points out that the two occur
 46 under different conditions and might be worth weighing against
 47 one another.

48 5. Lifetime well-being: life expectancy and fertility

49 We now examine individual well-being as measured by the
 50 means and variances of life expectancy and total fertility rate.
 51 These quantities reflect aspects of the quality of life that were
 52 surely directly relevant to individual lives.

53 The life expectancy at birth is approximately the sum over all
 54 ages of survivorship to each age. Survivorship l_x is the cumulative
 55 product of the food-dependent survival rates to age x . Period
 56 measures apply a given year's conditions to every age, as if a
 57 population experienced that year's conditions throughout life.
 58 Cohort measures track conditions in each year as an individual
 59 ages. This distinction matters for cumulative statistics such as
 60 survivorship, life expectancy and total fertility rate.

61 A second-order approximation of stochastic survivorship (see
 62 Appendix) has three components. The first is the shift in the
 63 survivorship schedule due to the fact that stochasticity alters
 64 mean food availability. The second is the covariance between

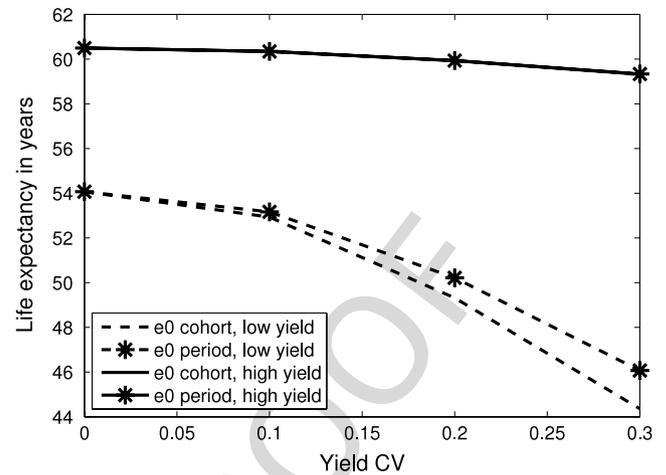


Fig. 4. In the expansion regime under favorable demographic conditions life expectancy is highly responsive to mean yield, less so to yield variation. When $Y/Y(0)$ is 1.2 (solid lines) vital rates are always near their maxima, even as variation in food supply increases. The difference between cohort and period approximations is quite small and the lines appear as one. When $Y/Y(0)$ is 0.8 (dashed lines) variation plays more of a role, reducing the constant-environment life expectancy by as much as 10 years at yield CV of 0.3. At the lower yield level we see the emergence of the expected difference in cohort and period measures.

65 perturbations at different ages weighted by the local survival
 66 elasticities, and the third is the contribution of variation in
 67 $\log E$, weighted by the curvature of the age-specific survival
 68 probabilities. All three contribute to period survivorship. In the
 69 period calculation survival at every age is determined by the food
 70 ratio in that period, and the second component is positive except
 71 at very low food availability. In the cohort calculation, survival
 72 at different ages responds to the food ratio in different years; if
 73 the autocorrelation in $\log E_t$ is zero, then in the cohort calculation
 74 the second component is zero. Hence in either the expansion
 75 or space-limitation regime, period survivorship exceeds cohort
 76 survivorship, due to the positive effect of correlated perturbations
 77 in the period calculation. In the expansion regime variation
 78 reduces average $\log E$, so the first component is negative and
 79 increases in magnitude with an increasing yield CV. The third
 80 component is negative above very low values of E and represents
 81 the asymmetrical effect of variation on survivorship due to the
 82 curvature of the survival functions.

83 The effects of varying yield are quite different in the expansion
 84 and limitation regimes. For the expansion regime, Fig. 4 displays
 85 the response of life expectancy to high and low mean yield and
 86 to yield variation. In the expansion, the first term changes little
 87 with yield CV because average $\log E$ changes little. At high yields
 88 under favorable demographic conditions the second term of the
 89 expansion is small so that period and cohort measures are very
 90 close. The third term is small and negative, so average period and
 91 cohort lifespan falls slightly in response to variation. At low yields
 92 the second term is larger and increases with CV, making period
 93 life expectancy larger than cohort life expectancy. Now the third
 94 term becomes more negative as variation increases, driving life
 95 expectancy down. Overall, in the expansion regime at high mean
 96 yield, e_0 is insensitive to CV, but at low mean yield e_0 decreases
 97 with an increasing CV. In contrast, in the space-limited regime
 98 (Fig. 5), the positive effect of variation on average E causes the
 99 first term of the expansion to increase with increasing CV. At high
 100 yields the first term dominates the other two, so both period and
 101 cohort e_0 increase with CV, with little difference between them.
 102 At low mean yields, life expectancy decreases as CV increases to
 103 about 0.2, and then increases with a further increase in yield CV.
 104 The contrast in the drivers of life expectancy in the two regimes
 105 is striking. In an expanding population, variance in food supply

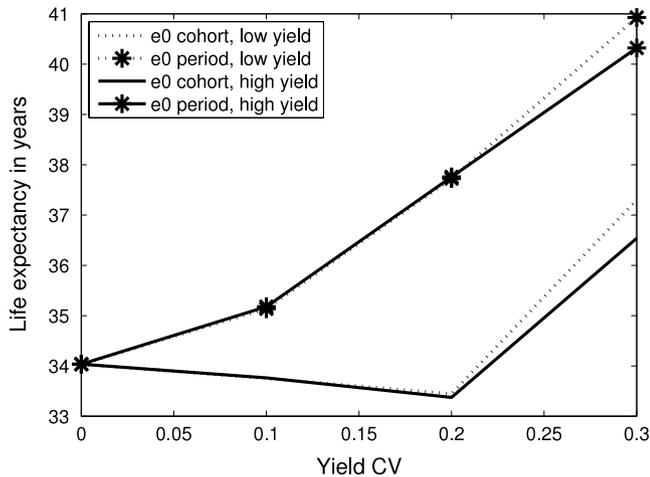


Fig. 5. In the limitation regime under favorable demographic conditions mean yield level has almost no effect on life expectancy. Variation generally increases life expectancy due to its strong positive effect on the food ratio. At low yield variation, cohort life expectancy changes very little from its deterministic level, as the increase in $\log E$ is balanced by the negative effect of variation on period survival. Period life expectancy exceeds the cohort measure due to the positive effect of correlated variation across the age classes. Even though the effect of environmental variation on life expectancy is positive here, at yield CV = 0.3 its value in the expansion regime still exceeds that in the limitation regime by several years.

drives life expectancy down from otherwise high levels due to the asymmetry in the survival curves. In the limitation regime, variance raises life expectancy from low levels due to increased average food availability.

Variance in life expectancy is another important measure of well-being in that it is an indicator of the predictability of quality of life over the time scale of periods and cohorts. In general form, variance of lifespan approximated to the second order is:

$$\text{Var}(e_0) = \left(\sum_{x=2} \bar{l}_x \sum_{y=1}^{x-1} \delta_{t-x+y} \frac{p'_y}{\bar{p}_y} \right)^2, \quad (16)$$

where in this expansion around the mean of $\log E$, as opposed to the equilibrium, \bar{l}_x and \bar{p}_x refer to survivorship and survival, respectively, evaluated at $\log E$, p'_x refers to the first derivative of the survival function evaluated at the same point, and $\delta_t = \log E_t - \log E$.

In the absence of serial correlation in $\log E$ we can see from (16) that the only expectations of products of δ_t that are non-zero occur when perturbations are squared. In cohort calculations products across age classes are expected to be zero. In the period approximation all the δ are identical and will remain. All remaining elements of (16) are greater than or equal to zero (the perturbations being squared in either case), so period variance exceeds cohort variance. In our parameter ranges the difference is approximately an order of magnitude.

Eq. (16) confirms the intuition that variance in life expectancy increases with variance in $\log E_t$, with mean or equilibrium life expectancy, and with the slope of survival probability at the mean log food ratio. We can also see that as in approximations of life expectancy, the contribution of younger age classes is iterated more than older ones, and thus more heavily weighted. In expanding populations high average yields dramatically reduce variation in life expectancy because the survival curves are generally flat when food is abundant. As mean yield falls, equilibrium life expectancy also falls but survival elasticities increase, resulting in a peak in variance at intermediate levels of yield and mean life expectancy. The concrete implication is that moderate to low mean yields not only shorten life expectancy on average but also increase inequality in well-being. This has

potential consequences for individuals' perceptions of and outlook on well-being, in addition to the temporal dynamics of any social motivation to increase mean yield or to decrease its variability during the growth phase of population dynamics. As space begins to limit population growth, this effect of mean yield diminishes, and both period and cohort variance remain relatively high because of the steep slope in life expectancy as a function of food. As in the expansion regime, the space-limited population's life expectancy variance is strongly humped, peaking at moderate to high levels of yield variation. As in the expansion regime, the peak is defined by the local slope of the survival curves, which approach zero as $\log E$ approaches zero.

We also expand age-specific fertility around its value at $\log E$ to second order to approximate the mean,

$$\text{Mean}(m_x) = \bar{m}_x + \frac{\langle \delta^2 \rangle}{2} m''_x, \quad (17)$$

where we define \bar{m}_x as the fertility at age x when $\log E_t = \log E$, and m''_x is the second derivative evaluated at the same point.

The sum of mean m_x is the total fertility rate, the number of children a woman would have if she lived to the end of her reproductive years. Fertility is a concave function, but curves more gradually throughout than survival probability. With variability mean TFR decreases from equilibrium in growing populations and increases in space-limited ones, again due to concavity in the former case and the increase in mean log food ratio in the latter. Mean TFR is identical whether measured by cohort or period, however, TFR variance follows the pattern of life expectancy, in which variation across age classes is included in the period calculation and absent in the cohort calculation. In either case, variance of lifetime fertility increases with variance in $\log E$ and with increasing slope of the age-specific fertility functions. As these elasticities are lowest near $E = 1$, variance is lowest under conditions of high food ratio when the population is expanding. In space-limited populations cohort variance is extremely small across a wide range of parameters. Period variance, however, is larger. Both measures of variance peak at moderate levels of variation, reflecting the flattening of the fertility curves as $\log E$ increases.

6. Discussion

Food-dependent demography provides quantitative measures of population dynamics and well-being in variable environments. We use these measures to identify that as populations grow to occupy available arable land, shifts occur in the relative importance of the factors that influence relative food availability, its fluctuation through time, and the resulting population dynamics. Our analysis emphasizes the important role of the slope and curvature of vital rates or the food ratio to variable driving forces. In particular, a population's inability to benefit beyond a maximum in good years prevents food surpluses from compensating for years of deficit.

Others have previously investigated the effects of environmental variability on human populations. Jorde and Harpending (1976) considered population growth to be resource dependent, but did not include the effects of population structure on resource production. Lee (1993) developed a general model of interdependent population and resource production and consumption, and showed that this feedback plays an important role in both population dynamics in variable environments and human evolution (Lee, 2003). Our model is more biologically explicit in specifying vital rates and their dependence on age and food, as well as the functional form of the food ratio in expansion and limitation population phases. This permits straightforward and concrete interpretation of quantitative results. For instance, Lee (1993) recognizes that the mean population size and well-being under limitation are not equal to their

deterministic equilibria; we are able not only to measure these shifts but also to explain their magnitude in terms of properties of the population and of the environment. As a further example, one could use our model to assess the effects on lifespan of the effects of the temporal scale and/or correlation structure of environmental variability, a question considered by both [Jorde and Harpending \(1976\)](#) and [Lee \(1993\)](#) but without the benefit of being able to examine life expectancy.

We have shown here that in expanding populations, crop yield is the controlling factor in both well-being and population growth; increasing the mean and decreasing the variance in yield are the most effective means of bettering well-being, but also result in faster growth and earlier transition into limitation by available space. During the limitation regime, tradeoffs develop between factors influencing food and factors influencing food-independent quantities. Agricultural productivity of the environment and agriculture-related activities influence population size and variation, but the shape of vital-rate functions and the influence of population dominate the dynamics of the food ratio. High crop yield and labor efficiency encourage large mean population size and variation, with very little effect on the dynamics of the food ratio; high maximal vital rates and low sensitivity to food shortage also encourage large population size but result in low mean food ratio and variance. Crop fluctuations can substantially increase average well-being, but the cost of this increase is widespread starvation.

Though we have not considered the effects of fluctuations in other environment-dependent quantities such as maximal life expectancy [here](#), we can infer them from the present analysis. In populations not limited by space, age structure dynamics are much less important to the food ratio and the population than environmental productivity and labor, so fluctuations in maximal life expectancy should have comparatively smaller effects. On the other hand when space is limiting, changing maximal life expectancy should affect both mean population size and the dynamics of the food ratio, decreasing the former and increasing the latter. Fluctuations in maximal fertility, whether through environmental or behavioral or social means, have similar effects.

Our analyses have assumed the local stability of deterministic equilibria, and do not take into account the effects of very large deviations. The effects of large perturbations can be profound, however. In the expansion regime, when unfavorable environmental and demographic factors bias a population strongly enough toward low growth rates, the constant-environment equilibrium loses stability, and sustained cycles in population structure and food ratio are possible ([Lee and Tuljapurkar, 2008](#)). These cycles may interact with environmental fluctuations in unexpected ways. During population limitation, severe food shortages can cause density reductions so dramatic that space ceases to limit population dynamics: in such cases, the population changes back into the expansion regime, and the associated increase in food ratio is sustained because population growth does not decrease per capita food production during expansion. Simulations confirm that an occasional transition out of the limitation regime, which is most likely when yield variation is high and demography is unfavorable, can drive an increase in the mean food ratio in highly productive environments. In less productive environments, a release from space limitation can still occur, but the effect on the food ratio is less because high average yield is the primary determinant of high food ratio in growing populations.

The precise social, economic, and political consequences of the dynamics we present here will vary between societies and environments. Our approach to food-dependent demography is general, and we are optimistic that it applies to a wide variety of societies and environments. In this last of three papers, we have extended our previous analyses of dynamics in constant

environments to include the effects of fluctuations in food supply, showing that environmental variability has little effect on average well-being in expanding populations although it slows growth, and increases average well-being in space-limited populations through widespread mortality. These and other findings improve our understanding of the role of short-term plenty and famine in early population dynamics and health, and eventually in human history and prehistory.

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Appendix. Outline of derivation and terms in text

For the expansion regime, we expand the functions \mathbf{A} , \mathbf{u} , and $\log E$ around their deterministic equilibrium values $\hat{\mathbf{A}}$, $\hat{\mathbf{u}}$, and $\log \hat{E}$,

$$\begin{aligned} \mathbf{u}_t &= \hat{\mathbf{u}} + \epsilon \mathbf{z}_t^{(1)} + \epsilon^2 \mathbf{z}_t^{(2)} + O(\epsilon^3), \\ \mathbf{A}_t &= \hat{\mathbf{A}} + \epsilon \mathbf{A}_t^{(1)} + \epsilon^2 \mathbf{A}_t^{(2)} + O(\epsilon^3), \\ \log E_t &= \log \hat{E} + \epsilon E_t^{(1)} + \epsilon^2 E_t^{(2)} + O(\epsilon^3), \end{aligned} \quad (18)$$

where ϵ is a small perturbation. We substitute the expansion for the age structure \mathbf{u}_t into expression (8) for the food ratio and expand logs to second order to obtain an expression for $\log E_t$ in terms of the age-structure deviations $\mathbf{z}_t^{(1)}$ and $\mathbf{z}_t^{(2)}$. Equating terms of equal order in ϵ yields the terms $\mathbf{h}^{(i)}$ and $\psi^{(i)}$. It helps to show from the first-order terms that

$$\mathbf{z}_{t+1}^{(1)} = \mathbf{S}_X \mathbf{z}_t^{(1)} + (\mathbf{I} - \hat{\mathbf{u}} \mathbf{e}^T) \frac{\mathcal{A}_1 \hat{\mathbf{u}}}{\lambda} W_t, \quad (19)$$

where

$$\mathbf{S}_X = \frac{1}{\lambda} (\mathbf{I} - \hat{\mathbf{u}} \mathbf{e}^T) \left[\hat{\mathbf{A}} + \mathcal{A}_1 \hat{\mathbf{u}} (\psi^{(2)})^T \right], \quad (20)$$

and where the derivation of \mathbf{S}_X appears in [Lee and Tuljapurkar \(2008\)](#).

The solution to (19) is

$$\mathbf{z}_t^{(1)} = \mathbf{S}_X^t \mathbf{z}_0^{(1)} + \sum_{j=1}^t W_j \mathbf{S}_X^{t-j} \frac{\mathcal{A}_1 \hat{\mathbf{u}}}{\lambda}, \quad (21)$$

and consequently $\bar{\mathbf{z}}_t^{(1)} = 0$. We can also use (19) in the appropriate Kronecker products to find $\bar{\mathbf{z}}_t^{(1)} \otimes \bar{\mathbf{z}}_t^{(1)} = \mathbf{h}^{(1)}$ in the text and to show that

$$\mathbf{h}^{(1)} = \overline{\mathbf{z}_{t+1}^{(1)} \otimes \mathbf{z}_t^{(1)}} = (\mathbf{S}_X \otimes \mathbf{I}) \mathbf{h}^{(1)}, \quad (22)$$

which we will use to find the stochastic growth rate, below.

Equating terms in (4) that are second-order in ϵ and doing some algebra, we find that

$$\mathbf{h}^{(2)} = \bar{\mathbf{z}}_t^{(2)} = (\mathbf{I} - \mathbf{S}_X)^{-1} \frac{1}{\lambda} (\mathbf{I} - \hat{\mathbf{u}} \mathbf{e}^T) \Omega_X \quad (23)$$

where, letting $\mathbf{H}^{(1)}$ be the square matrix corresponding to $\mathbf{h}^{(1)}$,

$$\begin{aligned} \Omega_X &= \mathcal{A}_1 \mathbf{H}^{(1)} \psi^{(2)} + \left(\langle \psi^{(1)}, \mathbf{h}^{(1)} \rangle_{\mathcal{A}_1} + \frac{1}{2} \langle \psi^{(3)}, \mathbf{h}^{(1)} \rangle_{\mathcal{A}_2} \right) \hat{\mathbf{u}} \\ &+ \frac{1}{2} (\mathcal{A}_2 - \mathcal{A}_1) \hat{\mathbf{u}} + \frac{1}{\lambda} [(\mathcal{A}_1 \hat{\mathbf{u}} \psi^{(2)} - \hat{\mathbf{A}}) \mathbf{H}^{(1)} \hat{\mathbf{A}}^T \mathbf{e} \\ &+ (\mathcal{A}_1 \hat{\mathbf{u}})^T \mathbf{e} \hat{\mathbf{A}} \mathbf{H}^{(1)} \psi^{(2)} + \mathcal{A}_1 \hat{\mathbf{u}} (1 + \langle \psi^{(3)}, \mathbf{h}^{(1)} \rangle)]. \end{aligned} \quad (24)$$

Here we define the second derivative of matrix elements with respect to $\log E$ evaluated at equilibrium,

$$\mathcal{A}_2 = \left(\frac{\partial^2 \mathbf{A}}{\partial (\log E)^2} \right)_{\hat{E}}. \quad (25)$$

The analysis proceeds similarly for the limitation regime, replacing the age-structure expansion with the following expression for the population vector:

$$\mathbf{n}_t = \hat{\mathbf{n}} + \epsilon \mathbf{Z}_t^{(1)} + \epsilon^2 \mathbf{Z}_t^{(2)} + O(\epsilon^3). \quad (26)$$

Puleston and Tuljapurkar (2008) show that the stability matrix of the limitation equilibrium is

$$\mathbf{S}_L = \hat{\mathbf{A}} + \mathcal{A}_1 \hat{\mathbf{n}} (\boldsymbol{\psi}^{(2)})^T, \quad (27)$$

where the $\boldsymbol{\psi}^{(2)}$ vector is of the form appropriate to the limitation regime. Finally,

$$\mathbf{h}^{(2)} = \bar{\mathbf{Z}}_t^{(2)} = (\mathbf{I} - \mathbf{S}_L)^{-1} \Omega_L, \quad (28)$$

where

$$\begin{aligned} \Omega_L = & \mathcal{A}_1 \mathbf{H}^{(1)} \boldsymbol{\psi}^{(2)} + \left(\langle \boldsymbol{\psi}^{(1)}, \mathbf{h}^{(1)} \rangle \mathcal{A}_1 + \frac{1}{2} \langle \boldsymbol{\psi}^{(3)}, \mathbf{h}^{(1)} \rangle \mathcal{A}_2 \right) \hat{\mathbf{n}} \\ & + \frac{1}{2} (\mathcal{A}_2 - \mathcal{A}_1) \hat{\mathbf{n}}. \end{aligned} \quad (29)$$

To find the stochastic growth rate in the expansion regime we follow the methods in Tuljapurkar (1990), which require a projection matrix that varies as

$$\mathbf{A}_t = \bar{\mathbf{A}} + \epsilon \mathbf{M}_t, \quad (30)$$

where the deviation matrix \mathbf{M}_t has mean 0. The stochastic growth rate depends on the dominant eigenvalue and corresponding right and left eigenvectors of the mean matrix $\bar{\mathbf{A}}$, as well as properties of \mathbf{M}_t . In our second-order analysis, the mean projection matrix is

$$\bar{\mathbf{A}} = \hat{\mathbf{A}} + \epsilon^2 \bar{\mathbf{A}}^{(2)}, \quad (31)$$

where

$$\begin{aligned} \bar{\mathbf{A}}^{(2)} = & C^2 \mathcal{A}_1 \left[-\frac{1}{2} + \langle \boldsymbol{\psi}^{(1)}, \mathbf{h}^{(1)} \rangle + \langle \boldsymbol{\psi}^{(2)}, \mathbf{h}^{(2)} \rangle \right] \\ & + \frac{C^2}{2} \mathcal{A}_2 \langle \boldsymbol{\psi}^{(3)}, \mathbf{h}^{(1)} \rangle, \end{aligned} \quad (32)$$

and the matrix deviations are

$$\mathbf{M}_t = \mathbf{A}_t^{(1)}. \quad (33)$$

where the perturbations $\mathbf{A}_t^{(1)}$ come from Eq. (18). By equating terms in (18) of equal order, we find that $\bar{\mathbf{M}} = \mathbf{0}$,

$$\bar{\mathbf{m}}^{(1)} = \overline{\mathbf{M}_t} \otimes \overline{\mathbf{M}_t} = [1 + \langle \boldsymbol{\psi}^{(3)}, \mathbf{h}^{(1)} \rangle] (\mathcal{A}_1 \otimes \mathcal{A}_1) \quad (34)$$

and

$$\begin{aligned} \bar{\mathbf{m}}^{(1)} = & \overline{\mathbf{M}_{t+1}} \otimes \overline{\mathbf{M}_t} \\ = & \left[\left\langle \boldsymbol{\psi}^{(2)}, (\mathbf{I} - \hat{\mathbf{u}} \mathbf{e}^T) \frac{\mathcal{A}_1 \hat{\mathbf{u}}}{\hat{\lambda}} \right\rangle + \langle \boldsymbol{\psi}^{(3)}, \mathbf{h}^{(1)} \rangle \right] (\mathcal{A}_1 \otimes \mathcal{A}_1). \end{aligned} \quad (35)$$

Letting λ_m , \mathbf{u}_m , and \mathbf{v}_m be the dominant eigenvalue and corresponding right and left eigenvectors of the mean matrix $\bar{\mathbf{A}}$, and after some algebra, the food-dependent stochastic growth rate is, to second order,

$$\begin{aligned} a = & \log \lambda_m - \epsilon^2 \frac{(\mathbf{v}_m \otimes \mathbf{v}_m)^T \bar{\mathbf{m}}^{(1)} (\mathbf{u}_m \otimes \mathbf{u}_m)}{2\lambda_m^2} \\ & + \epsilon^2 \frac{[(\boldsymbol{\psi}^{(3)})^T \otimes \mathbf{v}_m^T \mathcal{A}_1] [\mathbf{I} - (\mathbf{S}_X \otimes \mathbf{I}) \otimes \mathbf{q}]^{-1} [\mathbf{h}^{(1)} \otimes \mathcal{A}_1 \mathbf{u}_m]}{\lambda_m^2} \\ & - \epsilon^2 \frac{(\mathbf{v}_m \otimes \mathbf{v}_m)^T \bar{\mathbf{m}}^{(1)} (\mathbf{u}_m \otimes \mathbf{u}_m)}{\lambda_m^2}, \end{aligned} \quad (36)$$

where the symbol \otimes indicates a Kronecker product, \mathcal{A}_1 and the vectors $\Sigma_H(0)$, $\Sigma_M(0)$, and $\Sigma_M(1)$ are given in Appendix, and

$$\mathbf{q} = \frac{\bar{\mathbf{A}}}{\lambda_m} - \mathbf{u}_m \mathbf{v}_m^T. \quad (37)$$

The general second-order expansion of survivorship around its value at $\log E$ is:

$$\begin{aligned} l_x(\log E_t) = & (\hat{l}_x + \Delta \bar{l}_x) \left(1 + \sum_{i=2}^{x-1} \delta_{t-x+i} \delta_{t-x+j} \frac{p'_i p'_j}{\bar{p}_i \bar{p}_j} \right. \\ & \left. + \frac{1}{2} \sum_{y=1}^{x-1} (\delta_{t-x+y})^2 \frac{p''_y}{\bar{p}_y} \right), \end{aligned} \quad (38)$$

where $\Delta \bar{l}_x = \bar{l}_x - \hat{l}_x$ (the difference between the equilibrium survivorship and its value at $\log E$), and $\delta_t = \log E_t - \log E$ is the deviation in \log food ratio from its mean. The terms p'_y and p''_y are the first and second derivatives, respectively, of period survival with respect to $\log E$, evaluated at $\log E$. In period calculations, all the $\log E_t$ are identical and all their products in (38) reduce to $(\Delta \log E_t)^2$, the variance of the perturbation.

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