Sustainability of culture-driven population dynamics☆

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ARTICLE INFO

ABSTRACT

We consider models of the interactions between human population dynamics and cultural evolution, asking whether they predict sustainable or unsustainable patterns of growth. Phenomenological models predict either unsustainable population growth or stabilization in the near future. The latter prediction, however, is based on extrapolation of current demographic trends and does not take into account causal processes of demographic and cultural dynamics. Most existing causal models assume (or derive from simplified models of the economy) a positive feedback between cultural evolution and demographic growth, and predict unlimited growth in both culture and population. We augment these models taking into account that: (1) cultural transmission is not perfect, i.e., culture can be lost; (2) culture does not always promote population growth. We show that taking these factors into account can cause radically different model behavior, such as population extinction rather than stability, and extinction rather than growth. We conclude that all models agree that a population capable of maintaining a large amount of culture, including a powerful technology, runs a high risk of being unsustainable. We suggest that future work must address more explicitly both the dynamics of resource consumption and the cultural evolution of beliefs implicated in reproductive behavior (e.g., ideas about the preferred family size) and in resource use (e.g., environmentalist stances).

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1. Introduction

Culture is a major force in human population dynamics. Cultural innovations such as agriculture, social organization, tool manufacture and other technologies have been considered for a long time as key factors in human population growth (Rogers, 1995; Bar-Yosef, 2002; Riede and Bentley, 2008). Population dynamics, in turn, has been considered a crucial factor in cultural evolution (Boserup, 1981; Shennan, 2001; Henrich, 2004; Powell et al., 2009). Culture, however, can potentially *detract* from population growth in several ways, for instance through over-exploitation of resources (Harrison and Pearce, 2000; Diamond, 2005) or the creation of cultural practices that divert resources from reproduction (Boyd and Richerson, 1985; Enquist et al., 2002), e.g., higher education (Castro Martin and Juarez, 1995; Lawler Dye, 2008).

While most theoretical models of human population dynamics acknowledge that demography and culture are intimately tied and often reinforce each other, our understanding of such demo-cultural dynamics is still limited. In particular, we cannot assess the sustainability of forecasted future population size (Cohen, 2002). The main obstacle is that cultural evolutionary theory is still immature, and this is especially true of the theory of cumulative culture. By "cumulative" we refer to humans' ability to continuously elaborate over what is handed over by previous generations, often resulting in increasing diversity and efficiency of cultural products (Lehman, 1947; Ogburn, 1950; Sahlins, 1960; Basalla, 1988; Boyd and Richerson, 1996; Tomasello, 1999; Carneiro, 2003). Cumulation makes human culture much more powerful, amplifying both its potential benefits and its risks (Enquist and Ghirlanda, 2007; Enquist et al., 2008).

Here we first survey some models of demo-cultural dynamics from the social and natural sciences. We stress that most models neglect two factors that have recently been investigated in cultural evolutionary theory: (1) that cultural transmission is imperfect; (2) that culture can inhibit, as well as promote, population growth. We introduce a model that takes both factors into account, showing that they modify substantially the possible long-term outcomes of a demo-cultural dynamical system. In particular, population extinction becomes possible.
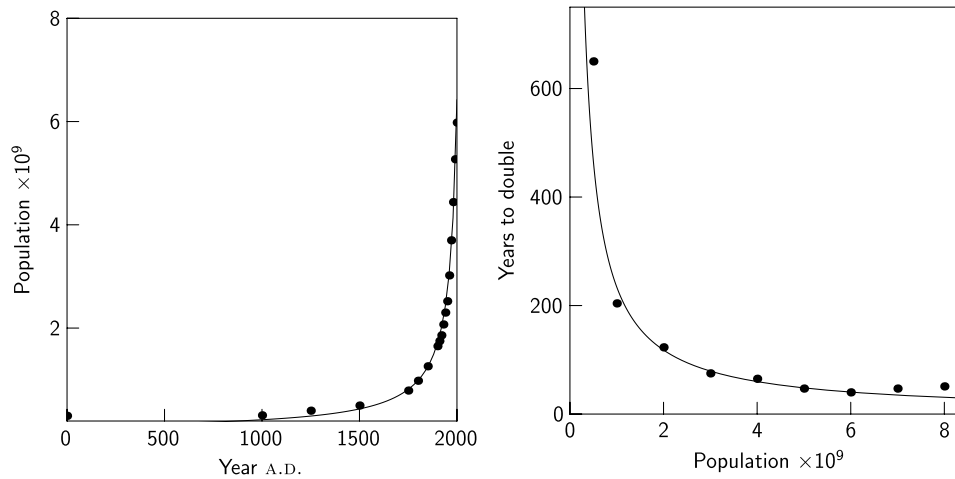
Fig. 1. Left: Human population growth. Points are empirical data, the line is Eq. (1) with $m = 1$, $A = 232.6 \times 10^9$, $t^\star = 2036.3$ AD. Right: Doubling times of world population. A point with coordinates (n, t) indicates that t years elapsed between populations of $n/2$ and n (world populations of 7 and 8 billions are estimated to be reached in 2012 and 2025, respectively). The line shows doubling times predicted by (1) with the above parameter values.
Data source: McEvedy and Jones (1978), U.S. Census Bureau Population Division (2008).

We conclude that both empirical data and theoretical models imply that a sustainable steady state is unlikely when technology is sufficiently advanced, unless culture itself brings about values and goals that promote sustainability. The last topic will be important in future research.

2. Overview of current theory

2.1. Phenomenological models

Fig. 1, left, shows the pattern of human population growth from about 0.3 to about 6 billion in the period 0–2000 AD. The right panel shows that the time required for population to double has decreased dramatically over history. Several authors have sought to characterize these data mathematically. In an influential paper, Von Foerster et al. (1960) noted that humans seem to defy density-dependent regulation mechanisms that limit the growth of animal populations (see also Hern, 1993; Kapitza, 2006). According to these authors, human population growth accelerates as the population grows because of the increased benefits of cooperating in larger groups (whether large-scale cooperation is to be expected, however, is an open question, cf. Axelrod, 1984). Assuming that population growth rate increases weakly with population size ($\dot{n} \simeq n^k$, $k > 1$), and fitting the resulting population dynamics to demographic data, Von Foerster et al. forecasted that the human population would become unsustainably large around 2025 AD. Formally, these authors' expressed population size n at time t as

$$n(t) = \frac{A}{(t^\star - t)^m} \tag{1}$$

which is valid for $t < t^\star$, where A is a constant, $t^\star$ is a parameter that represents a time at which the population is predicted to become, formally, infinite, and m describes the speed at which such population explosion takes place. Von Foerster et al. (1960) estimated $t_0 \simeq 2025$ AD and $m \simeq 1$. Since $m = 1$ represents a hyperbola, human population growth is often described as "hyperbolic." As just mentioned, hyperbolic growth achieves infinity in a finite time, and therefore it is faster than exponential growth. The lines in Fig. 1 show our fit of Eq. (1) to current data.

Actual hyperbolic growth would require organisms to reproduce arbitrarily fast in the last stages of growth, and thus is unattainable in practice. The fact that humans have a maximum reproductive rate implies that hyperbolic growth must eventually give way to (at most) exponential growth (Karev, 2005; Kapitza, 2006). Empirically, the doubling time of human population has apparently stabilized at a value of about 40–50 years (Fig. 1, right), mostly due to the "second demographic transition"—a reduction in fertility with increased standards of living that has occurred in many countries (Borgerhoff Mulder, 1998; Cohen, 2002). Despite this recent slowdown in population growth, Eq. (1) fits human population growth well from about 10^6 years ago to about 1960 AD (Kremer, 1993), and most models of human population dynamics are primarily intended to account for hyperbolic growth.

Current phenomenological models estimate a human population of 8–11 billion around 2050 AD (Kapitza, 2006; United Nations Population Division, 2008; U.S. Census Bureau Population Division, 2008). Such estimates are obtained by either projecting current (or presumed) demographic trends into the future, or by forecasting other quantities, e.g., income, which are then assumed to determine population growth. These methods fail to account for feedback between population, cultural and environmental dynamics, and have not been very successful in the past (Cohen, 2002). We summarize below some models in which population is part of a larger dynamical system that also includes cultural and environmental variables.

2.2. Culture that promotes growth

Many macroscopic models of human population dynamics can be understood as modifications of population dynamics models based on the logistic equation:

$$\dot{n} = rn \left(1 - \frac{n}{k}\right) \tag{2}$$

where n is population size, $\dot{n}$ its rate of change, r is the population's growth rate in the absence of resource limits ("intrinsic" growth rate), and k is the environment's "carrying capacity", i.e., the maximum population size that can be sustained in a given environment. According to (2), an initially small population grows in time until, eventually, it reaches the carrying capacity and stops growing. Such a limit to growth is usually attributed to resources per individual becoming scarcer as population size increases. In the case of human population growth, however, it is natural to assume that technology, social organization, and other aspects of culture have allowed humans to increase the environment's carrying capacity. All models considered below have modified (2) in this sense.

Both Kremer (1993) and Korotayev (2005) study models in which technological (i.e., cultural) innovation is the driving force behind human population growth. Empirically, major population expansions have often coincided with technological change, e.g., in the case of the out-of-Africa expansion and of agriculture (Rogers, 1995; Bar-Yosef, 2002). Specifically, these authors assume a positive feedback between technology and population: people create technology which allows to sustain more people, who, in turn, produce more technology (Kuznets, 1960; Simon, 1977). Formally, these models can be summarized as

$$\dot{k} = cnk \tag{3}$$

$$\dot{n} = rkn\left(1 - \frac{n}{k}\right). \tag{4}$$

Eq. (3) says that carrying capacity increases proportionally to its current level and to population size. This effect is assumed to derive from increase in technology (for simplicity, technology and carrying capacity are conflated in this model). Eq. (4) departs from (2) in assuming that the intrinsic rate of increase is also proportional to current carrying capacity (r in (2) is replaced by rk in (4)). Eq. (4) is commonly written as $\dot{n} = rn(k - n)$ (Cohen, 1995; Korotayev, 2005)—we use an alternative form to better highlight the relationship with the standard logistic equation.

The outcome of this model, as mentioned above, is very fast (hyperbolic) demographic and technological growth. The model shows that the interaction between culture and demography is crucial to understand human population dynamics, but ignores several potentially important factors. For instance, it only considers culture that promotes population growth (technology), and it assumes that technology is perfectly transmitted between generations. We address these shortcomings below, but first we consider the logic underlying Eqs. (3) and (4).

2.3. The generation of culture

Why do technological and demographic growth reinforce each other, as assumed above? The better developed arguments for this assumption come from macroeconomic models. A very short description of such models is that people are assumed to consume goods for various ends (including reproduction) and to produce goods (including technology) based on available resources, including the current level of technology. The laws governing production and consumption are derived from macroeconomic theory. For example, Kremer (1993) arrived at a model equivalent to Eqs. (3) and (4) through the following hypotheses:

(1) Individuals produce goods in such a way that the total economic output of a population is kn^α, with $0 < \alpha < 1$.
(2) Each individual produces new technology at a rate proportional to k^ϕ, $0 < \phi \leq 1$.
(3) Population grows when individual income exceeds a given level.

Hypotheses 1 and 2 exemplify the widespread use of power laws, which are often observed empirically (Gabaix, 2008). In particular, an exponent smaller than 1 embodies the principle of diminishing returns to investment: increasing the input into an economic activity by fixed amounts yields smaller and smaller increases in output. Hypothesis 1 exemplifies also the common assumption that technology acts as a multiplier on economic processes. Lastly, Hypothesis 3 links economic and demographic growth (see Kremer, 1993, for details and more general models).

Many macroeconomic models of population dynamics make similar assumptions, as well as other such as perfect competition and economic equilibrium. Such simplifications are necessary due to the difficulty of taking into account individual-level processes of cultural transmission, creativity, decision making, etc.

(Bisin and Verdier, 2001; Strimling et al., 2009). In particular, to link individual behavior to population-level outcomes, economists have often adopted the hypothesis that individuals behave rationally, together with assumptions about what they try to achieve. Models of technological and demographic growth of this kind have been proposed by, for instance, Brander and Taylor (1998), D'Alessandro (2006) and Krutilla and Reuveny (2006). The most comprehensive model is probably "unified growth theory" (Galor and Weil, 2000). This model predicts first a transition from slow to fast growth in both population and technology, through a positive feedback between population and technological as in the models discussed above. A second transition leads eventually to an equilibrium population size as a consequence of parents investing resources in the education ("quality") rather than in the quantity of children. The rationale for the latter transition is that parents are assumed to optimize children's "human capital" (the capacity to generate income), which in a highly developed technological society requires substantial education.

In the following, we will continue to consider simple population-level models, to which we will add insights from recent work in cultural evolutionary theory that most existing models neglect. It should be borne in mind, however, that ultimately individual-level processes will need to be taken into account in greater detail to arrive at a satisfactory understanding of demo-cultural dynamics.

2.4. The maintenance of culture

Ghirlanda and Enquist (2007) studied a model of demo-cultural dynamics based on previous work on the dynamics of cumulative culture. The model differs from Eqs. (3) and (4) in two respects. First, cultural transmission is not perfect, hence knowledge can be lost (Nowak, 2000; Henrich, 2004; Enquist et al., 2008; Powell et al., 2009). In this model, the amount of culture, x, changes according to

$$\dot{x} = -\lambda x + \delta n \tag{5}$$

meaning that culture is created by individuals at a rate of δ per individual, and is lost at a rate λ (perfect cultural transmission is described by $\lambda = 0$). It can be showed that (5) is a good description of the dynamics of the expected number of cultural traits in a finite population, under the assumption that individuals can both invent new cultural traits and learn them from others (Strimling et al., 2009). Second, population growth is governed by the logistic equation, with carrying capacity given by $1 + \alpha x$:

$$\dot{n} = rn\left(1 - \frac{n}{1 + \alpha x}\right). \tag{6}$$

The parameter α describes how strongly culture affects the environment's carrying capacity. We will call it the "subsistence potential" of culture. The carrying capacity in (6) has a minimum value of 1, corresponding to $x = 0$. Thus an equilibrium population size of $n > 1$ can occur only when culture contributes positively to the carrying capacity. A population size of $0 < n < 1$ corresponds to a population in which culture is detrimental to demographic growth (an equilibrium with $n < 1$ is impossible in this model, but can occur in the model in Section 3). Note that, according to (6), culture causes population growth only through increase in the carrying capacity; in contrast with Eq. (4), reproductive rate does not increase with culture. We will return to this point below, when discussing the pattern of population growth.

The main merit of this model is to highlight some conditions under which a population in demographic equilibrium can start to grow. The model, in fact, exhibits two regimes: stability and unlimited growth. The latter occurs when $\alpha\delta > \lambda$, i.e., when the positive feedback between cultural and demographic dynamics is strong enough to overcome the loss of culture due to faulty transmission.
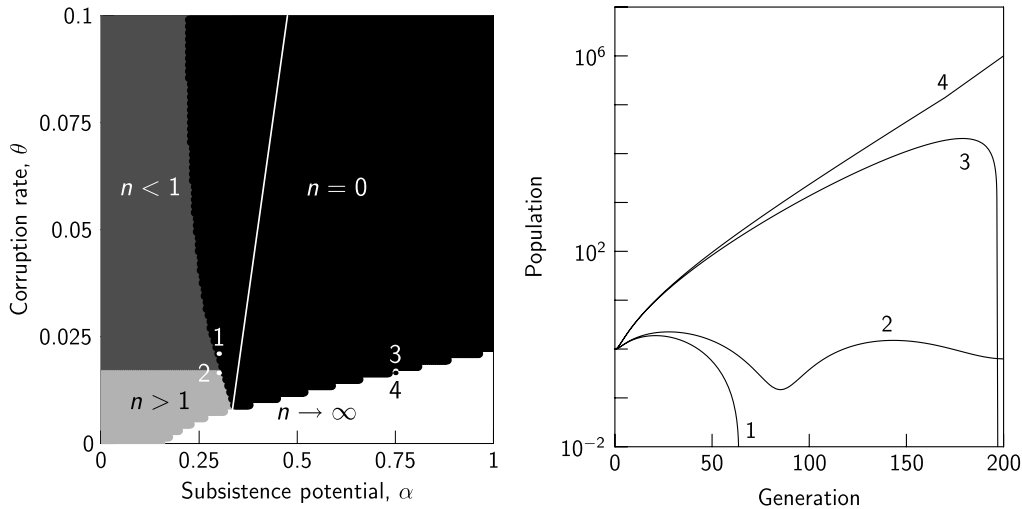
Fig. 2. Left: outcome of dynamical simulations as a function of culture's subsistence potential and corruption rate (respectively, α and θ in Eqs. (7)–(9)). White: unbounded population growth; black: population extinction; dark gray: finite population size, smaller than that of an acultural population ($n < 1$); light gray: finite population size, larger than that of an acultural population ($n > 1$). The boundary between the latter two regions is a straight line, as the condition for culture being adaptive when a stable equilibrium exists is independent of the parameter α (see text after Eq. (A.8)). To the left of the white line the system has formally a stable equilibrium with finite population size, but the system trajectory brings n to 0 *en route* to the equilibrium. Right: Population dynamics vs. time for the 4 points labeled in the left panel. Parameter values: $q = 2/3$, $\lambda = 0.05$, $\delta = 1$ and $r = \ln 2$. The latter amounts to choose the time scale so that the doubling time of an exponentially growing population is 1 time unit.

When $\alpha\delta < \lambda$, instead, the population settles at a stable equilibrium. Ghirlanda and Enquist (2007) used this result to suggest that the transition from the relatively stable population size characteristic of apes to the explosive growth characteristic of humans could result both from improvements in cultural transmission (decrease in the loss rate λ) and from improvements in creativity (increase in δ, corresponding to more cultural output, or increase in α, corresponding to culture that exerts a larger influence on the carrying capacity).

Imperfect transmission of culture can also be introduced in other models, often with dramatic effects. For instance, if in Eq. (3) we assume that technology is lost at a rate proportional to its amount ($\dot{k} = cnk - \lambda k$), we obtain that a population that starts with poor technology (approximately, lower than about λ/c) can become extinct rather than grow (see Appendix; the dependence on initial population size is weak).

3. A model with growth-inhibiting culture

Culture is not only technology that, by increasing resource production and utilization, favors population growth. Cultural traits can inhibit population growth. For instance, they can cause individuals to invest resources in activities other than reproduction, such as higher education (Castro Martin and Juarez, 1995; Lawler Dye, 2008). Additionally, a cultural trait that promotes population growth at one time may later come to inhibit growth because of intervening environmental or cultural changes (Boyd and Richerson, 1985; Rogers, 1988; Boyd and Richerson, 1995; Richerson and Boyd, 2005; Enquist and Ghirlanda, 2007). A technology that exploits a particular resource, for example, becomes less useful as the resource becomes more scarce. The consequences can be catastrophic, such as the Irish Great Famine of 1846–1850 AD, when a fungus destroyed the potato crops on which over half of Irish population relied. Potato farming had previously been a very productive technology, yielding the same nutritional value of corn for one third of the cost, thereby allowing Ireland to export larger quantities of wheat (Ó'Gráda, 1995). Cultural traits can also lose value as a consequence of cultural evolution itself, rather than because of exogenous environmental change. For instance, traditional food fermentation techniques became a significant health hazard among Alaska natives after earthen pits used for storage were replaced by plastic bags, which favor the growth of botulism bacteria. The rate of death by botulism in some parts of Alaska is now more than 20 times higher than in the rest of the USA (Lancaster, 1990; Chiou et al., 2002).

Enquist and Ghirlanda (2007) sought to capture such processes in a model in which culture that promotes population growth and culture that inhibits population growth are different yet interacting dynamical variables. A population of n individuals is assumed to invent new cultural traits at a rate of δn per generation; a fraction q of these traits contributes to growth, while the remaining fraction $1 - q$ detracts from growth. Processes that transform growth-promoting into growth-inhibiting culture are modeled by assuming that the former is continuously transformed into the latter at a rate θ, which we refer to as the "corruption rate" of culture. Additionally, both growth-promoting and growth-inhibiting culture are forgotten at a rate λ. These assumptions give the following differential equations for the expected number u and v of growth-promoting and growth-inhibiting traits, respectively:

$$\dot{u} = -\lambda u - \theta u + q\delta n \tag{7}$$
$$\dot{v} = -\lambda v + \theta u + (1-q)\delta n \tag{8}$$

where the terms $-\lambda u$ and $-\lambda v$ represent the loss of culture due to faulty transmission, the terms $-\theta u$ and $+\theta u$ represent the transformation of growth-promoting into growth-inhibiting culture, and the terms $+q\delta n$ and $+(1-q)\delta n$ refer to the creation of growth-promoting and growth-inhibiting traits by individuals.

Enquist and Ghirlanda (2007) did not consider population dynamics (they assumed $\delta n = \gamma$, a constant), but we can easily generalize Eq. (6) to read

$$\dot{n} = rn\left(1 - \frac{n}{1 + \alpha(u - v)}\right) \tag{9}$$

so that growth-promoting and growth-inhibiting culture have opposite effects on the carrying capacity. Assuming $q = 1$ and $\theta = 0$ returns Eqs. (5) and (6), with $x = v$.

3.1. Extinction, stability, and growth

We simulated the model starting from a population size of $n = 1$ (corresponding to the environment's carrying capacity in the
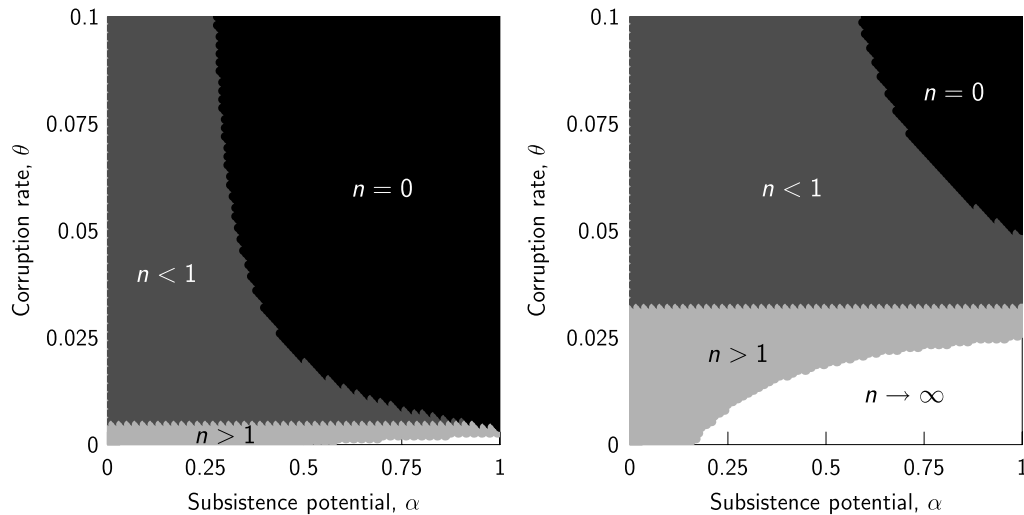
Fig. 3. Left: demo-cultural evolution when only 55% of innovations are adaptive ($q = 0.55$ in Eqs. (7) and (8), compare with $q = 2/3$ in Fig. 2). Right: demo-cultural evolution with 55% of adaptive innovations and the addition of adaptive filtering ($q = 0.55$ and $\psi = 0.2$ in Eq. (10)). Other parameter values are as in Fig. 2.

absence of culture) and varying the impact of culture on carrying capacity, α, and the corruption rate of culture, θ. Three long-term outcomes are possible, as shown in Fig. 2:

Stable equilibrium (gray areas in Fig. 2). The population can be larger (dark gray) or smaller (light gray) than a population without culture. A stable equilibrium is possible as long as the subsistence potential of culture, α, is small, almost independently of the corruption rate, θ. This may model a population with relatively inefficient technology. Oscillations are often observed before reaching equilibrium (trajectory 2 in Fig. 2).

Unlimited growth (white). Population size, as well as the difference between growth-promoting and growth-inhibiting culture, increases exponentially with time. This occurs for small θ (growth-promoting culture becomes growth-inhibiting slowly) and α too large to yield stability (trajectory 4).

Extinction (black). The population goes extinct when θ and α are large enough. Under such conditions, growth-promoting culture initially increases, leading to an increase in population size, but is eventually overcome by growth-inhibiting culture and therefore population collapse. When α is large, collapse can be preceded by a very large increase in population (trajectory 3), when α is small the initial increase is modest (trajectory 1).

The role of oscillations in system dynamics is noteworthy. We show in the Appendix that oscillations occur for many values of α and θ (everywhere above the line $\theta = \alpha/5$ for the case in Fig. 2). Moreover, numerical analysis shows that, whenever oscillations occur, the system has an equilibrium point with positive population size. To the right of the white line in Fig. 2, the equilibrium point is unstable and the system eventually collapses to zero population size (e.g., trajectory 3 in Fig. 2). To the left of the white line, the equilibrium point is stable, and is reached by damped oscillations. The latter, however, can be large enough to drive the system to extinction *en route* to the equilibrium point (black region to the left of the white line, exemplified in trajectory 1). In summary, it is not generally possible to infer system fate from a simple equilibrium analysis. Rather, trajectories must be tracked to ascertain whether the system reaches a zero population size anytime during its history.

Our results complement those of Lehmann and Feldman (2009), who also model the effect of growth-promoting and growth-inhibiting culture on population size. These authors study gene-culture coevolution assuming that individuals follow one of three genetically determined strategies of cultural transmission and innovation: "producer" (learns from others and produces cultural innovations), "scrounger" (learns from others but does not innovate), and "innate" (neither learns from others nor innovates). Similarly to Eqs. (7) and (8), both growth-promoting and growth-inhibiting traits can be invented. The fitness of individuals depends on how much time they invest in social learning and innovation as well as on the amount of growth-promoting and growth-inhibiting culture they acquire. Lehmann and Feldman focus mostly on gene-culture coevolution over evolutionary time (hundreds or thousands of generations), while our model is mainly geared toward historical time (hundreds or thousands of years). We have, therefore, neglected genetic evolution and examined changes in population size induced by cultural evolution alone. This simplification has resulted in a model with fewer parameters, whose effect on population growth could be analyzed more systematically, including varying the impact of culture on population growth (parameter α in Fig. 2, see also Fig. 3).

Results from the two models appear fully compatible. For instance, Lehmann and Feldman's result that gene-culture coevolution yields most often populations where producers are present (possibly with scroungers and/or innates) agrees with our starting assumption of a population capable of both cultural transmission and innovation. Likewise, Lehmann and Feldman report either approach to a stable population size or oscillations around an average size (the latter are due to periodic changes in strategy frequencies, and have no parallel in our model). According to the balance between growth-inhibiting and growth-promoting culture, which follows a similar logic to our Eqs. (7) and (8), average population size can be lower or higher than that of an acultural population. Additionally, oscillation minima may be very low, putting the population at risk of extinction. Unlimited growth is not reported in the presence of growth-inhibiting culture, but it seems likely that it can occur, at least for parameter values that are very favorable to the development of growth-promoting vs. growth-inhibiting culture.

3.2. Adaptiveness of innovations and adaptive filtering of culture

In Fig. 2 we have assumed that a proportion $q = 2/3$ of all innovations is adaptive. A lower proportion of adaptive innovations corresponds to an expansion of the regions where the population goes
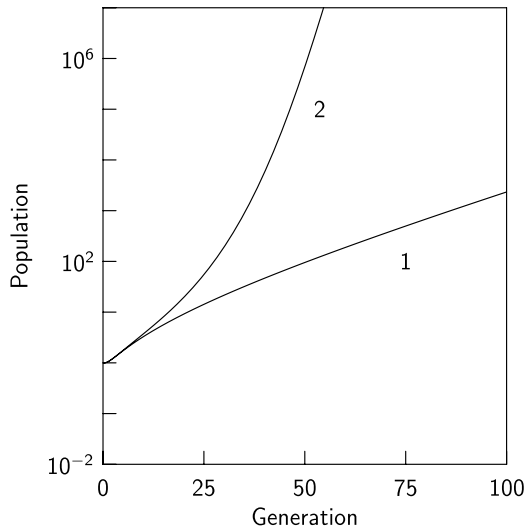
Fig. 4. Comparison of growth under linear and superlinear generation of cultural innovations. Trajectory 1 is produced by Eqs. (7)–(9) in the parameter region yielding unbounded growth ($\alpha = 0.75$, $\theta = 0.0165$; inside the white region in Fig. 2). Trajectory 2 corresponds to superlinear production of culture (n replaced by $n^{1.2}$ in Eqs. (7) and (8)), with the same system parameters. Because population is represented on a logarithmic scale, exponential growth takes the form of a straight line.

extinct, or settles at a lower size than a population without culture. Indeed, Enquist and Ghirlanda (2007) noted that Eqs. (7) and (8) lead to growth-inhibiting culture exceeding growth-promoting culture for most many values. For example, if $q < 0.5$ a cultural population has always a lower viability than a population without culture. Fig. 3, left, repeats the analysis in Fig. 2, left, with $q = 0.55$, showing that substantial population growth is possible only for a small subset of parameter values.

Enquist and Ghirlanda (2007) also showed that the adaptive value of culture can be increased by processes of "adaptive filtering" that allow individuals to discard growth-inhibiting culture. Assuming such a process modifies (8) as follows:

$$\dot{v} = -(\lambda + \psi)v + \theta u + (1 - q)\delta n \qquad (10)$$

where the positive parameter ψ models the increased loss rate of growth-inhibiting culture due to adaptive filtering. When population dynamics is introduced in such a model, the qualitative picture is similar to Fig. 2, but the parameter region in which population grows without bound expands (monotonically in ψ) at the expense of the regions where the population goes extinct or reaches a stable state (Fig. 3, right, which also demonstrates that adaptive filtering can compensate for a low proportion of adaptive innovations). Thus an increase in the ability to discard growth-inhibiting culture, which is favored by natural selection (Enquist and Ghirlanda, 2007), promotes an unsustainable regime of unlimited growth.

3.3. Faster-than-exponential growth

As mentioned above, human population has grown faster than exponentially up to about 1960 AD. To explain this finding, most current models assume that culture augments linearly both the environment's carrying capacity and the intrinsic rate of population increase, e.g., as in Eq. (3). Empirical data suggest another possible cause of faster-than-exponential growth: that the rate of cultural innovation increases faster than linearly with population size. Bettencourt et al. (2007), indeed, show that the rate of innovation in a city of population n is approximately proportional to $n^{1.2}$. Several measures of innovation follow this pattern: number of people employed in research and development activities, number of patented inventions, and number of patent holders. This finding is reminiscent of Von Foerster et al.'s (1960) suggestion that faster-than-exponential growth is due to the benefits of cooperation between individuals (the output of n individuals is more than n times the output of one individual).

If we replace the rate of innovation δn in Eqs. (7) and (8) with $\delta n^{1.2}$, growth trajectories exhibit a period of faster-than-exponential growth (Fig. 4) and decreasing doubling times, similarly to observed data (Fig. 1). After some time, growth slows down and becomes exponential. Model behavior is otherwise very similar; the picture in Fig. 2, left, applies almost unchanged, although boundaries between regions shift somewhat.

4. Discussion

The challenge for models of human sustainability is to account for the interactions between demography, culture and resources, while remaining tractable enough to bring understanding and make predictions. Existing models are all highly simplified, but their message seems clear, and consistent with intuition: a population capable of maintaining a large amount of culture, including a powerful technology, runs a high risk of being unsustainable. The dynamical models surveyed above, in fact, predict either extinction or unlimited (unsustainable) population growth when culture is allowed to have a strong impact on population dynamics.

Improving our understanding of human population dynamics will require considering two kinds of factors neglected by the models surveyed above. First, models should explicitly consider resource dynamics. Implicitly, the models considered here assume that technology is capable of producing unlimited resources. This is acceptable when studying the past, because population dynamics has been more affected by the ability to exploit existing resources than by shortage of resources. However, to understand the future of human populations it will be crucial to model resource dynamics explicitly. Here we have simply interpreted unlimited population growth as unsustainable, as it must eventually be curbed by resource shortage. Economic models that have considered populations exploiting renewable and/or exhaustible resources show that a variety of steady states are possible, for instance depending on individual preferences about consumption (Brander and Taylor, 1998; D'Alessandro, 2006). The cultural dynamics in these models, however, is either very simple (simpler than what considered here) or absent. Cultural dynamics, indeed, is the second key shortcoming of existing models of sustainability. In particular, existing models either neglect the cultural evolution of human values and goals or extrapolate such evolution from what has happened in the past, assuming, e.g., that humans will always invest in technological innovation.

The importance of these shortcomings becomes apparent when we consider predictions of future population size. Most studies project that the human population will stabilize at 8–11 billion individuals around 2050 AD. These projections are potentially misleading for two reasons. First, they have little to say about sustainability. Demographic stability is necessary, but not sufficient for sustainability, because a fixed population of individuals can still exploit resources in an unsustainable way. Second, these projections are based on the assumption that fertility will decline everywhere in the world as it has done in industrialized countries, and that will thereafter remain low. As far as we know, however, nothing prevents a reversal of the demographic transition. If fertility is tied to income, for instance, a global economic recession could trigger an increase in fertility (as predicted, for instance, by the theory of Galor and Weil, 2000, if jobs requiring higher educations become unavailable). Alternatively, beliefs may come into fashion that promote high fertility (Kaufmann, 2006).

In conclusion, assessing the sustainability of culture-driven population dynamics requires a deeper understanding of cultural evolution in at least two areas: ideas about reproduction, e.g., concerning the preferred family size, and ideas that influence resource use, such as beliefs about acceptable energy consumption.
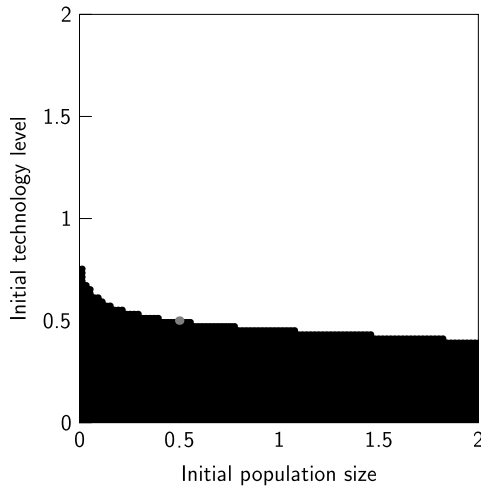
Fig. A.1. Outcome of demo-cultural evolution for the model in Eq. (A.1) as a function of initial conditions, with $c = 0.1$, $\lambda = 0.05$ and $r = \ln 2$. Black: population goes extinct. White: population grows without bound. The gray dot is the unstable equilibrium point $k = n = \lambda/c$.

Appendix

A.1. Impact of errors in cultural transmission

Allowing errors in cultural transmission in Eq. (3) yields the model

$$\dot{k} = cnk - \lambda k$$
$$\dot{n} = rkn\left(1 - \frac{n}{k}\right). \tag{A.1}$$

The equilibrium points are $(0, 0)$ and $(\lambda/c, \lambda/c)$. The system Jacobian is

$$J = \begin{pmatrix} r(k - 2n) & rn \\ ck & cn - \lambda \end{pmatrix} \tag{A.2}$$

which, calculated at the nonzero equilibrium is

$$J^\star = \begin{pmatrix} -\dfrac{r\lambda}{c} & \dfrac{r\lambda}{c} \\ \lambda & 0 \end{pmatrix} \tag{A.3}$$

with eigenvalues

$$e_{1,2} = -\frac{r\lambda}{c}\left(1 \pm \sqrt{1 + \frac{4c}{r}}\right). \tag{A.4}$$

One eigenvalue is always positive, the other always negative, hence the equilibrium is a saddle point. From any starting condition, the population either grows without bound or goes extinct, as shown in Fig. A.1.

A.2. Impact of growth-inhibiting culture

The model in Eqs. (7)–(9) can be recast in terms of the total amount of culture $x = u + v$ and the difference between growth-promoting and growth-inhibiting culture $a = u - v$ (Enquist and Ghirlanda, 2007). In these variables, the model has an equilibrium point given by

$$a^\star = f(\lambda, \theta, q)n^\star \tag{A.5}$$

$$x^\star = \frac{n^\star}{\lambda} \tag{A.6}$$

$$n^\star = \frac{1}{1 - \alpha f(\lambda, \theta, q)} \tag{A.7}$$
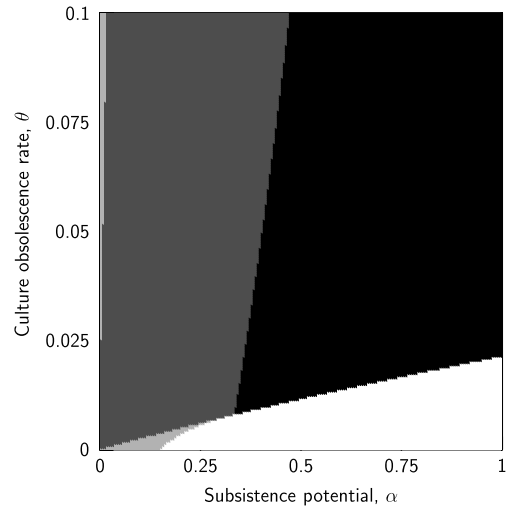

Fig. A.2. Classification of the equilibrium point of Eqs. (7)–(9) by eigenvalue analysis of the Jacobian matrix, Eq. (A.10). White: unstable focus; black: unstable node; light gray: stable focus; dark gray: stable node.

with

$$f(\lambda, \theta, q) = \frac{(2q - 1)\lambda - \theta}{\lambda(\lambda + \theta)}. \tag{A.8}$$

A positive equilibrium, therefore, exists when $f(\lambda, \theta, q) < 1/\alpha$; a cultural equilibrium with higher population than an acultural population ($n^\star > 1$) exists when $f(\lambda, \theta, q) > 0$. The dependence of $f(\lambda, \alpha, q)$ on system parameters has been characterized in Enquist and Ghirlanda (2007). The system Jacobian is

$$J(a, x, n) = \begin{pmatrix} -\theta - \lambda & -\theta & 2q - 1 \\ 0 & -\lambda & 1 \\ \dfrac{r\alpha n^2}{(1 + \alpha a)^2} & 0 & \dfrac{r(1 + \alpha a - 2n)}{1 + \alpha a} \end{pmatrix} \tag{A.9}$$

which, evaluated at the equilibrium point is

$$J(a, x, n) = \begin{pmatrix} -\theta - \lambda & -\theta & 2q - 1 \\ 0 & -\lambda & 1 \\ r\alpha & 0 & -r \end{pmatrix}. \tag{A.10}$$

Fig. A.2 shows the classification of the equilibrium point (Eqs. (A.5)–(A.7)) according to the eigenvalues of the Jacobian matrix. We find numerically that where $f(\lambda, \theta, q) < 0$ the equilibrium is an unstable focus, corresponding to the white region in Fig. A.2. This parallels the analysis by Ghirlanda and Enquist (2007), who found that in Eqs. (5)–(6) a negative equilibrium corresponds to unbounded population growth. Comparing Fig. 2 and Fig. A.2 shows that a positive equilibrium does not generally correspond to a sustainable system (see main text).

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