

Coevolution of adaptive technology, maladaptive culture, and population size in a producer-scrounger game

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April 26, 2009

Abstract

Technology (i.e., tools, methods of cultivation and domestication, systems of construction and appropriation, machines) has increased the vital rates of humans, and is one of the defining features of the transition from Malthusian ecological stagnation to a potentially perpetual rising population growth. Maladaptations, on the other hand, encompass behaviors, customs, and practices that decrease the vital rates of individuals. Technology and maladaptations are part of the total stock of culture carried by the individuals in a population. Here, we develop a quantitative model for the coevolution of cumulative adaptive technology and maladaptive culture in a “producer/scrounger” game, which can also usefully be interpreted as an “individual/social” learner interaction. Producers (individual learners) are assumed to invent new adaptive technology or cultural practices by trial-and-error learning, insight, or deduction, and they pay the cost of innovation. Scroungers (social learners) are assumed to copy or imitate (cultural transmission) both the adaptations and maladaptations generated by producers. We show that the coevolutionary dynamics of producers and scroungers in the presence of cultural transmission can have a variety of effects on population carrying-capacity. From stable polymorphism, where scroungers bring an advantage to the population (increase in carrying-capacity) to periodic cycling, where scroungers decrease carrying-capacity, we find that selection driven cultural innovation and transmission may send a population on the path of growth or to extinction.

Keywords: Producer-scrounger game, technology, adaption, maladaptation, individual and social learning, carrying capacity, cyclic dynamics.

Introduction

Over the last million years the human lineage has learned to transform natural resources into technology; that is, tools, methods of cultivation and domestication, systems of construction and appropriation, machines, modes of social organization. From Oldowan stone tools, to steam engines, to genetic research, humans have mastered technology to the point of being able to leave the surface of the earth and explore outer space. Technology is also the basis of economic growth (Solow, 1956; Galor and Weil, 2000; Romer, 2006); without technological innovations the human population would probably have long ago reached a stable size (Kremer, 1993). Technology is thus one of the defining features of the transition from Malthusian ecological stagnation to a potentially continuous economic and population growth (Galor and Weil, 2000; Galor and Moav, 2002).

Technology can be interpreted as being a *nonrival* good: in economics a good is considered to be nonrival if its consumption or use by one individual makes its use by someone else no less difficult (Pindyck and Rubinfeld, 2001). For instance, the control of fire by one individual does not in itself make its use by another individual more problematic. By contrast, one individual's consumption of some natural resources, such as a chunk of meat or a piece of wood for the fire, does prevent the use of those resources by another individual (consumption of natural resources is a zero-sum game: the gain or loss by one individual is exactly balanced by the losses or gains to others). Before the advent of modern societies, technology was probably also a *nonexcludable* good: a good is considered to be nonexcludable if its use by one individual who has not paid for it is ineluctable (Pindyck and Rubinfeld, 2001). The invention of the wheel certainly took the inventor some time and effort, but use of wheels by others would have been difficult to prevent. Goods that are both nonrival and nonexcludable are called public goods (Pindyck and Rubinfeld, 2001).

For most of human evolution technology was probably a public good. The technology produced by one individual could easily be copied and used by others in the population. Because technology is probably costlier to produce, in terms of time and energy, than to copy or imitate, the interaction between the individuals in a population producing and using technology can be regarded as a "producer/scrounger" game. In this game, the individuals of one type (the scroungers) make use of the behavioral investment of individuals of another type, the producers (Barnard and Sibly, 1981; Giraldeau et al., 1994). Because the technology developed by producers might be copied by scroungers, the interaction between

them can also usefully be regarded as an “individual/social” learner interaction. Here, the individuals of one type (the social learners) copy or imitate the behaviors or artifacts that have been generated by the other type (the individual learners), through trial-and-error learning, insight, or deduction (Rogers, 1988; Stephens, 1991; Boyd and Richerson, 1995; Wakano et al., 2004; Enquist and Ghirlanda, 2007). The evolution of technology (and the origins of economic growth) can thus be framed in terms of the producer/scrounger game, as well as in terms of the coevolution of individual learning and cultural transmission, in which technology can be regarded as a suite of cultural practices.

Throughout human evolution, technology is also likely to have increased the vital rates of individuals; that is, it is adaptive. But technology may become maladaptive, and decrease the vital rates of individuals using it. For instance, agricultural practices, such as the clearing of land, and irrigation, which increased productivity, might also have brought increased contact between human populations and animal reservoirs of disease such as schistosomiasis and malaria, which raised the mortality rate of the resident population (Huang and Manderson, 1993; Livingstone, 1958). Instead of traditional earthen pits, Alaskan natives now often use plastic bags as food containers. These allow the growth of botulism bacteria that increase the rate of death due to botulism (Lancaster, 1990). The suite of cultural practices carried by the individuals in a population, therefore, may involve both adaptive and maladaptive components (Boyd and Richerson, 1985; Diamond, 2005; Enquist and Ghirlanda, 2007). We may thus postulate that producers of technology (individual learners) not only produce adaptive cultural traits but, as a byproduct, may generate maladaptive traits, which may be copied or imitated by scroungers (social learners).

The impact of adaptive and maladaptive cultural traits on human evolution has been repeatedly stressed (Cavalli-Sforza and Feldman, 1981; Lumsden and Wilson, 1981; Boyd and Richerson, 1985; Richerson and Boyd, 2005), but its cumulative nature has virtually never been taken explicitly into account in evolutionary models of cultural transmission. Further, the feedback of cultural adaptations and maladaptions on population dynamics is also very likely to have affected human demography (Tainter, 1988; Diamond, 1997, 2005), but this also has rarely been analyzed in an evolutionary context. There is a clear lack of quantitative theory in this area and a need to gain a better understanding of how the evolutionary dynamics drives the accumulation of culture, and how this feeds back on population demography. This gap has started to be filled with the construction of macro-level models for

cumulative cultural dynamics (Enquist et al., 2008; Ghirlanda and Enquist, 2007; Enquist and Ghirlanda, 2007). Here, we pursue this line of research by focusing more on micro-level individual actions, and explore the coevolution of technological innovation, byproduct maladaptation and population growth under a producer/scrounger game dynamics. The producers are assumed to invent new technology or cultural practices, and pay a cost for innovation. The scroungers are assumed to copy both the technology and maladaptations generated by producers. We ask what are the equilibrium frequencies of producers and scroungers that are selected for in the population, and how does the presence of scroungers (cultural transmission) feed back on the equilibrium levels of adaptations, maladaptations, and population size (carrying-capacity).

Model

Biological setting

We consider a panmictic population of large enough size to ignore the stochastic effects introduced by finite population size. We assume that the amount of resources available to an individual to produce offspring in this population depends on the amount of adaptive and maladaptive cultural traits he/she expresses. Cultural adaptations (also referred to as adaptive technology) encompasses such items as techniques to build arrows, a list of poisonous foods, irrigation methods, or any other knowledge involved in hunting, gathering, and cultivation of resources, which may increase the number of resources available to an individual. Maladaptations, on the other hand represent behaviors, customs, or mystical beliefs, which reduce the amount of resources invested into vital rates.

We assume that there are three types of individuals in the population. The first are innates: these are individuals who do not express any cultural traits, be they adaptations or maladaptations. The second are producers (individual learners), namely those individuals that use adaptive technology and will augment its stock by trial-and-error learning, insight or deduction. In so doing, producers are also likely to generate maladaptive behaviors. In other words, producers augment both the stock of adaptive and maladaptive culture, and pay a fitness cost c_i for it. The third type of individuals are scroungers (social learners) who copy or imitate the cultural traits invented by producers. The strategies of the three

types of individuals, innates, producers, scroungers, can be interpreted here as being either genetically or culturally determined; in any case we consider that the inheritance of these strategies occurs vertically from parent to offspring.

The events of the life-cycle of individuals in the population unfold in the following order: (1) Reproduction occurs with the number of offspring produced by an individual depending on the amount of resources he/she has gathered and that are not diverted into expressing maladaptations. (2) Offspring grow and develop. Juveniles are subject to an enculturation period during which producers and scroungers acquire and assimilate adaptive and maladaptive cultural items from the individuals of the parental population, either by vertical transmission, with probability v , and by oblique transmission, with complementary probability $1 - v$. (3) Juveniles become adults and produce resources. Innates spend all their time producing resources. Producers spend a fraction z_i of their time inventing new adaptive technology (during which they might produce maladaptations) and a complementary fraction $1 - z_i$ of their units of time producing resources. Scroungers spend a fraction z_s of their time scrounging, during which they imitate both adaptive and maladaptive practices developed by producers, and a complementary fraction $1 - z_s$ of their time producing resources.

Population dynamics

The fitness of an individual is defined here as the expected number of its offspring that reach the stage of reproduction. We assume that this is an increasing, linear function of the total amount of resources available to him/her (introducing diminishing returns does not change the qualitative results reported here). We suppose that individuals are endowed with two factors of production allowing them to produce resources: land and labor. The number of units of land available to an individual is assumed to decrease with total population size N (negative density-dependent competition), with the effective units of land available to him/her being given by $1/(1 + \eta N)$, where η measures the strength of density-dependent competition ($0 \leq \eta \leq \infty$, see Table 1 for a list of symbols). Hence, in the absence of density-dependence ($\eta = 0$) each individual is endowed with one baseline unit of land, and the functional form of density-dependence follows the standard Beverton-Holt model from ecology (discrete-time analogue of the logistic model, Begon et al., 1996; Brännström and Sumpter, 2005).

Each individual is also endowed with one baseline unit of labor, which is decreased by the time spent producing cultural items (or scrounging) and augmented by its level of adaptive technology, with the effective units of labor being given by $(1 + A)(1 - z)$, where A is the stock of adaptations and $(1 - z)$ is the fraction of time spent in labor. Hence, an innate ($A = 0$ and $z = 0$) is endowed with one baseline unit of labor. We assume that effective units of land and effective units of labor combine multiplicatively to give the total amount of resources $(1 + A)(1 - z)/(1 + \eta N)$ available to an individual. With these assumptions, the production of resources follows the standard Cobb-Douglas model from economics with unit exponent (Cobb and Douglas, 1928; Pindyck and Rubinfeld, 2001; Romer, 2006; with exponential components for the production function, i.e. with functional form $\{(1 + A)(1 - z)\}^{\gamma_1}/(1 + \eta N)^{\gamma_2}$, the qualitative results reported here do not change). The main motivation behind endorsing the above simplifying assumptions is to make the model analytically tractable by using well established functional forms.

Having specified the functional relationships mapping factors of production into resource availability, it remains to specify how the benefits of producing resources, the cost c_i to producers, and the cost of expressing maladaptations affect fitness. Two main possibilities are usually considered in evolutionary biology: additive and multiplicative effects of costs and benefits on fitness. We investigated these two cases, but present only the additive case in the main text as it turns out to be analytically more tractable thus allowing us to develop intuitions about the dynamics of the system. Introducing multiplicative effects does not change the qualitative results reported here (see the Appendix).

With our assumptions, the fitness of an innate at time t is given by

$$w_{g,t} = \frac{\alpha}{1 + \eta N_t}, \quad (1)$$

where α is a scaling factor converting the amount of resources available to an individual into offspring production, and can be thought of as the maximum rate of offspring production with one unit of resource ($0 \leq \alpha \leq \infty$). The fitness of a producer is

$$w_{i,t} = \alpha \left[\frac{(1 + A_{i,t})(1 - z_i)}{1 + \eta N_t} - c_M M_{i,t} - c_i \right], \quad (2)$$

where $A_{i,t}$ is the stock of adaptations used by a producer at time t ; c_M is a scaling factor, which converts maladaptations into a decrease in the amount of resources used in offspring production ($0 \leq c_M \leq \infty$); and $M_{i,t}$ is the amount of maladaptations carried by a producer at time t . The net cost of expressing maladaptations is thus given by $c_M M_{i,t}$. Finally, c_i is

the fitness cost of being a producer relative to being a scrounger (see eq. A-1 in the Appendix for the multiplicative version of the fitness function). The fitness of a scrounger is

$$w_{s,t} = \alpha \left[\frac{(1 + A_{s,t})(1 - z_s)}{1 + \eta N_t} - c_M M_{s,t} \right], \quad (3)$$

where $A_{s,t}$ is the stock of adaptations used by a scrounger at time t and $M_{s,t}$ is the stock of maladaptations carried by him/her (see eq. A-2 for the multiplicative version of the fitness function). Notice that these fitness functions entail, first, that being a producer has a fitness cost relative to being a scrounger, and, second, that both producing and scrounging are costly relative to being a innate (when everything else is the same) because less time is spent extracting resources.

With these fitness functions we can obtain the frequency p_t (q_t) of producers (scroungers) in the population at time t by evaluating the ratio of the number of their offspring to the total number of offspring in the population as

$$p_{t+1} = \frac{w_{i,t} p_t}{\bar{w}_t}, \quad (4)$$

and

$$q_{t+1} = \frac{w_{s,t} q_t}{\bar{w}_t}, \quad (5)$$

where

$$\bar{w}_t = (1 - p_t - q_t)w_{g,t} + p_t w_{i,t} + q_t w_{s,t} \quad (6)$$

is the mean fitness in the population. From this equation, we obtain the total population size in the next time generation as

$$N_{t+1} = \bar{w}_t N_t. \quad (7)$$

In the absence of producers and scroungers, $p_t = q_t = 0$ for all t , the population is monomorphic for innates. Then, from eq. 1, eq. 6, and eq. 7, and if $\alpha > 1$ and $\eta > 0$, population size converges to the stable value (carrying-capacity):

$$\hat{N} = \frac{\alpha - 1}{\eta}, \quad (8)$$

where throughout the paper the caret denotes an equilibrium value.

Adaptation dynamics

We now present expressions for the dynamics of adaptive technology used by producers ($A_{i,t}$) and scroungers ($A_{s,t}$). In order to obtain these expressions we denote by

$$A_t = p_t A_{i,t} + q_t A_{s,t} \quad (9)$$

the stock of adaptations used by an individual sampled at random from the population at time t (average stock of adaptations).

The stock of adaptations used by a producer consists of two parts. First, a producer living at time t acquires adaptations from the individuals of the parental generation (stage (2) of the life-cycle). With probability v it copies its parent and otherwise copies an individual sampled at random from the parental population, and then acquires an amount A_{t-1} of adaptations (see eq. 9). Second, a producer living at time t generates an amount $I_{A,t}$ of adaptations by itself, which is the per capita rate of adaptive technological innovation. As a result, the stock of adaptations used by a producer at time t is

$$A_{i,t} = (1 - \epsilon_A) [v A_{i,t-1} + (1 - v) A_{t-1}] + I_{A,t}, \quad (10)$$

where ϵ_A is an exogenous decay rate of adaptations ($0 \leq \epsilon_A \leq 1$). This parameter can be interpreted as the rate of obsolescence of technology from one generation to the next (for instance because the exogenous environment changes), as an error rate in copying technology from the parental generation, or even as a pure loss of knowledge due to lack of memory if the system of knowledge, e.g., list of poisonous food, is mainly stored in peoples' heads (for simplicity, we do not consider an endogenous decay rate).

As was the case for a producer, we assume that the stock of adaptations used by a scrounger consists of two parts. First, a scrounger living at time t acquires cultural traits from the parental generation either by vertical and/or oblique transmission. Second, a scrounger may scrounge on the total stock $p_t N_t I_{A,t}$ of adaptations generated at time t by all producers in the population. Then, the stock of adaptations used by a scrounger at time t is

$$A_{s,t} = (1 - \epsilon_A) [v A_{s,t-1} + (1 - v) A_{t-1}] + z_s \beta_A p_t N_t I_{A,t}, \quad (11)$$

where β_A is a transmission parameter ($0 \leq \beta_A \leq 1$), which can be interpreted as the contact rate between producers and scroungers multiplied by the probability of transmission

of cultural items from producers to scroungers. The transmission probability may depend on the concealment of traits by producers or the degree of excludability of adaptations. If technology becomes more excludable, then β_A decreases, holding everything else constant, and complete excludability would correspond to $\beta_A = 0$. Eq. 11 entails that a scrounger may assimilate the technology of several different individuals, and implicit in the use of $p_t N_t I_{A,t}$ is the assumption that the technology expressed independently by different producers can be combined additively. We found no micro-foundations in the economics or cultural evolution literature to justify any particular functional form for the aggregation of cultural items. Thus, additive aggregation is the natural starting point as it is the most analytically tractable.

Finally, we need an expression for $I_{A,t}$, which we assume takes the form

$$I_{A,t} = z_i [\mu(1-x) + \varphi_A \{vA_{i,t-1} + (1-v)A_{t-1}\}], \quad (12)$$

where μ is the rate of innovation per unit time invested into learning, which is independent of the adaptations acquired from the parental generation ($0 \leq \mu \leq \infty$), and x is the fraction of these innovations that are maladaptive. The parameter φ_A is a rate of innovation, which converts existing adaptations into new ones ($0 \leq \varphi_A \leq \infty$). The parameterization of eq. 12, where new adaptive technology is created *de novo* (at rate $\mu(1-x)$ per unit investment) and from existing technology (at rate φ_A) follows the work of Enquist and Ghirlanda (2007, eq. 8-9) and Enquist et al. (2008, eq. 18), who developed macroscopic models for the dynamics of adaptations and maladaptations aiming at fitting empirical data. We mention that economists endorse quiet similar assumptions for the dynamics of technology (e.g., Galor and Weil, 2000; Romer, 2006), but tend to exponentiate the existing technology, which does not alter the qualitative results reported here.

Maladaptation dynamics

Here, we present expressions for the amount of maladaptions carried by producers ($M_{i,t}$) and scroungers ($M_{s,t}$) in the population. Similarly to the average stock of adaptations introduced above (eq. 9), we denote by

$$M_t = p_t M_{i,t} + q_t M_{s,t} \quad (13)$$

the stock of maladaptations carried by an individual sampled at random from the population at time t (average maladaptation).

As was the case for adaptations, we assume that the stock of maladaptations carried by a producer consists of two parts. First, an individual acquires maladaptions from individuals of the parental generation by vertical and/or oblique transmission. Second, producers develop $I_{M,t}$ new maladaptations during generation t . Combining these, the stock of maladaptations used by a producer at time t is

$$M_{i,t} = (1 - \epsilon_M) [vM_{i,t-1} + (1 - v)M_{t-1}] + I_{M,t}, \quad (14)$$

where ϵ_M is a decay rate of maladaptations, which can be interpreted as the rate of loss of maladaptations due to errors in copying exemplar individuals or selective filtering, which corresponds to a higher probability of adopting adaptive rather than maladaptive cultural traits (Enquist and Ghirlanda, 2007). In addition to inheriting maladaptations from the parental generation, scroungers are assumed to copy them from the total stock $p_t N_t I_{M,t}$ of maladaptations generated at time t by all producers in the population. The stock of maladaptations used by a scrounger at time t is then given by

$$M_{s,t} = (1 - \epsilon_M)M_{t-1} + z_s \beta_M p_t N_t I_{M,t}, \quad (15)$$

where β_M is the transmission rate of maladaptions from producers to scroungers ($0 \leq \beta_M \leq 1$), which can be thought of as the contact rate between producers and scroungers multiplied by the per individual transmission rate of maladaptations from producers to scroungers.

Finally, the amount of maladaptations developed by a producer in generation t is assumed to be given by

$$I_{M,t} = z_i [\mu x + \varphi_M \{vM_{i,t-1} + (1 - v)M_{t-1}\}]. \quad (16)$$

where φ_M is the rate of conversion of existing maladaptations into new ones. In eq. 16, we ignored, for simplicity, the possibility that existing adaptations may generate new maladaptations (again, introducing such a feature does not alter the main qualitative results reported here).

Our model tracks the non-linear dynamical system characterized by the variables p_t , q_t , N_t , $A_{i,t}$, $A_{s,t}$, $M_{i,t}$, $M_{s,t}$ (eq. 4, eq. 5, eq. 7, eq. 10, eq. 11, eq. 14, and eq. 15), and allows us to track the dynamics of p_t , q_t , N_t , A_t , and M_t , which eventually converge to some equilibrium point given by \hat{p} , \hat{q} , \hat{N} , \hat{T} , \hat{M} . Depending on the parameter values, this system can be complicated, and we studied its dynamics and equilibrium points using analytical expressions when we were able to derive them (or when they are not too complicated), and used numerical analysis for the more complicated cases.

Results

Adaptations without maladaptations

In this section we present results for the case where there are no maladaptations ($x = 0$, $\varphi_M = 0$, and $M_0 = 0$) so that only the dynamics of p_t , q_t , N_t , and A_t are involved.

Analytical results

If we further assume that the investment into producing and scrounging are the same ($z_i = z_s = z$) and that there is no cost to individual learning ($c_i = 0$), the analysis simplifies considerably. In the absence of scroungers ($q_0 = 0$), a small fraction of producers ($p_0 \rightarrow 0$) will invade a population of innates if $w_{i,t} > w_{g,t}$ (eq. 1 and eq. 2). That is, if $(1 + z\mu)(1 - z) > 1$, which reflects a trade off between the gains from inventing new adaptive technology (first parentheses) and the loss of productivity incurred from spending time inventing technology (second parentheses). By rearranging, the gains outweigh the losses when

$$\mu > \frac{1}{1 - z}, \quad (17)$$

where the parameters ϵ_A and φ_A do not affect this invasion condition the stock of adaptive technology of the parental generation is initially set to zero (no producers and no scroungers in the parental generation).

If the condition of invasion of producers is satisfied, it can also be shown that producers will not only spread where rare but will also go to fixation in the population, in which case $\hat{p} = 1$. This occurs because the fitness of producers will be higher than that of innates at all frequencies of innates in the population (the accumulation of adaptations can only further increase the fitness of producers relative to that of innates). If the invasion condition is not satisfied, the producers will be expelled from the population, in which case $\hat{p} = 0$. Therefore, no polymorphism is maintained and, depending on the balance between fitness costs and benefits of producing (see eq. 17), the population will be either fixed for innates ($\hat{p} = 0$) or fixed for producers ($\hat{p} = 1$) in the long-term. In the latter event, we find from eq. 7, eq. 10, and eq. 12 that the carrying-capacity is given by

$$\hat{N} = \frac{1}{\eta} \left(\alpha(1 - z)(1 + \hat{A}) - 1 \right), \quad (18)$$

where the equilibrium level \hat{A} of average adaptations is

$$\hat{A} = \frac{z\mu}{\epsilon_A - z\varphi_A}. \quad (19)$$

Thus, by generating \hat{A} , producers increase the carrying-capacity; that is, they bring an advantage to the population (compare eq. 18 to eq. 8). Notably, the intensity of vertical transmission v does not appear in eqs. 18–19, and thus has no effect on equilibrium values; it only affects the rate of convergence to equilibrium. For ease of presentation, we set $v = 0$ in the rest of the paper; that is, juveniles copy only an individual sampled at random from the population (the value of v does not affect any of the analytical equilibrium points reported in this paper nor does it affect the qualitative results observed under non-equilibrium dynamics reported below).

Eqs. 18–19 show that, given values of η , μ , and z , the stable population size will be mainly affected by the difference $\epsilon_A - z\varphi_A$ between the exogenous decay rate ϵ_A and the endogenous growth rate $z\varphi_A$ of existing adaptations. As this difference goes to zero, both the level of cultural adaptations and population size approaches infinity. Hence, a theoretical possibility is the realization of Marquis de Condorcet’s view that cogitation will generate innovations (μ and φ_A), which will remove any obstacle (ϵ_A) to technological improvement, and then break the Malthusian iron limit. This is a classical result from macroeconomic theory (Kremer, 1993; Romer, 2006) and termed the “demo-cultural explosion” by Ghirlanda and Enquist (2007).

Introducing scroungers into a population fixed for producers ($\hat{p} = 1$) results in the invasion by scroungers, and in a unique stable polymorphism between producers and scroungers characterized by

$$\hat{p} = \frac{1}{z\beta_A\hat{N}}, \quad (20)$$

where \hat{N} is given by eq. 18. Thus \hat{p} varies inversely with the rate of transmission β_A of technology to scroungers and with \hat{N} , but, crucially, neither \hat{N} nor \hat{A} is affected by β_A and the frequency of scroungers. If $z_i = z_s = z$ and $c_i = 0$, scrounging has no effect on population carrying-capacity: it brings neither an advantage nor a disadvantage to the population. This feature is illustrated in Figure 1, where producers first invade a population of innates, then go to fixation, and are subsequently invaded by scroungers, with the presence of scroungers not perturbing the equilibrium population size.

The equilibrium adaptive technology and population size are unaffected by the presence of scroungers because these individuals aggregate the adaptive technology of many different producers in the population, and then pass it to the next generations. Hence, the decrease in amount of adaptations inherited from the parental generation that stems from a reduction in the number of producers can be compensated by the increase in adaptations due to their aggregation by scroungers. At equilibrium, the same amount of adaptations will be maintained with fewer individuals producing it. This accords with previous results delineating several situations where cultural transmission does not increase population fitness even if it is selected for (Rogers, 1988; Stephens, 1991; Boyd and Richerson, 1995; Wakano et al., 2004; Enquist and Ghirlanda, 2007)

Numerical results

If we assume that the proportion of time spent producing adaptive technology is different from that spent scrounging it ($z_i \neq z_s$), the analysis becomes more complicated and we present only numerical results for this case. When $z_s > z_i$, we observe that \hat{p} decreases as z_s increases while z_i is held constant (Fig. 2). But \hat{N} and \hat{A} behave in the opposite way with both increasing as z_s increases while z_i is held constant (Fig. 2). Consequently, increased scrounging has the potential to increase the average level of adaptation and population size (Fig. 3). This occurs because the more time that scroungers spend scrounging, the more they aggregate adaptations from different producers (see the second term on the right hand side of eq. 11), thereby raising the average stock of adaptations in the population (which varies directly with z_s). This, in turn, increases the amount of adaptive technology that both producers and scroungers inherit from the parental generation (eq. 10 and eq. 11), and the rate of innovation when $I_{A,t} > 0$ (eq. 12). Hence, when $z_s > z_i$, scrounging increases carrying-capacity. By contrast, when $z_s < z_i$, we observe that \hat{p} decreases as z_s decreases while z_i is held constant, but the equilibrium values \hat{N} and \hat{A} are reduced instead of increased (Fig. 3).

The main effect of introducing a fitness cost to being a producer relative to being a scrounger ($c_i > 0$) is that it decreases \hat{p} (Fig. 4), which decreases the equilibrium stock of adaptive technology, and consequently \hat{N} . By contrast to the case where there is no cost to producers, the equilibrium values \hat{N} and \hat{A} will be affected by introducing scroungers into the population even for $z_s = z_i$. The presence of scroungers actually decreases both \hat{N}

and \hat{A} , everything else being constant (Fig. 4). Hence, when producers bear a fitness cost relative to scroungers, scrounging decreases the carrying-capacity, everything else being held constant.

Adaptations with maladaptations

We now allow maladaptations to affect the coevolutionary dynamics of producers and scroungers, and analyze the dynamics of p_t , q_t , N_t , A_t and M_t .

Analytical results

Again we start by assuming that $z_i = z_s = z$ and $c_i = 0$, and further that $\epsilon_A = \epsilon_M = \epsilon$ (rate of obsolescence of adaptations equals the rate of loss of maladaptations), $\varphi_A = \varphi_M = 0$ (rate of growth of adaptations and maladaptations do not depend on past adaptations), and that $\beta_A = \beta_M = \beta$ (the rate of transfer of adaptations and maladaptations from producers to scroungers is the same). In the absence of scroungers, a small fraction of producers may invade a population of innates; this occurs if $(1+z(1-x)\mu)(1-z) - z\mu x c_M > 1$, which reflects a trade off between the gains from inventing new adaptive technology (first parentheses of the first term) and two types of costs: loss of productivity incurred by spending time inventing cultural traits (second parentheses of the first term) and cost due to expressing maladaptations. The gains outweigh the losses when

$$\mu > \frac{1}{(1-z)(1-x) - x c_M}, \quad (21)$$

where ϵ does not affect this invasion condition because the level of adaptations and of maladaptations of the parental generation is initially set to zero (no producers and no scroungers in the parental generation).

The main qualitative difference between eq. 21 and the invasion condition without maladaptations (eq. 17) is the cost due to generating maladaptations, which decreases the selective advantage of producers. If the invasion condition is satisfied, it can again be shown that the fitness of producers will be higher than that of innates at all frequencies of innates in the population, so that producers will go to fixation in the population. In this event we have $\hat{p} = 1$ and from eq. 7, eq. 10, eq. 11, and eq. 16, fixation of producers results in the

carrying-capacity being given by

$$\hat{N} = \frac{1}{\eta} \left(\frac{\alpha(1-z)(1+\hat{A})}{1+\alpha c_M \hat{M}} - 1 \right), \quad (22)$$

where

$$\hat{A} = \frac{z\mu(1-x)}{\epsilon} \quad (23)$$

and

$$\hat{M} = \frac{z\mu x}{\epsilon}. \quad (24)$$

The main qualitative difference between eqs. 18–19 and eqs. 22–24 is that \hat{N} is now a decreasing function of the equilibrium average stock of maladaptations in the population.

Introducing scroungers into a population of producers, allows us again to find a unique stable polymorphism between producers and scroungers, which is characterized by

$$\hat{p} = \frac{1}{z\beta\hat{N}}, \quad (25)$$

where \hat{N} is given by eq. 22. Qualitatively this is the same result as eq. 20. Quantitatively, the presence of maladaptation increases the equilibrium level of producers \hat{p} : increasing the rate of production x of maladaptations and/or the cost c_M of maladaptations decreases \hat{N} , which causes \hat{p} to increase. Eqs. 22–25 show that when $\beta_A = \beta_M = \beta$ the rate of transmission of cultural variants from producers to scroungers does not affect \hat{A} and \hat{M} , which is the same result as that found without maladaptation. But if the rates of transmission of adaptations and maladaptations from producers to scroungers are different ($\beta_A \neq \beta_M$), then \hat{A} and \hat{M} will be affected by β_A and β_M (see eqs. A-6–A-5 of the Appendix).

Numerical results

More generally, the rates of loss of technology and maladaptations may be different ($\epsilon_A \neq \epsilon_M$) and the appearance of new adaptations and maladaptations may be dependent on the amount of existing cultural traits ($\varphi_A > 0$ and $\varphi_M > 0$) or a combination of these factors. In all these cases, and assuming no scroungers ($q_0 = 0$), we find that either there is a stable polymorphism between innates and producers, or innates and producers coexist in a stable periodic cycle (Fig. 5). Producers do not fix in a population of innates when the increase in fitness benefits brought by adaptations is balanced by the fitness costs resulting from the

expression of maladaptations. Both fitness costs and benefits are frequency-dependent, with the consequence that the fitness of producers becomes equivalent to that of innates (negative frequency-dependence on producers) before producers fix in the population. This will cause the carrying-capacity to be either the same as that determined by innates (eq. 8, if there is a stable polymorphism between innates and producers), or result in periodic cycling around this value (Fig. 5).

There is a large range of parameter values for $\epsilon_A \neq \epsilon_M$, or $\varphi_A > 0$ and $\varphi_M > 0$, or a combinations of these, where periodic cycling of producers, technology, maladaptation and population size occurs ($\varphi_A, \varphi_M, \epsilon_A, \epsilon_M$ are so-called bifurcation parameters). This follows from the following considerations. Initially producers increase technology and invade the population of innates (without enough maladaptations to prevent the initial increase in producer frequency). Then maladaptions accumulate (for instance if the rate of production of new maladaptations is low, but their rate of decay is not lower than that of technology: $\epsilon_A > \epsilon_M$) in which case a calculable point is eventually reached where the fitness of producers declines drastically, causing their decrease in frequency, followed by a rapid decline in adaptations and subsequently of maladaptions (Fig. 5). This results in a situation where the stock of maladaptations is again too low to prevent the increase in frequency of producers: the cycle starts again.

Introducing scroungers into a population polymorphic for innates and producers can result in the coexistence between the three types, either in a stable polymorphism or in a periodic cycle (Fig. 6). As was observed in the presence of maladaptations, the typical time dynamics of the system when small fractions of producers and scroungers are introduced into the population is that producers invade first, and are then invaded by scroungers, with the population finally settling either at a stable polymorphic equilibrium or into a state where the frequencies of the three types oscillate periodically (Fig. 6). We observed cycling under a large range of parameter values, and there are situations where the population size rises and falls sharply, possibly reaching the point of extinction.

Finally, we mention that assuming that $z_s > z_i$ or $c_i > 0$ in the presence of maladaptations changes the dynamics of the system qualitatively in exactly the same way as was observed in the absence of maladaptations with everything else held constant. That is, producers and scroungers may still invade a population of innates and, depending on parameter values, may settle either at a stable equilibrium or at a cyclic polymorphism involving the three

strategies. In general, we observed that, holding everything else constant, $z_s > z_i$ will augment the amplitude of the oscillations. Hence, scrounging leads to greater fluctuations in carrying-capacity.

Discussion

We have presented a model for the evolution of adaptive technology and maladaptive culture, both of which were assumed to be generated by producers, copied or imitated by scroungers within generations, and culturally transmitted by learning between generations. Adaptive technology represents any tool, method of cultivation, system of construction and appropriation, or mode of social organization, which may result in an increase in the resources obtained by the individuals in the population, and hence in their vital rates. On the other hand, maladaptive culture represent behaviors, customs, or mystical beliefs, which reduce the amount of resources invested into survival or reproduction, and may therefore decrease the vital rates of individuals. The accumulation of adaptive and maladaptive cultural traits can be interpreted as giving the total stock of culture carried by the individuals in the population. We have analyzed how this stock of culture is selected for through the interaction between innates (individuals using neither adaptations nor maladaptations), producers, and scroungers, and how the resulting dynamics feed back on equilibrium population size. We introduced the “innates” mainly in order to have a benchmark population of individuals, which do not express cultural traits and where the carrying capacity is determined by construction by exogenous factors. But the model and results applies without the innates, by considering only producers and scroungers, which is probably the case for humans.

Adaptations without maladaptations

Our results suggest that in the absence of maladaptions, producers are likely to invade a population of innates and will then go to fixation causing population size to increase (eq. 17 and Fig. 1). By allowing individuals in the population to obtain more resources, the benefits of adaptive technology may offset the cost of innovation (loss of time devoted to labour), and increase the vital rates of individuals. Scroungers may then invade a population of producers with the consequence that the population will approach a stable polymorphism (Fig. 1). Is adding scroungers advantageous or disadvantageous to the population; that is, how does

cultural transmission affect population size? Our results show that this is sensitive to the parameter values. When producing has some intrinsic cost relative to scrounging ($c_i > 0$, eq. 2), adding scroungers might actually undermine population productivity and thus reduce equilibrium population size (Fig. 4). Here, cultural transmission is detrimental to the population. In the absence of costs, and with equal effort required for producing and scrounging, the population size is not affected by the presence of scroungers: the demographic consequences of cultural transmission are neutral (Fig. 4), although any frequency of scroungers can be maintained at equilibrium by tuning the transmission parameter β_A (eq. 20). However, when scroungers put more effort into scrounging than producers do into producing, and everything else is held constant, scroungers may greatly increase population size: here cultural transmission brings an advantage to the population (Fig. 3). This occurs because scroungers aggregate the technology of many different producers in the population, thereby increasing the average level of technology, which is then passed on to the next generations. Scroungers can be regarded as fitness amplifiers in this case.

Adaptations with maladaptations

Adding maladaptations (as byproducts of technological innovation or corruption of past technology) markedly affects the co-evolutionary dynamics of innates, producers, and scroungers. Qualitative changes in the dynamics occur in at least two different ways. First, innates may coexist with producers at a stable polymorphism, or with producers and scroungers so that all three strategies are maintained in the population. Innates will be retained in the population only if the fitnesses of the other strategies are not greater than theirs, which entails that the population size will not be increased by the presence of producers or scroungers. This occurs when the gains in productivity brought about by adaptation are exactly offset by the loss of resources resulting from the expression of maladaptations, with the result that cultural practices and transmission are neutral with respect to their effects on equilibrium population size. Neither producers nor scroungers bring an advantage or disadvantage to the population.

The second way in which adding maladaptations affects the coevolutionary dynamics is that they may cause periodic cycling of strategies and demographic variables for a large range of parameter values (Fig. 5 and Fig. 6). Cycling may occur in our model with all three types of strategies in the population, and it may result in sharp oscillations of population

size, above and below the value attained by a population of innates. Cycling occurs when technology first grows faster than maladaptations, but maladaptations accumulate subsequently (for instance if the rate of production of new maladaptations is low, but their rate of decay is slower than that of adaptations) in which case a point is reached where the fitness of producers declines and causes their decrease in frequency, which is followed by a decline in adaptive technology and of production of maladaptations (Fig. 5). The stock of maladaptations then reaches a threshold value that it is too low to prevent the increase in frequency of producers, which increase in frequency again and concomitantly brings technology into the population, so that the cycle can repeat itself. In these situations, cultural innovations and transmission bring periodic advantages and disadvantages to the population possibly placing the population at risk of extinction. The presence of scroungers sometimes amplifies these oscillations, so they can be seen as fitness disrupters in this case.

Learning and macroeconomic models

Our formalization is related to two distinct previous modeling approaches. First, it has features in common with previous models on the evolution of individual and social learning (e.g., Rogers, 1988; Stephens, 1991; Boyd and Richerson, 1995; Wakano et al., 2004; Enquist and Ghirlanda, 2007). Such models usually assume fluctuating environments to which individual learners can adapt by trial-and-error learning or insight. Social learners are then assumed to copy individual learners without paying the cost of individual learning (analogous to our parameter c_i , and which can be thought of as the “cost of plasticity”). This can result in either a stable or a cyclic polymorphism between the strategies in the population. As in our model, individual learners can be seen as producers (inventing new behaviors), and social learners as scroungers (copying the new behaviors), so that the basic underlying game structure in these classical models is similar to ours. The crucial difference is that we do not invoke exogenous environmental fluctuations, but consider explicitly the cumulative aspect of culture. That is, producers (individual learners) produce adaptive technology and maladaptations that accumulate over generations so that the environment (stock of culture) is endogenously determined. This defining feature of our model may result in different qualitative outcomes concerning the coexistence of social and individual learners from those obtained in previous formalizations. In particular, in previous work social learners are not selected for in the absence of costs to individual learning (e.g., $c_i = 0$, $z_i = z_s$) because they

have the same fitness as producers in that case. In our model, by contrast, social learners may still be favored by selection as they can aggregate adaptive cultural traits from different individuals, so that when rare they may have higher fitness than producers.

Second, because we formalized the cumulative aspect of technology and maladaptations explicitly, our model has features in common with models of economic growth such as those traditionally employed in macroeconomics to study economics growth (e.g., Solow, 1956; Kremer, 1993; Galor and Weil, 2000; De La Croix and Michel, 2002; Romer, 2006). These models often take into account the cumulative aspect of technology and its feedback on demography. Technology (in combination with other factors of production) then affects the output of individuals and/or their vital rates, in the same or in a more refined way than we considered in our fitness functions (eq. 2 and eq. 3). Our formalization thus delineates a link between such models and those of cultural transmission. Future models may go further and take into account both geographic and age structure, which are crucial demographic features affecting the evolution of populations (e.g., Wright, 1931; Charlesworth, 1980; Rousset, 2004) and economic growth dynamics (e.g., De La Croix and Michel, 2002; Romer, 2006).

Implications and outlook

Although our model is based on a series of simplifying assumptions, the general qualitative features seem robust to changes in functional forms, which suggests two main implications of our results. First, as mentioned above, a classical result of cultural evolution theory is that individual and social learning are favored under conditions of fluctuating exogenous environments, and cultural transmission does often not increase population fitness (Rogers, 1988; Stephens, 1991; Wakano et al., 2004, see Boyd and Richerson, 1995; Enquist et al., 2007 for exceptions to the rule). Our results point to broader conditions for selection on individual and social learning, which may actually evolve under a stable exogenous environments if individual learners (producers) generate a stock of adaptive cultural traits, which can itself be seen as an endogenous environment. With the environment (or part of it) being an endogenous dynamical variable, the effects of social learning (scroungers) on fitness is also changed. Our results show that the coevolution of producers and scroungers may then result in a wide variety of dynamics, in which selection-driven cultural innovation and transmission evolve to be advantageous (increase in carrying capacity) as well as detrimental to the population (decrease in carrying capacity). From a theoretical point of view, our analysis

thus singles out unrecognized conditions for the evolution of individual and social learning, and where cultural innovation and transmission can greatly increase population size. There is a set of parameter values where this process results in infinite population size (e.g., eq. 18 and eq. 19).

Second, taking the dynamics of maladaptions explicitly into account, and thus considering the observation that not all aspects of culture are beneficial to population growth (Kaplan and Lancaster, 1999, Richerson and Boyd, 2005, chapter 5), led us to identify feedbacks on population demography that generate cycling under a large set of parameter values. In a stochastic world this means an increase in the extinction probability of the population. This feature might be of empirical relevance for understanding the rise and fall of populations due to endogenous factors. As exemplified by the massive diversion of natural resources to ceremonial construction on Easter Island, that are linked to the final collapse of this society, maladaptations are likely to affect population demography (Tainter, 1988; Diamond, 2005). Importantly, cycling occurs in our model (Fig. 5 and Fig. 6) and it is an outcome of the evolutionary dynamics, made possible by cultural maladaptations being a by-product of the production of cultural adaptations. Modeling maladaptations as a fraction of the innovation that are not adaptive (see eq. 16 and also Enquist and Ghirlanda, 2007) seems to us to be a very plausible assumption; in the biological context it is well-known that most novel genetic mutations are deleterious (Eyre-Walker and Keightley, 2007). This suggests that population extinctions due to the accumulation of cultural maladaptations might have been recurrent events because there are likely to be selection-driven, not the consequence of some local contingency. Our results thus support quantitatively the view that maladaptations may have repeatedly affected human demographic history (Tainter, 1988; Diamond, 2005).

More generally, the effect of endogenous factors on population demography needs further theoretical investigation as several of them might lead to population cycling. For instance, Turchin (2003) studied a demographic-fiscal model where producers' surplus (e.g., surplus of grains produced by peasants, commoners) are absorbed by state expenditures, and where feedback loops lead to over-taxation eventually generating population collapse (see also Tainter, 1988). Collapse was more likely to occur in Turchin's (2003) model in the presence of elite classes scrounging on the behavioral investment of producers. Future work might thus combine different sides of the "producer/scrounger" game, including the possibility of expressing mixed strategies (e.g. critical social learning, Enquist et al., 2007), in order to gain

a better understanding of the effect of individual behavior on demographic-cultural-fiscal coevolution. As illustrated by the problem of the sex-ratio in China and India, son preference is widespread and culturally transmitted (Coale and Banister, 1994). With the easy availability of sex selection technology, many people are choosing to use it to manifest son preference, which has maladaptive consequences at several levels. These include a strong squeeze on males in the marriage market (which makes the trait maladaptive at the individual level), eventual reduction in population growth, and an array of other societal problems (Tuljapurkar et al., 1995; Li et al., 2000).

Acknowledgements

We thank R. Kaeuffer for helpful discussions, U. Steiner for helpful comments on the manuscript, and all reviewers for constructive criticism that improved this paper. LL is supported by a grant from the Swiss NSF and by NIH grant GM28016 to M. W. Feldman.

Appendix

Multiplicative effects on fitness

When fitness costs and benefits combine multiplicatively, but everything else is the same, eq. 2 and eq. 3 are replaced by

$$w_{i,t} = \frac{\alpha(1 + A_{i,t})(1 - z_i)(1 - c_M M_{i,t})(1 - c_i)}{1 + \eta N_t}, \quad (\text{A-1})$$

and

$$w_{s,t} = \frac{\alpha(1 + A_{s,t})(1 - z_s)(1 - c_M M_{s,t})}{1 + \eta N_t}. \quad (\text{A-2})$$

We checked with numerical analysis that with these fitness functions the critical qualitative results reported in the main text are not altered. That is, when $z_i = z_s = z$, $c_i = 0$, $\varphi_A = \varphi_M = 0$, and $\epsilon_A = \epsilon_M = \epsilon$, scroungers do not affect the equilibrium population size, which is illustrated in the additive case by eqs. 22–25, and that when these equalities are not satisfied, periodic cycling of the strategies and demographic variables occurs under a large set of parameters values.

Producer-scrounger equilibrium for unequal transmission rates

When $\beta_M \neq \beta_T$, but everything else is the same, eqs. 22–25 are replaced by

$$\hat{N} = \frac{1}{\eta} \left(\frac{\alpha(1 - z)\{\epsilon + z\mu(1 - x)\}}{\epsilon + \alpha c_M z \mu x} - 1 \right), \quad (\text{A-3})$$

$$\hat{A} = \frac{\hat{p}z\mu(1 - x)(1 + z\beta_T(1 - \hat{p})\hat{N})}{\epsilon}, \quad (\text{A-4})$$

$$\hat{M} = \frac{\hat{p}z\mu x(1 + z\beta_M(1 - \hat{p})\hat{N})}{\epsilon}, \quad (\text{A-5})$$

and

$$\hat{p} = \frac{1}{z\hat{N}} \left(\frac{x(1 + \eta\hat{N})c_M - (1 - x)(1 - z)}{x(1 + \eta\hat{N})c_M\beta_M - (1 - x)(1 - z)\beta_T} \right). \quad (\text{A-6})$$

References

- Barnard, C. J. and R. M. Sibly. 1981. Producers and scroungers: a general model and its application to captive flocks of house sparrows. *Animal Behaviour* 29:543–550.
- Begon, M., J. L. Harper, and C. R. Townsend. 1996. Ecology: Individuals, Populations and Communities. Blackwell Science, 6th edn.
- Boyd, R. and P. J. Richerson. 1985. Culture and the Evolutionary Process. University of Chicago Press, Chicago.
- Boyd, R. and P. J. Richerson. 1995. Why does culture increase human adaptability? *Ethology and Sociobiology* 16:125–143.
- Brännström, A. and D. J. Sumpter. 2005. The role of competition and clustering in population dynamics. *Proceedings of the Royal Society B-Biological Sciences* 272:2065–2072.
- Cavalli-Sforza, L. and M. W. Feldman. 1981. Cultural Transmission and Evolution. Princeton University Press, NJ.
- Charlesworth, B. 1980. Evolution in age-structured populations. Cambridge University Press, Cambridge.
- Coale, A. J. and J. Banister. 1994. Five decades of missing females in China. *Demography* 31:459–479.
- Cobb, C. W. and P. H. Douglas. 1928. A Theory of Production. *The American Economic Review* 18:139–165.
- De La Croix, M. and P. Michel. 2002. A theory of economic growth. Cambridge University Press, Cambridge.
- Diamond, J. 1997. Guns, Germs, and Steel. W. W. Norton.
- Diamond, J. 2005. How Societies Choose to Fail or Succeed. Penguin, New York.
- Enquist, M., K. Eriksson, and S. Ghirlanda. 2007. Critical social learning: a solution to Rogers’s paradox of nonadaptive culture. *American Anthropologist* 109:727–734.
- Enquist, M. and S. Ghirlanda. 2007. Evolution of social learning does not explain the origin of human cumulative culture. *Journal of Theoretical Biology* 246:129–135.

- Enquist, M., S. Ghirlanda, A. Jarrick, and C. A. Wachtmeister. 2008. Why does human culture increase exponentially? *Theoretical Population Biology* 74:46–55.
- Eyre-Walker, A. and P. Keightley. 2007. The distribution of fitness effects of new mutations. *Nature Review Genetics* 8:610–618.
- Galor, O. and O. Moav. 2002. Natural selection and the origin of economic growth. *Quarterly Journal of Economics* 117:1133–1191.
- Galor, O. and D. N. Weil. 2000. Population, technology, and growth: from Malthusian stagnation to the demographic transition and beyond. *American Economic Association* 90:806–828.
- Ghirlanda, S. and M. Enquist. 2007. Cumulative culture and explosive demographic transitions. *Quality and Quantity* 41:581–600.
- Giraldeau, L., T. Caraco, T., and T. Valone. 1994. Social foraging: individual learning and cultural transmission of innovations. *Behavioral Ecology* 5:35–43.
- Huang, Y. and L. Manderson. 1993. Schistosomiasis and the social patterning of infection. *Acta tropica* 52:317–317. Acta Tropica.
- Kaplan, H. S. and J. B. Lancaster. 1999. The evolutionary economics and psychology of the demographic transition to low fertility. In Cronk, L., N. Chagnon, and W. Irons (eds.), *Adaptation and human behavior: An anthropological perspective*, pp. 283–322. Aldine de Gruyter, New York.
- Kremer, M. 1993. Population growth and technological change: one Million BC to 1990. *The Quarterly Review of Economics* 108:681–716.
- Lancaster, M. J. 1990. Botulism: north to Alaska. *American Journal of Nursing* 90:60–62.
- Li, N., M. W. Feldman, and S. Li. 2000. Cultural transmission in a demographic study of sex ratio at birth in China's future. *Theoretical Population Biology* 58:161–172.
- Livingstone, F. B. 1958. Anthropological implications of sickle cell gene distribution in West Africa. *American Anthropologist* 60:533–562.
- Lumsden, C. J. and E. O. Wilson. 1981. *Genes, Mind and Culture*. Harvard University Press, MA.

- Pindyck, R. S. and D. L. Rubinfeld. 2001. *Microeconomics*. Prentice Hall, Upper Saddle River, NJ.
- Richerson, P. J. and R. Boyd. 2005. *Not by Genes Alone*. University of Chicago Press, Chicago.
- Rogers, A. R. 1988. Does biology constrain culture. *American Anthropologist* 90:819–831.
- Romer, D. 2006. *Advanced Macroeconomics*. McGraw-Hill, 3th edn.
- Rousset, F. 2004. *Genetic Structure and Selection in Subdivided Populations*. Princeton University Press, Princeton, NJ.
- Solow, R. M. 1956. A contribution to the theory of economic growth. *Quarterly Journal of Economics* 70:65–94.
- Stephens, D. W. 1991. Change, regularity, and value in the evolution of animal learning. *Behavioral Ecology* 2:77–89.
- Tainter, J. A. 1988. *The Collapse of Complex Societies*. Cambridge University Press, Cambridge.
- Tuljapurkar, S., N. Li, and M. W. Feldman. 1995. High sex ratios in China's future. *Science* 267:874–876.
- Turchin, P. 2003. *Historical Dynamics: Why States Rise and Fall*. Princeton University Press, NJ.
- Wakano, J. Y., K. Aoki, and M. W. Feldman. 2004. Evolution of social learning: a mathematical analysis. *Theoretical Population Biology* 66:249–258.
- Wright, S. 1931. Evolution in Mendelian populations. *Genetics* 16:97–159.

Table 1: List of symbols

Symbol	Definition
p	Frequency of producers in the population.
q	Frequency of scroungers in the population.
N	Population size.
A	Average level of adaptations (adaptive technology) in the population.
M	Average level of maladaptations in the population.
v	Probability of vertical transmission of cultural traits.
α	Scaling factor converting resources produced into offspring number.
η	Strength of density-dependent competition for land.
μ	Rate of <i>de novo</i> innovation per unit time invested into learning.
x	Fraction of innovations that are maladaptive.
φ_A	Rate of innovation converting existing adaptations into new adaptations.
φ_M	Rate of conversion of existing adaptations into maladaptations.
ϵ_A	Rate of obsolescence of adaptations.
ϵ_M	Rate of loss of maladaptations.
β_A	Transmission rate of adaptations from producers to scroungers.
β_M	Transmission rate of maladaptations from producers to scroungers.
z_i	Proportion of time spent by a producer into generating adaptations/maladaptations.
z_s	Proportion of time spent by a scrounger scrounging adaptations/maladaptations.
c_M	Scaling factor converting maladaptations into fitness costs.
c_i	Fitness cost of being a producer instead of being a scrounger.

Figure legends

Figure 1: Time dynamics of the frequency of producers and scroungers (p_t and q_t , first panel), population size (N_t , second panel), and technology (A_t , third panel) with equal scrounging and producing time ($z_i = z_s = z$), no individual cost to producers ($c_i = 0$), and no maladaptations ($x = 0$, $\varphi_M = 0$, and $M_0 = 0$). Parameter values are $\alpha = 3$, $\eta = 0.001$, $\epsilon = 0.1$, $\mu = 1.2$, $\varphi_A = 0$, $\beta_A = 0.025$, $z = 0.05$. We introduced both producers and scroungers at low frequency in a population of innates, and the initial variable values were set to $p_0 = 0.001$, $q_0 = 0.001$, $N_0 = 2000$ (which is the carrying capacity in a population of innates, see eq. 8), $A_{i,0} = I_{A,0} = z_i\mu$, and $A_{s,0} = z_s\beta_A I_{A,0}p_0N_0$. The figure illustrates the typical time dynamics of the model: in a first time producers, p_t , invade the population of innates and then go to quasi fixation, which is followed by population size and technology reaching a steady state ($t = 650$ to $t = 1000$). In a second time scroungers, q_t , then invade the population of producers, during which population size and technology go through a transitory peak, to finally resettle at their steady state values observed before the rise of scroungers. These steady state values, $\hat{N} = 3560$ and $\hat{A} = 0.6$, are predicted by eqs. 18–19 of the text, and they describe the equilibrium population size and technology regardless of the initial frequencies of scroungers.

Figure 2: Equilibrium values \hat{p} , \hat{N} , \hat{A} graphed as functions of the fraction z_s of time that scroungers spend scrounging, while holding the fraction z_i of time producers spend producing constant. Parameter values are the same as those in Fig. 1 except that z_s varies while $z_i = 0.05$ is held constant. To gauge the effect on \hat{N} and \hat{A} of letting z_s vary, the horizontal lines in the second and third panel give the values of \hat{N} and \hat{A} for $z_i = z_s = 0.05$ (see Fig. 1). When $z_s > z_i$ the equilibrium values of both \hat{N} and \hat{A} increase, while for $z_s < z_i$ the equilibrium values of both \hat{N} and \hat{A} decrease.

Figure 3: Dynamics of p_t , q_t , N_t and A_t when scroungers spend more time scrounging than producers do producing ($z_s > z_i$). Here $z_s = 0.1$ and $z_i = 0.05$ while the other parameter values are the same as those in Fig. 1. As was the case in Fig. 1, producers first invade the population of innates, and go to quasi fixation, which is followed by population size and technology reaching a steady state. Scroungers subsequently invade the population of producers. However, after the invasion of scroungers, the equilibrium values \hat{N} and \hat{A} are now larger than they were before the invasion of scroungers. Scroungers bring an advantage to the population.

Figure 4: Equilibrium values \hat{p} , \hat{N} , \hat{A} as functions of the fitness cost c_i to producers. Other parameter values are the same as those in Fig. 1. The top curves in the second and third panels represent the situation where there are no scroungers in the population ($\hat{p} = 1$), and thus represent benchmarks against which the effect on carrying-capacity of including scroungers can be assessed. The lower curves in the second and third panels represents the situation where there are scroungers in the population, and show that in the presence of fitness costs to producers, adding scroungers decreases the values of both \hat{N} and \hat{A} . This differs qualitatively feature from the case where there is no intrinsic cost to producers (see eqs. 20–19). We mention that for the value of the cost where the frequency of producers is zero, \hat{N} is lower than in a population of innates, which stems from the fact that scroungers do no spend all their time in labor, and the population would thus be invaded by innates.

Figure 5: Dynamics of producers in the absence of scroungers ($q_0 = 0$); and N_t , A_t and M_t in the presence of maladaptations, $x = 0.1$, and cost to maladaptations, $c_M = 1$. Parameter values are $\alpha = 3$, $\eta = 0.001$, $\epsilon_A = 0.1$, $\epsilon_M = 0.01$, $\mu = 2$, $\varphi_A = 0$, $\varphi_M = 0$, $z_i = 0.05$, and $c_i = 0$, otherwise the initial values are those given in Fig. 1. Producers invade a population of innates. In so doing, they first increase the level of technology, and subsequently that of maladaptations. The dynamics of all variables then oscillate to finally settle in stable periodic cycles, which are reached regardless of the initial mixture of innates and producers in the population (no chaos was observed).

Figure 6: Dynamics of p_t , q_t , N_t , A_t and M_t in the presence of maladaptations, $x = 0.1$, and cost to maladaptations, $c_M = 1$. Parameter values are $\alpha = 3$, $\eta = 0.001$, $\epsilon_A = 0.1$, $\epsilon_M = 0.01$, $\mu = 2$, $\varphi_A = 0.1$, $\varphi_M = 0.1$, $\beta_A = 0.025$, $\beta_M = 0.02$, $z_i = z_s = 0.05$, and $c_i = 0$. The initial values are those given in Fig. 1. Besides the addition of scroungers, the only difference between the parameters values in this figure and those of Fig. 5 is the presence of density-dependence ($\varphi_A > 0$ and $\varphi_M > 0$). All dynamical variables approach a stable periodic cycle regardless of the initial mixture of innates, producers and scroungers in the population. However, removing scroungers under these parameter values would remove the stable cycling. As can be seen in the figure, the oscillations tend to dampen after the invasion of producers (from $t = 1000$ to $t = 1500$), and the population would approach a stable polymorphism in an oscillatory way if we set $q_0 = 0$ (no scroungers) for all initial mixtures of innates and producers. But scroungers tend to amplify the oscillations: after the invasion of scroungers ($t \approx 1500$), the oscillations of N_t , A_t and M_t increase and reach

a higher amplitude than those due to producers.

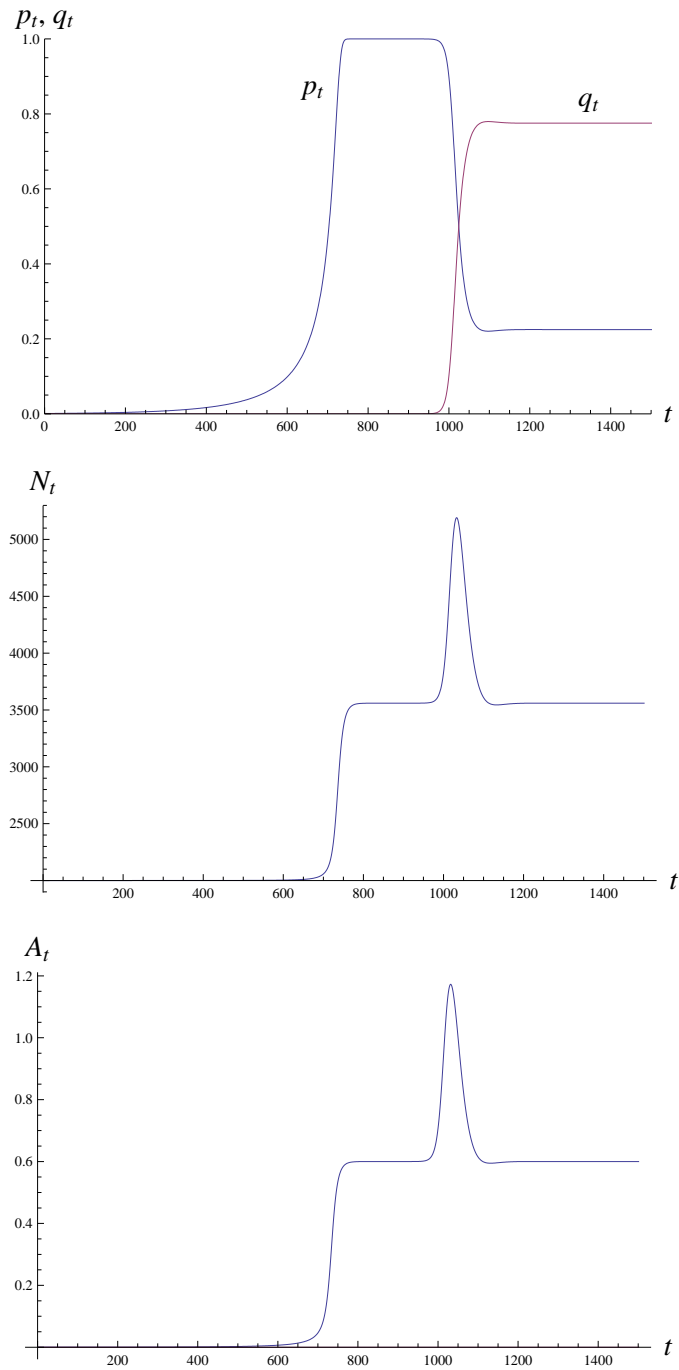


Figure 1:

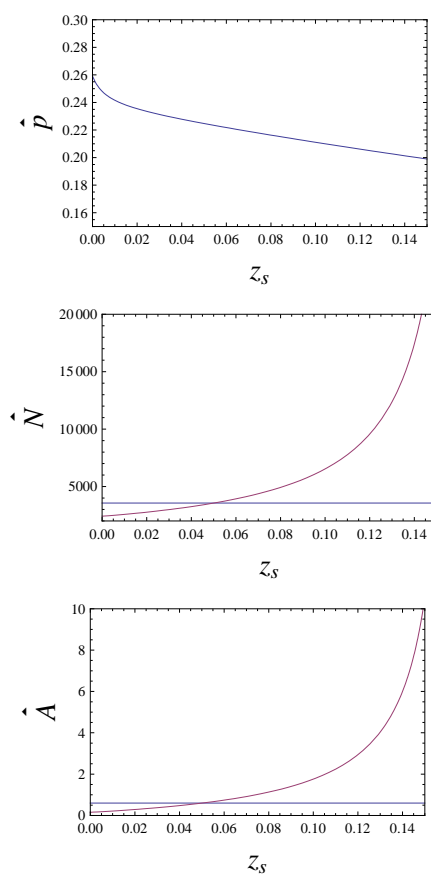


Figure 2:

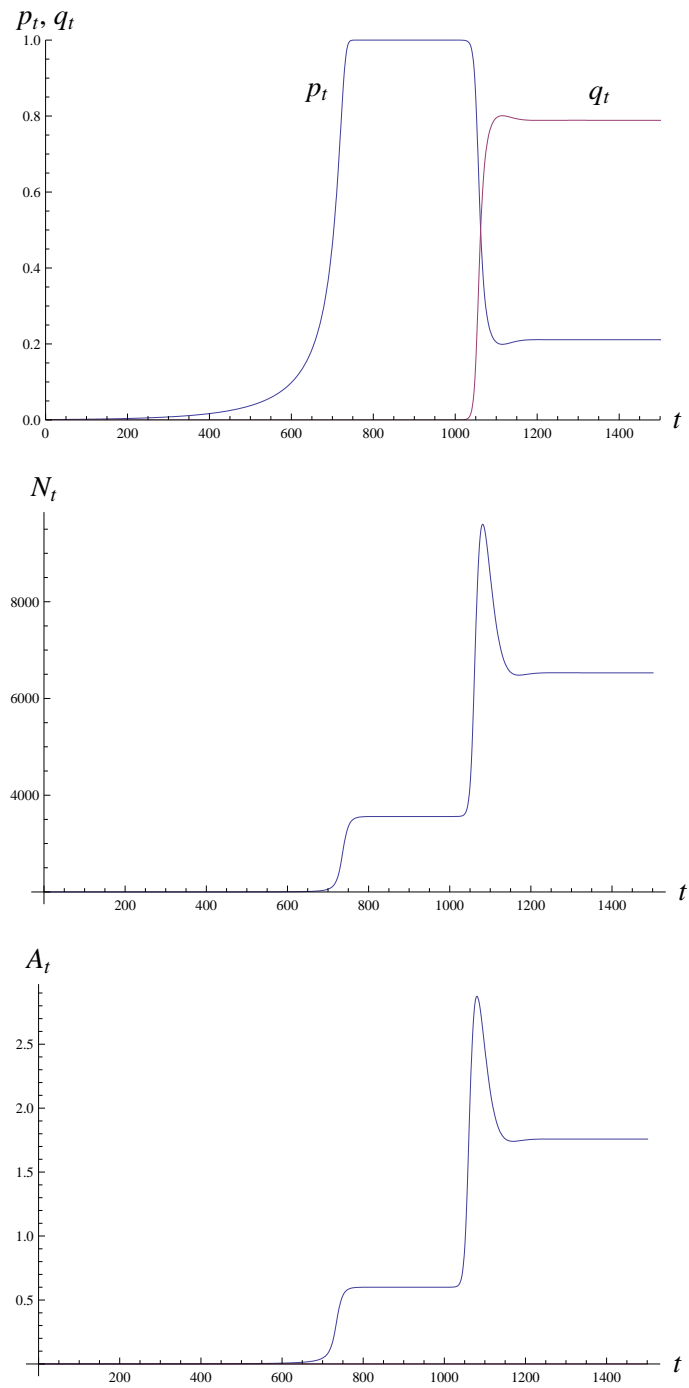


Figure 3:

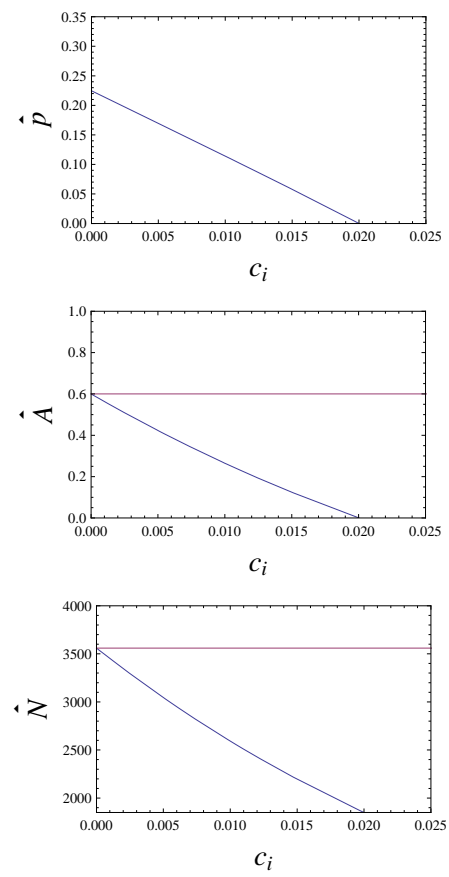


Figure 4:

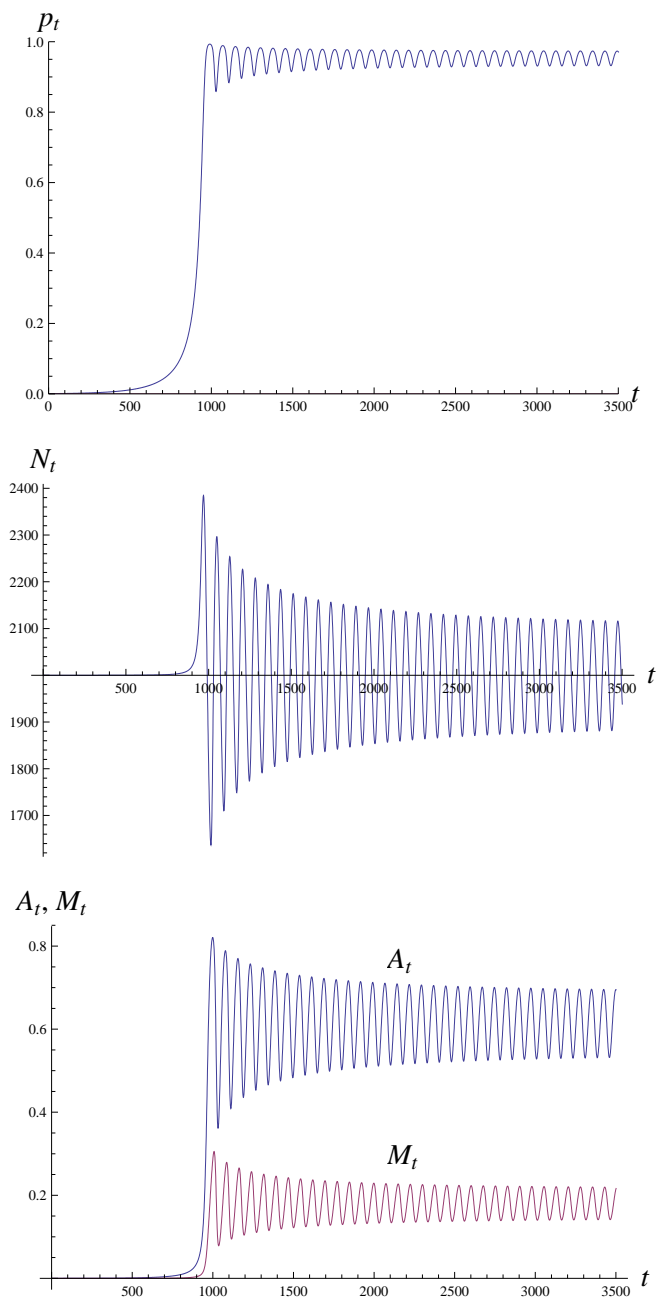


Figure 5:

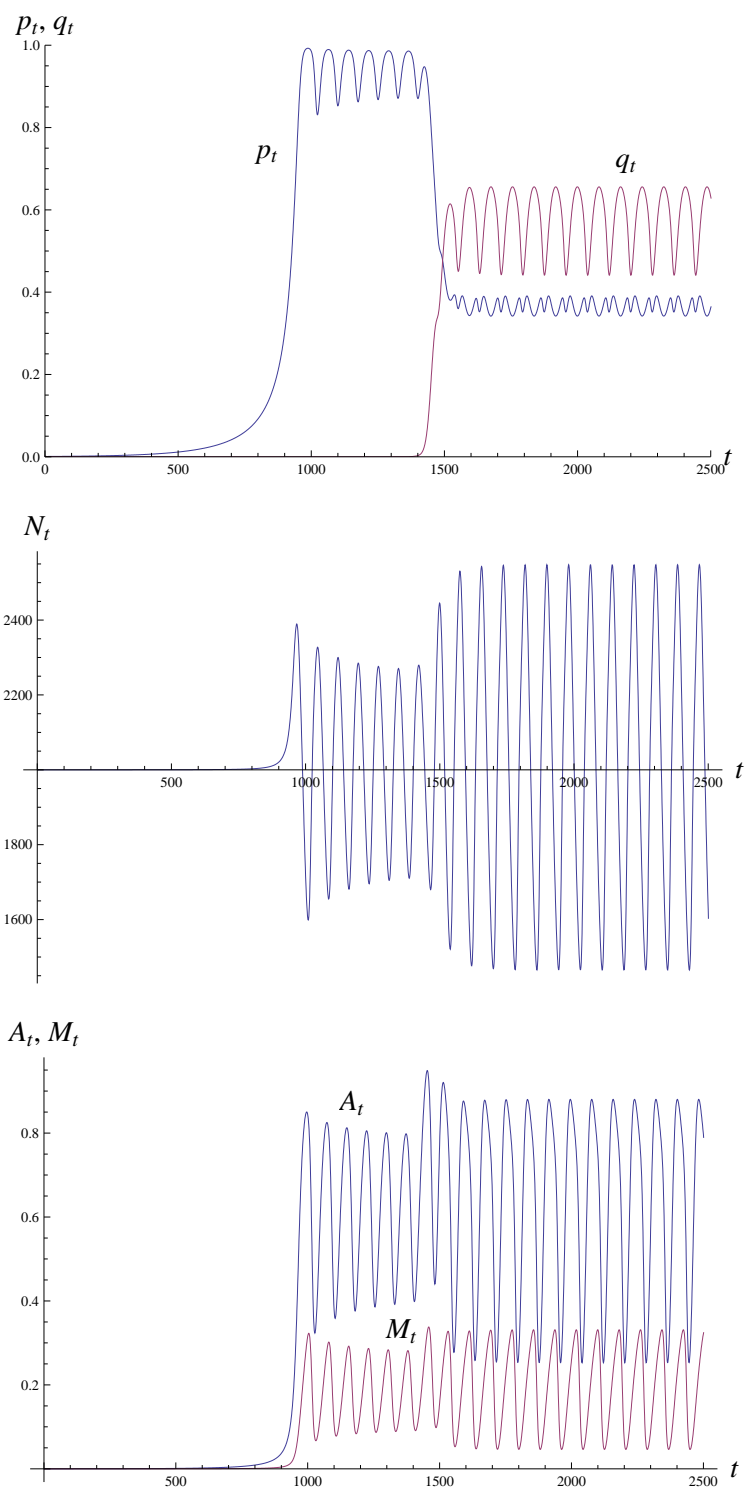


Figure 6: