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

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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 behaviours, 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 adaptations and maladaptations 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 indefinite growth or to extinction.

Keywords: producer–scrounger game; technology; adaptation; maladaptation; individual and social learning; cyclic dynamics

1. 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 and 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 & Weil 2000; Romer 2006); without technological innovations, the human population would probably have reached a stable size long ago (Kremer 1993). Technology is thus one of the defining features of the transition from Malthusian ecological stagnation to potentially continuous economic and population growth (Galor & Weil 2000; Galor & Moav 2002).

Technology can be interpreted as being a *non-rival* good: in economics, a good is considered to be non-rival if its consumption or use by one individual makes its use by anyone else no less difficult (Pindyck & 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 (unless people expand resources, consumption of natural resources tends to be a zero-sum game: the gain or loss by one individual is balanced by the losses or gains to others). Before the advent of modern societies, technology was probably also a *non-excludable* good: a good is considered to be non-excludable if its use by one individual who has not paid for it is ineluctable (Pindyck & Rubinfeld 2001). The invention of the wheel certainly took the inventor some time and effort, but later use of wheels by others would have been difficult to prevent. Goods that are both non-rival and non-excludable are called public goods (Pindyck & 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 behavioural investment of individuals of another type, the producers (Barnard & Sibly 1981; Giraldeau et al. 1994). Because scroungers might copy the technology developed by producers, the interaction between the two types can also usefully be regarded as an 'individual–social' learner interaction. Here, the individuals of one type (the social learners) copy or imitate the behaviours or artefacts that have been generated by the other type

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1

(the individual learners) through trial-and-error learning, insight or deduction (Rogers 1988; Stephens 1991; Boyd & Richerson 1995; Wakano *et al*. 2004; Enquist & 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 (Livingstone 1958; Huang & Manderson 1993). Instead of traditional earthen pits, Alaskan natives now often use plastic bags as food containers. These allow the growth of botulism bacteria, which increase the rate of death owing to botulism (Lancaster 1990). The collection of cultural practices carried by the individuals in a population, therefore, may involve both adaptive and maladaptive components (Boyd & Richerson 1985; Diamond 2005; Enquist & Ghirlanda 2007). We may thus postulate that producers of technology (individual learners) not only produce adaptive cultural traits but, as a by-product, may generate maladaptive traits, which may be copied or imitated by scroungers (social learners).

The impact of adaptive and maladaptative cultural traits on human evolution has been repeatedly stressed (Cavalli-Sforza & Feldman 1981; Lumsden & Wilson 1981; Boyd & Richerson 1985; Richerson & Boyd 2005), but its cumulative nature has virtually never been taken into account explicitly in evolutionary models of cultural transmission. Further, the feedback of cultural adaptations and maladaptations on population dynamics is also very likely to have affected human demography (Tainter 1988; Diamond 1997, 2005), but this also has rarely been analysed in an evolutionary context. There is a clear lack of quantitative theory in this area and a need to gain better understanding of how the evolutionary dynamics drive 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 & Ghirlanda 2007; Ghirlanda & Enquist 2007; Enquist *et al*. 2008). Here, we pursue this line of research but focus on micro-level, individual actions, and explore the coevolution of technological innovation, by-product maladaptation and population growth under producer–scrounger game dynamics.

2. MODEL

(a) *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) encompass such items as techniques to build arrows, a list N of poisonous foods, irrigation methods and any other knowledge involved in hunting, gathering and cultivation of resources that may increase the amount of resources available to an individual. Maladaptations, on the other hand, represent behaviours, customs or mystical beliefs that 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 express no cultural traits (neither adaptations nor 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 behaviours. 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 are scroungers (social learners), who copy or imitate the cultural traits invented by producers. The strategies of the three types of individuals—innates, producers and 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. (i) Reproduction occurs with the number of offspring produced by an individual depending on the amount of resources he/she has gathered and that they are not diverted into expressing maladaptations. (ii) 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, or by oblique transmission, with complementary probability $1 - v$. (iii) 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 also 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.

(b) *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 labour. 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 ($0 \leq \eta \leq \infty$). 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 & Sumpter 2005).

Each individual is also endowed with one baseline unit of labour, 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 labour being assumed to be given by the multiplicative form $(1 + A)(1 - z)$, where A is the stock of adaptations and $(1 - z)$ is the fraction of time spent in labour. Hence, an innate ($A = 0$ and $z = 0$) is endowed with one baseline unit of labour. We assume that effective units of land and effective units of labour combine also multiplicatively to give the total amount of resources $(1 + A)(1 - z)/(1 + \eta N)$ available to an individual. With the above assumptions, the production of resources follows the standard Cobb–Douglas model from economics with unit exponent (Cobb & Douglas 1928; Pindyck & Rubinfeld 2001; Romer 2006); with exponential components for the production function, i.e. with functional form $(1 + A)^{\gamma_1} (1 - z)^{\gamma_2}/(1 + \eta N)^{\gamma_3}$, the main qualitative results reported here do not change. The main motivation behind adopting the above simplifying assumptions is to make the model analytically tractable by using well-established functional forms.

Having specified the functional relationships that map 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, which makes it easier to develop intuitions about the dynamics of the system. Introducing multiplicative effects does not change the qualitative results reported here (electronic supplementary material).

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

$$w_{g,t} = \frac{\alpha}{1 + \eta N_t}, \qquad (2.1)$$

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

$$w_{i,t} = \alpha \left[\frac{(1 + A_{i,t})(1 - z_i)}{1 + \eta N_t} - c_M M_{i,t} - c_i \right], \qquad (2.2)$$

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 equation (A 1) in electronic supplementary material for the multiplicative version of the fitness function). The fitness of a scrounger is

$$w_{s,t} = \alpha \left[\frac{(1 + A_{s,t})(1 - z_s)}{1 + \eta N_t} - c_M M_{s,t} \right], \qquad (2.3)$$

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 equation (A 2) in the electronic supplementary material for the multiplicative version of the fitness function).

Notice that these fitness functions (equations (2.1)–(2.3)) 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 (in the absence of stocks of cultures) because producers and scroungers spend less time extracting resources. For this reason and for simplicity, we did not introduce an additional cost to scroungers (a parameter c_s, which would parallel c_i, where both can be thought of as the costs of plasticity, or of the physiological mechanisms that allow invention and imitation) as this will not change the main qualitative results reported here, although adding such a cost would make the model biologically more realistic.

With the 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

$$p_{t+1} = \frac{w_{i,t} p_t}{\bar{w}_t}, \qquad (2.4)$$

and

$$q_{t+1} = \frac{w_{s,t} q_t}{\bar{w}_t}, \qquad (2.5)$$

where

$$\bar{w}_t = (1 - p_t - q_t) w_{g,t} + p_t w_{i,t} + q_t w_{s,t} \qquad (2.6)$$

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

$$N_{t+1} = \bar{w}_t N_t. \qquad (2.7)$$

In the absence of producers and scroungers, $p_t = q_t = 0$ for all t, the population is monomorphic for innates. Then, from equations (2.1), (2.6) and (2.7), and if $\alpha > 1$ and $\eta > 0$, population size converges to the stable value (carrying capacity)

$$\hat{N} = \frac{\alpha - 1}{\eta}, \qquad (2.8)$$

where throughout the paper the caret denotes an equilibrium value.

(c) *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

$$A_t = p_t A_{i,t} + q_t A_{s,t} \qquad (2.9)$$

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 equation (2.9)). 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

$$A_{i,t} = (1 - \epsilon_A)[vA_{i,t-1} + (1 - v)A_{t-1}] + I_{A,t}, \quad (2.10)$$

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 adaptive technology from one generation to the next (for instance, because the exogenous environment changes), as an error rate in copying adaptations from the parental generation or even as a pure loss of knowledge owing 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 at time t consists of two parts. First, a scrounger living at time t acquires cultural traits from the parental generation by vertical and/or by 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

$$\begin{aligned} A_{s,t} = {} & (1 - \epsilon_A)[vA_{s,t-1} + (1 - v)A_{t-1}] \\ & + z_s \beta_A p_t N_t I_{A,t}, \end{aligned} \quad (2.11)$$

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 adaptations become more excludable, then β_A decreases and complete excludability would correspond to $\beta_A = 0$. Equation (2.11) entails that a scrounger may assimilate the adaptations of several different individuals, and implicit in the use of $p_t N_t I_{A,t}$ is the assumption that the adaptations 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

$$I_{A,t} = z_i[\mu(1 - x) + \varphi_A\{vA_{i,t-1} + (1 - v)A_{t-1}\}], \quad (2.12)$$

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 parametrization in equations (2.10) and (2.12), where the existing adaptive technology decays exogenously (at rate ϵ_A), and new technology is created *de novo* (at rate $\mu(1 - x)$ per unit investment) and from the existing adaptive technology (at rate φ_A), follows the work of Enquist & Ghirlanda (2007, equations (8) and (9)) and Enquist *et al.* (2008, equation (18)), who developed macroscopic models for the dynamics of adaptations and maladaptations aimed at fitting the empirical data. We mention that economists endorse quite similar assumptions for the dynamics of technology (e.g. Galor & Weil 2000; Romer 2006), but tend to exponentiate the existing technology, which does not alter the main qualitative results reported here.

(d) Maladaptation dynamics

Here, we present expressions for the amount of maladaptations carried by producers ($M_{i,t}$) and scroungers ($M_{s,t}$) in the population. Similar to the average stock of adaptations introduced above (equation (2.9)), we denote by

$$M_t = p_t M_{i,t} + q_t M_{s,t} \quad (2.13)$$

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 maladaptations 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

$$M_{i,t} = (1 - \epsilon_M)[vM_{i,t-1} + (1 - v)M_{t-1}] + I_{M,t}, \quad (2.14)$$

where ϵ_M is a decay rate of maladaptations, which can be interpreted as the rate of loss of maladaptations owing to errors in copying exemplar individuals or selective filtering through a higher probability of adopting adaptive rather than maladaptive cultural traits (Enquist & 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

$$\begin{aligned} M_{s,t} = {} & (1 - \epsilon_M)[vM_{s,t-1} + (1 - v)M_{t-1}] \\ & + z_s \beta_M p_t N_t I_{M,t}, \end{aligned} \quad (2.15)$$

where β_M is the transmission rate of maladaptations 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

$$I_{M,t} = z_i[\mu x + \varphi_M\{vM_{i,t-1} + (1 - v)M_{t-1}\}], \quad (2.16)$$

where φ_M is the rate of conversion of existing maladaptations into new ones. In equation (2.16), we ignore, for simplicity, the possibility that existing adaptations may generate new maladaptations (again, adding such a feature does not alter the main qualitative results reported here).

Our model tracks the nonlinear dynamical system characterized by the variables p_t, q_t, N_t, $A_{i,t}$, $A_{s,t}$, $M_{i,t}$, $M_{s,t}$ (equations (2.4), (2.5), (2.7), (2.10), (2.11), (2.14) and (2.15), respectively) 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 $\hat{p}$, $\hat{q}$, $\hat{N}$, $\hat{A}$ and $\hat{M}$. 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.

3. RESULTS

(a) *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. If we further assume that the investments 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 ($p_0 \to 0$) will invade a population of innates if $w_{i,t} > w_{g,t}$, where the fitnesses are evaluated at the demographic equilibrium of the innates (equation (2.8)). That is, producers invade 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

$$\mu > \frac{1}{1 - z}, \tag{3.1}$$

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

If the condition for invasion by producers is satisfied, it can also be shown that producers will not only spread when 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 can be maintained in the population in the long run, and it will be fixed either for innates ($\hat{p} = 0$) or for producers ($\hat{p} = 1$). In the latter event, we find from equations (2.7), (2.10) and (2.12) that the carrying capacity is given by

$$\hat{N} = \frac{1}{\eta}\left(\alpha(1 - z)(1 + \hat{A}) - 1\right), \tag{3.2}$$

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

$$\hat{A} = \frac{z\mu}{\epsilon_A - z\varphi_A}. \tag{3.3}$$

By generating $\hat{A}$, producers thus increase the carrying capacity; that is, they bring an advantage to the population (compare equation (3.2) with (2.8)). Note that the intensity of vertical transmission, v, does not appear in equations (3.2) and (3.3), 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 properties of the non-equilibrium dynamics reported below).

Equations (3.2) and (3.3) 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 Marquis de Condorcet's view that cogitation (μ and φ_A) will remove any obstacle to technological improvement and 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 & Enquist (2007).

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

$$\hat{p} = \frac{1}{z\beta_A\hat{N}}, \tag{3.4}$$

where $\hat{N}$ is given by equation (3.2). Thus, $\hat{p}$ varies inversely with the rate of transmission β_A of adaptations 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, whose presence does not perturb the equilibrium population size.

The equilibrium level of adaptive technology and population size are not affected by the presence of scroungers nor the transmission rate β_A because scroungers aggregate adaptations from several different producers in the population in a given generation (the term $\beta_A p_t N_t$ in equation (2.11)), and then pass it to the next generation. An increase in the transmission rate β_A decreases the selective pressure on producers, whose frequency then decreases in the population. But the concomitant decrease in the average stock of adaptations inherited from the parental generation will then be compensated by an increase in their aggregation by scroungers (higher β_A value). Thus, at equilibrium, the same amount of adaptations can be maintained with fewer individuals producing it. This accords with previous
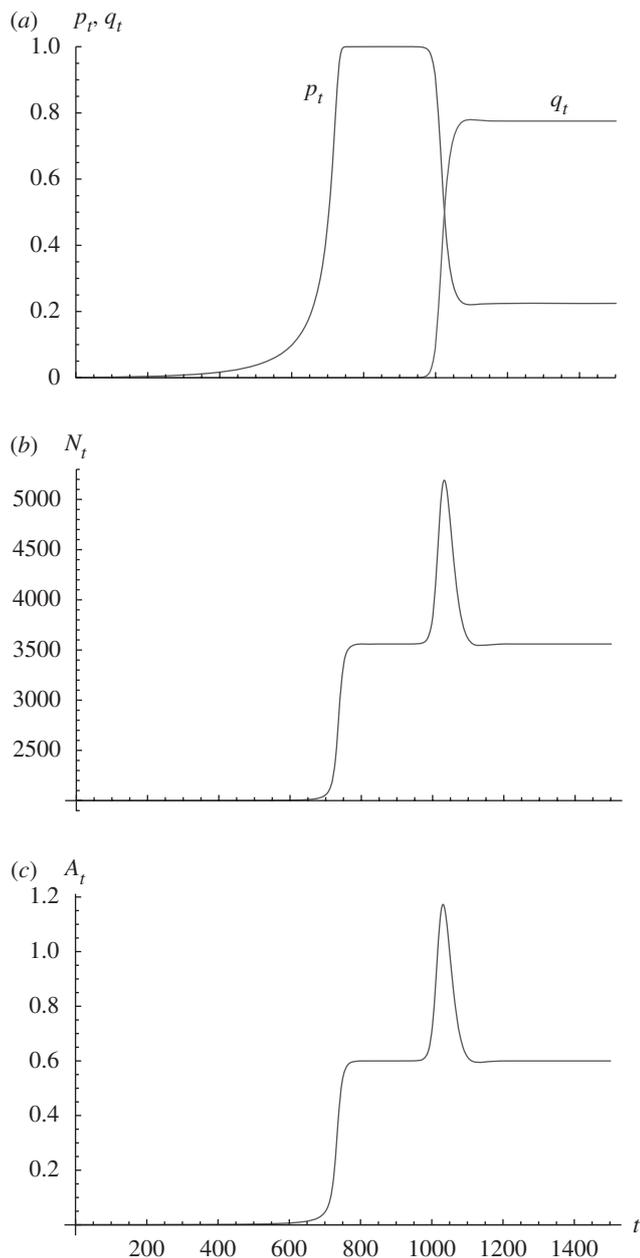
(a) p_t, q_t

(b) N_t

(c) A_t

Figure 1. Time dynamics of (*a*) the frequencies of producers and scroungers (p_t and q_t), (*b*) population size (N_t) and (*c*) average stock of adaptations (A_t), 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 $\alpha = 3$, $\eta = 0.001$, $\epsilon = 0.1$, $\mu = 1.2$, $\varphi_A = 0$, $\beta_A = 0.025$ and $z = 0.05$. 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, equation (2.8)), $A_{i,0} = I_{A,0} = z_i \mu$ and $A_{s,0} = z_s \beta_A I_{A,0} p_0 N_0$. The figure illustrates the typical time dynamics of the model: in the first period, producers, p_t, invade the population of innates and go to quasi-fixation, which is followed by population size and stock of adaptations reaching a steady state ($t = 650$ to $t = 1000$). In the second period, scroungers, q_t, then invade the population of producers, after which population size and adaptations 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 equations (3.2) and (3.3), and they describe the equilibrium population size and stock of adaptations regardless of the initial frequencies of scroungers.

studies that identified several situations where cultural transmission does not increase population fitness even if it is selected (Rogers 1988; Stephens 1991; Boyd & Richerson 1995; Wakano *et al.* 2004; Enquist & Ghirlanda 2007). In the electronic supplementary material we analyse how varying both the cost of producing and the proportion of time spent producing relative to that spent scrounging affect the equilibrium point of the dynamical system just discussed.

(b) *Adaptations with maladaptations*
We now allow maladaptations to affect the coevolutionary dynamics of producers and scroungers, and analyse the dynamics of p_t, q_t, N_t, A_t and M_t.

(i) *Analytical results*
Again we start by assuming that $z_i = z_s = z$ and $c_i = 0$, and further that $\epsilon_A = \epsilon_M = \epsilon$ (rates 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 if $w_{i,t} > w_{g,t}$ at the demographic equilibrium of the innates (equation (2.8)); 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 a 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 owing to expressing maladaptations. The gains outweigh the losses when

$$\mu > \frac{1}{(1 - z)(1 - x) - x c_M}. \qquad (3.5)$$

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

The main qualitative difference between equation (3.5) and the invasion condition without maladaptations (equation (3.1)) is the cost owing 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 equations (2.7), (2.10), (2.12), (2.14) and (2.16), fixation of producers results in the carrying capacity being given by

$$\hat{N} = \frac{1}{\eta}\left(\frac{\alpha(1 - z)(1 + \hat{A})}{1 + \alpha c_M \hat{M}} - 1\right), \qquad (3.6)$$

where

$$\hat{A} = \frac{z\mu(1 - x)}{\epsilon} \qquad (3.7)$$

and

$$\hat{M} = \frac{z\mu x}{\epsilon}. \qquad (3.8)$$

The main qualitative difference between equations (3.2), (3.3) and equations (3.6)–(3.8) is that $\hat{N}$ is now a decreasing function of the equilibrium average stock $\hat{M}$ 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

$$\hat{p} = \frac{1}{z\beta\hat{N}}, \tag{3.9}$$

where $\hat{N}$ is given by equation (3.6). Qualitatively, this is the same result as equation (3.4). Quantitatively, however, 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. Equations (3.6)–(3.9) 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 we found without maladaptation. As was the case for adaptations, this stems from the fact that scroungers aggregate adaptations and maladaptations from several different producers in the population (the terms of the form $\beta p_t N_t$ in equations (2.11) and (2.15), which are the same when $\beta_A = \beta_M = \beta$). At equilibrium, the same amount of adaptations and maladaptations can be maintained in the population with various combinations of frequencies of producers and values of β. 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 equations (A 4)–(A 6) of the electronic supplementary material).

(ii) *Numerical results*

More generally, the rates of loss of adaptations 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 (figure S4 in the electronic supplementary material). 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 (equation (2.8), if there is a stable polymorphism between innates and producers) or result in periodic cycling around this value (figure S4 in the electronic supplementary material).

There is a large range of parameter values with $\epsilon_M > \epsilon_A$ or $\varphi_M > \varphi_A$, where periodic cycling of producers, adaptations, maladaptations and population size occurs (φ_A, φ_M, ϵ_A, ϵ_M are so-called bifurcation parameters). This follows from the following considerations. Initially, producers increase adaptive technology and invade the population of innates (without enough maladaptations to prevent the initial increase in producer frequency). Then, maladaptations accumulate (for instance, if the rate of production of new maladaptations is low, but their rate of decay is not lower than that of adaptations: $\epsilon_A > \epsilon_M$), 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 maladaptations (figure S4 in the electronic supplementary material). This results in a situation where the stock of maladaptations is again too low to prevent the increase in the frequency of producers: the cycle starts again.

Introducing scroungers into a population polymorphic for innates and producers can result in coexistence between the three types, either in a stable polymorphism or in a periodic cycle (figure 2). 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 (figure 2). 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.

4. DISCUSSION

(a) *Adaptations without maladaptations*

Our results suggest that, in the absence of maladaptations, producers are likely to invade a population of innates and will then go to fixation, causing population size to increase (equation (3.2) and figure 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 (figure 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 ($c_i > 0$, equation (2.2)), adding scroungers might actually undermine population productivity and reduce equilibrium population size (figure S3 in the electronic supplementary material). 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 (figure 1), although any frequency of scroungers can be maintained at equilibrium by tuning the transmission parameter β_A (equation (3.4)). 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
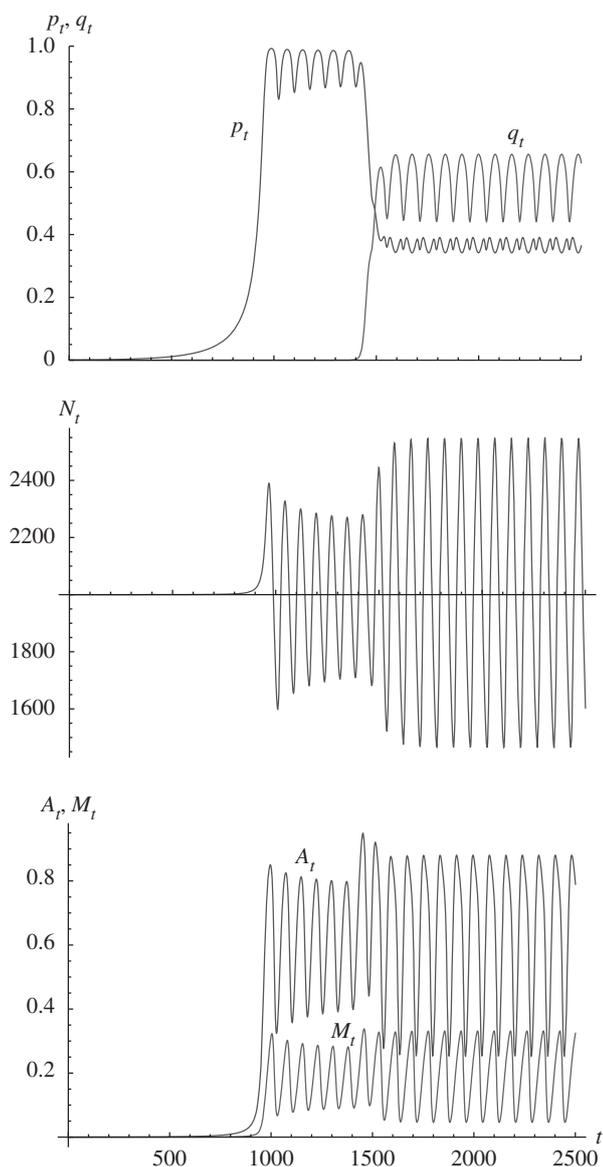
Figure 2. (*a*–*c*) Dynamics of p_t, q_t, N_t, A_t and M_t in the presence of maladaptations, $x = 0.1$, and cost to maladaptations, $c_M = 1$. Parameter values are $\alpha = 3$, $\eta = 0.001$, $\epsilon_A = 0.1$, $\epsilon_M = 0.01$, $\mu = 2$, $\varphi_A = 0.1$, $\varphi_M = 0.1$, $\beta_A = 0.025$, $\beta_M = 0.02$, $z_i = z_s = 0.05$ and $c_i = 0$. The initial values are those given in figure 1. Besides the addition of scroungers, the only difference between the parameters values in this figure and those of figure S4 in the electronic supplementary material is the presence of density dependence affecting the rates of innovations ($\varphi_A > 0$ 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 reduce the amplitude of the oscillations. 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 approaches a stable cycle if we set $q_0 = 0$ (no scroungers) for all initial mixtures of innates and producers. But scroungers tend to amplify the oscillations: after they invade ($t \approx 1500$), the oscillations of N_t, A_t and M_t increase and reach a higher amplitude than those owing to producers.

transmission brings an advantage to the population (figure S2 in the electronic supplementary material). This occurs because scroungers aggregate the adaptive technology of many different producers in the population,

thereby increasing the average level of adaptations, which is then passed on to the next generations. Scroungers can be regarded as fitness amplifiers in this case.

(b) *Adaptations with maladaptations*

Adding maladaptations (as by-products of adaptive technological innovation) markedly affects the coevolutionary 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 (figure 2). 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. In the presence of cycling, cultural innovations and transmission bring periodic advantages and disadvantages to the population, possibly placing it at risk of extinction. The presence of scroungers sometimes amplifies these oscillations, so they can be seen as fitness disrupters in these cases.

(c) *Learning and macroeconomic models*

Our formalization is related to two distinct previous modelling 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 & Richerson 1995; Wakano *et al.* 2004; Enquist & 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 behaviours) and social learners as scroungers (copying the new behaviours), 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 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 favoured 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 from economics such as those traditionally employed in macroeconomics to study economic growth (e.g. Solow 1956; Kremer 1993; Galor & Weil 2000; De La Croix & 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 way as, or in a more refined way than, we considered in our fitness functions (equations (2.2) and (2.3)). Our formalization thus provides a link between such models and those of cultural transmission. This could be further expanded by taking into account geographical and age structure, as these two features affect both the evolution of populations (e.g. Wright 1931; Charlesworth 1980; Rousset 2004) and economic growth dynamics (e.g. De La Croix & Michel 2002; Romer 2006).

(d) *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, our results suggest broader conditions for selection on individual and social learning than the constraint of fluctuating environments emphasized previously (e.g. Rogers 1988; Stephens 1991; Boyd & Richerson 1995; Wakano *et al.* 2004; Enquist *et al.* 2007). Indeed, these strategies may also evolve under a stable exogenous environment if individual learners (producers) generate a stock of adaptive cultural traits, which can be interpreted as being an endogenously determined environment. With the environment (or part of it) being an endogenous dynamical variable, the effect of social learning (scroungers) on fitness is 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) or detrimental (decrease in carrying capacity) to the population. 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 increase population size. There is a set of parameter values where this process results in infinite population size (e.g. equations (3.2) and (3.3)); that is, in a 'demo-cultural explosion' (Ghirlanda & Enquist 2007).

Second, taking the dynamics of maladaptations explicitly into account, and observing that not all aspects of culture are beneficial to population growth (Kaplan & Lancaster 1999; Richerson & Boyd 2005, chapter 5;

Enquist & Ghirlanda 2007), led us to identify feedbacks on population demography that generate cycling under a large set of parameter values. In a stochastic world, this could mean an increase in the extinction probability of the population, which might be of empirical relevance for understanding the rise and fall of populations owing to endogenous factors. As exemplified by the massive diversion of natural resources to ceremonial construction on Easter Island, which is 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 as an outcome of the evolutionary dynamics because it is selection-driven (figure 2), and is made possible by cultural maladaptations being a by-product of the production of cultural adaptations. Modelling maladaptations as a fraction of the innovations that are not adaptive (see equation (2.16); see also Enquist & Ghirlanda 2007) seems a plausible assumption; in the biological context, it is well known that most novel genetic mutations are deleterious (Eyre-Walker & Keightley 2007). This suggests that population extinction owing to the accumulation of cultural maladaptations might have been a recurrent phenomenon, not the consequence of some local contingency, unless selective filtering of cultural traits was strong (Enquist & Ghirlanda 2007). Our results thus support quantitatively the view that maladaptations may have repeatedly affected human demographic history (Tainter 1988; Diamond 2005) and suggest that, as cultural transmission and innovation became more prevalent, local extinctions may have increased.

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There are three appendixes (A1 to A3) followed by four figures (S1 to S4) in this supplement.

A.1. Numerical results for unequal producing and scrounging times and fitness costs

In the sub-section "Adaptations without maladaptations" of the "Results" section in the main text, we presented analytical results with equal investment into producing and scrounging ($z_i = z_s = z$) and no cost to individual learning ($c_i = 0$). Here, we relax these assumptions.

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. S1). 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. S1). Consequently, increased scrounging has the potential to increase the average level of adaptations and population size (Fig. S2). 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. 2.11 of the main text), 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. 2.10 and eq. 2.11 of the main text), and the rate of innovation when $I_{A,t} > 0$ (eq. 2.12). Hence, when $z_s > z_i$, scrounging increases carrying-capacity. By contrast, when $z_s < z_i$, we observe that $\hat{p}$ increases 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. S1).

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. S3), which decreases the equilibrium stock of adaptive technology, and consequently $\hat{N}$. In contrast to the case where there is no cost to producers, the equilibrium values $\hat{N}$ and $\hat{A}$ will now 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. S3). Hence, under these conditions when producers bear a fitness cost relative to scroungers, scrounging decreases the carrying-capacity.

A.2. Multiplicative effects on fitness

When fitness costs and benefits combine multiplicatively, but everything else is the same, eq. 2.2 and eq. 2.3 of the main text are replaced by

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

and

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

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. 3.6–3.9 of the main text, and that when these equalities are not satisfied, periodic cycling of the strategies and demographic variables occurs under a large set of parameters values with $\epsilon_M > \epsilon_A$ or $\varphi_M > \varphi_A$.

A.3. Producer-scrounger equilibrium for unequal transmission rates

When $\beta_M \neq \beta_T$, but everything else is the same, eqs. 3.6–3.9 are replaced by

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

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

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

and

$$\hat{p} = \frac{1}{z\hat{N}}\left(\frac{x(1+\eta\hat{N})c_M - (1-x)(1-z)}{x(1+\eta\hat{N})c_M\beta_M - (1-x)(1-z)\beta_T}\right). \tag{A-6}$$
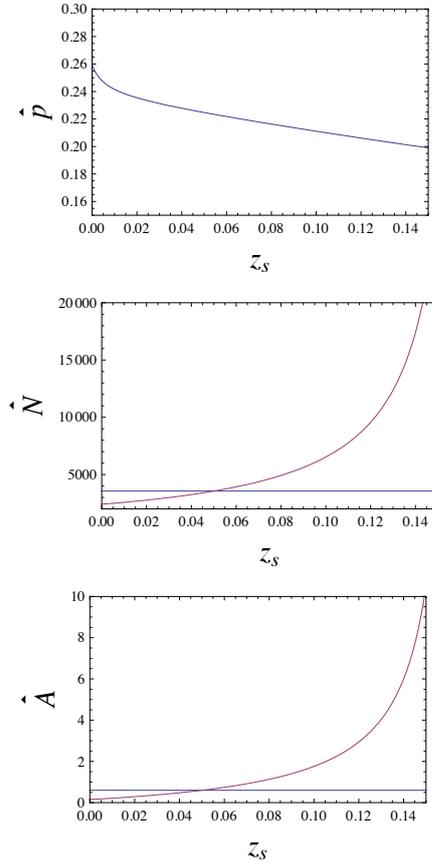
Figure S1: Equilibrium values $\hat{p}$, $\hat{N}$, $\hat{A}$ graphed as functions of the fraction z_{s} of time that scroungers spend scrounging, while holding constant the fraction z_{i} of time producers spend producing. Parameter values are the same as those in Fig. 1 of the main text except that z_{s} varies while $z_{\mathrm{i}} = 0.05$ 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 $z_{\mathrm{i}} = z_{\mathrm{s}} = 0.05$ (see Fig. 1). When $z_{\mathrm{s}} > z_{\mathrm{i}}$ the equilibrium values of both $\hat{N}$ and $\hat{A}$ increase, while for $z_{\mathrm{s}} < z_{\mathrm{i}}$ the equilibrium values of both $\hat{N}$ and $\hat{A}$ decrease.
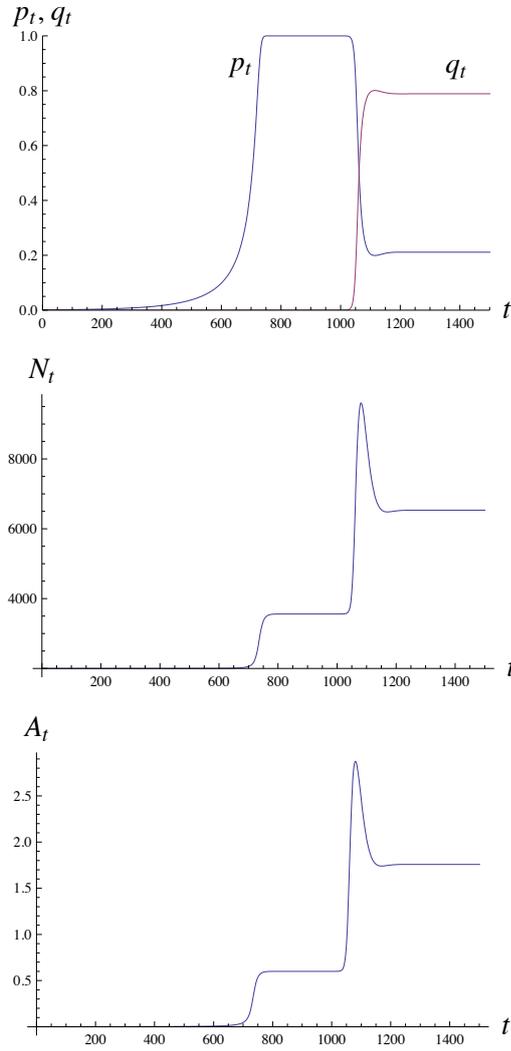
Figure S2: Dynamics of p_t, q_t, N_t and A_t when scroungers spend more time scrounging than producers do producing ($z_s > z_i$). Here $z_s = 0.1$ and $z_i = 0.05$ while the other parameter values are the same as those in Fig. 1 of the main text. As was the case in Fig. 1, producers first invade the population of innates, and go to quasi fixation, which is followed by population size and adaptive 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.
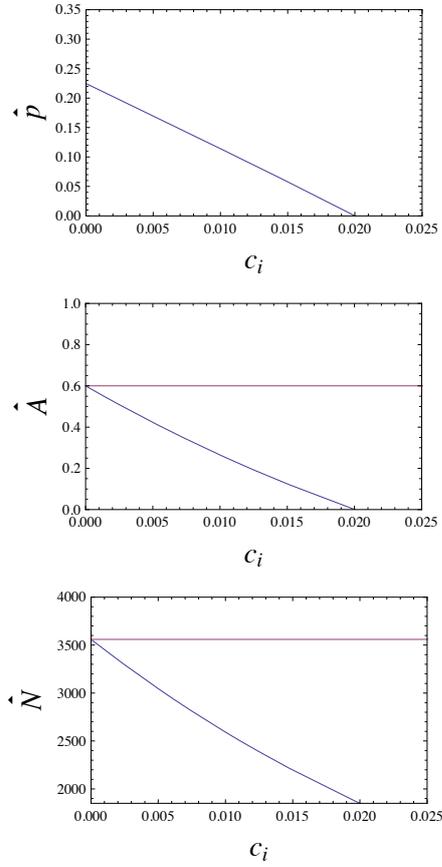
Figure S3: Equilibrium values $\hat{p}$, $\hat{N}$, $\hat{A}$ as functions of the fitness cost c_i to producers. Other parameter values are the same as those in Fig. 1 of the main text. The top curves in the second and third panels represent the situation where there are no scroungers in the population ($\hat{p} = 1$), 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 (eqs. 3.3–3.4 of the main text). 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.
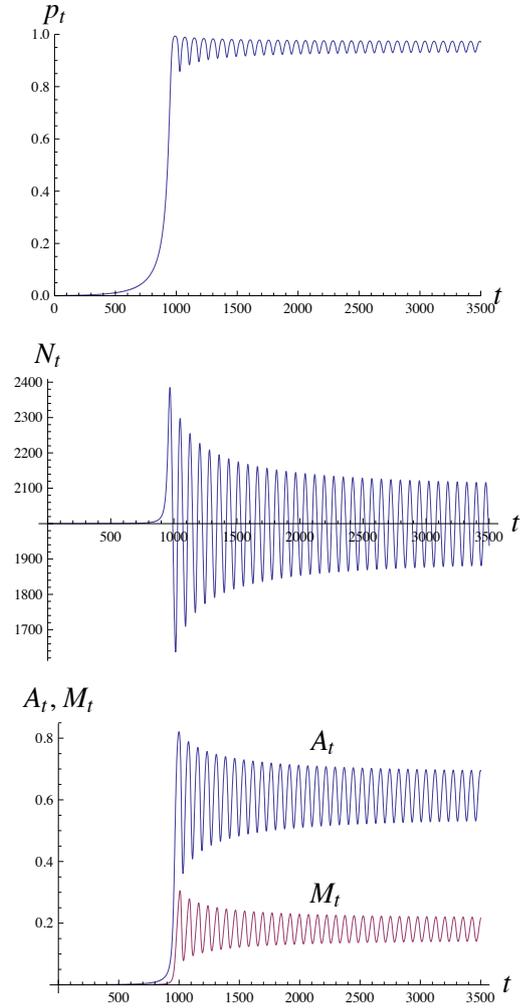
Figure S4: Dynamics of producers in the absence of scroungers ($q_0 = 0$); and N_t, A_t and M_t in the presence of maladaptations, $x = 0.1$, and cost to maladaptations, $c_M = 1$. Parameter values are $\alpha = 3$, $\eta = 0.001$, $\epsilon_A = 0.1$, $\epsilon_M = 0.01$, $\mu = 2$, $\varphi_A = 0$, $\varphi_M = 0$, $z_i = 0.05$, and $c_i = 0$, otherwise the initial values are those given in Fig. 1 of the main text. Producers invade a population of innates. In so doing, they first increase the level of adaptive 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).