Cultural evolution by capital accumulation

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This paper aims to understand the dynamics of cultural accumulation when cultural knowledge is costly to produce and costly to learn. We first show that the cost of social learning prevents any significant cultural accumulation, as individuals rapidly reach a maximum amount of knowledge that they can barely learn over the course of their lives, without being able to go any further. However, we then show that cultural knowledge can accumulate durably and even experience phases of acceleration if it improves individuals' productivity. That is, if culture is a *capital*. In this case, cultural knowledge creates wealth that can then be invested into the production of further knowledge, generating a positive feedback loop allowing significant acumulation and acceleration. These results prompt us to change the way we see cultural evolution. Instead of an accumulation of uninteded random "mutations," as in genetics, cultural evolution should rather be seen as an accumulation of assets that gradually improve productivity and allow individuals to learn, master and create an increasingly higher amount of further assets.

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In economic terms, the soma of biological organisms constitutes a *capital*, an asset that enhances the organism's ability to perform useful activities (Kaplan et al., 2000, 2003). Organisms invest in it because it allows them to better exploit the environment and ultimately to reproduce more. Biological growth is therefore a form of capital accumulation. But biological capital is often limited in its lifespan: it is *disposable* in the sense that it is not passed onto the next generation (Kirkwood, 1977). In many species and at least in all mammals, natural selection has favored a life history strategy whereby organisms build their biological capital and then let it degrade (Jones et al., 2014). Only a very small fraction of an organism's biological capital, its germ cells, survives the death of the organism and is passed on to its offspring. For all the rest, each generation must start from scratch.

But this is not the case for all forms of capital built by biological organisms. Some forms of capital are functionally independent of the biological body, and can therefore retain value after the death of the individual who produced them. That is, they are *non-disposable*. For these investments, each generation can start a little higher than the former. Hence, these investments will be referred to in this paper as "cumulative".

Investments in knowledge are the most typical forms of cumulative investments. New knowledge, not always but in many cases, remains useful long after the death of the person who produced it. But knowledge is not the only form of non-disposable capital. All the investments made in improving the quality of the environment (sometimes called niche construction; Laland et al., 2000) can be cumulative. Clearing part of a forest, building a house, opening a path, fighting infectious diseases, etc., are all cumulative investments. In this article we focus primarily on cumulative knowledge, but to understand its dynamics, we argue that it must be seen as one form, among others, of investments in non-disposable capital.

Most models of cumulative cultural evolution do not see the production of new knowledge as an investment into a capital. This is because they are based on a parallel between cultural evolution and genetic evolution (Boyd and Richerson, 1985, Cavalli-Sforza and Feldman, 1981). In genetics, the vast majority of mutations are harmful, and organisms are therefore under a directional selection pressure to reduce their mutation rate, that is not to "innovate" (except under certain extreme conditions, André and Godelle, 2006, Taddei et al., 1997). Genetic innovations are not a voluntary investment in a "genetic capital" but rather an unintended by-product of the normal activity of the DNA replication machinery. Because they are based on a parallel with genetics, the majority of models on cultural evolution therefore also consider cultural innovations as accidental by-products of individual activities.

In reality, however, cultural innovations are far from being as involuntary as genetic mutations (see Fogarty et al., 2015 for a discussion). While the precise content of discoveries can never be predicted in advance (otherwise there would be precisely no need to make a discovery), in the vast majority of cases, innovations are the result of efforts made by individuals to solve a problem (Allen, 2009, Bloom et al., 2017, Mokyr, 1992). Even the inventions that famously have a strong serendipitious component (e.g. the discovery of penicilin, microwave ovens, velcro, saccharin, superglue, etc.), are always the work of engineers, researchers, or more generally of people who pay attention to an accidental observation, and put enough effort to transform it into an actual discovery.

Similarly, because they are based on a parallel with genetics, models of cumulative cultural evolution also tend to neglect the cost of social learning. In genetics, the transmission of genes to the next generation cannot be considered an investment. The genetic information of parents is simply passed on to offspring. In the case of cultural knowledge, on the other hand, acquiring knowledge socially can hardly be considered a passive phenomenon. During their growth, humans invest in the development of their behavioral skills at the expense of other investments, resulting in particular in a delay of reproduction (Kaplan et al., 2000). In Drosophila, Mery and Kawecki (2004) experimentally showed that learning has an operating cost: drosophila placed in conditions where they must learn have a reduced egg laying rate.

Only a few models of cumulative cultural evolution explicitly consider the costs of innovation and social learning. Aoki

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et al. (2012) and Lehmann et al. (2013) focus on the evolution of individuals' investment strategies (into learning and innovating) and on the consequences of these investments on cultural dynamics. They show that the optimal investment schedule consists of starting with social learning and then innovating secondarily, which is precisely the schedule that makes cumulative culture possible. In a highly original approach, Mesoudi (2011) shows that the cost of social learning constitutes a constraint that limits the total amount of knowledge that a population is able to maintain. But, in both cases, these models do not consider the fact that individuals have other things to do in their life than invest in knowledge. That is, they do not consider the competition between investments in disposable versus non-disposable capital.

In fact, most of the models that consider knowledge as a form of capital are not in the field of cultural evolution but in the field of economics, in the so-called *endogenous growth* litterature. In Romer's classic model (Romer, 1986), the growth of knowledge is the result of individuals' decision to invest in savings rather than in consumption (that is, in non-disposable rather than disposable capital). This way of seeing knowledge is still relatively rare in the field of cultural evolution.

In this article we consider cultural knowledge as a cumulative capital voluntarily produced by individuals by paying a cost, and we take into account the fact that individuals can also invest in non-cumulative capital. The rate of cultural evolution thus eventually depends on the fraction of their investments that individuals make in cumulative versus non-cumulative capital.

To characterize these investment decisions, we assume that individuals have been shaped by natural selection to invest at all times in the form of capital that has the strongest marginal effect on their fitness. This approach, typical of the study of life history strategies (see also Lehmann et al., 2013), allows us to capture the essential mechanisms that affect individuals' investment decisions, and ultimately to describe the dynamics of cultural evolution.

We first show that culture can hardly be cumulative if it does not affect the cultural productivity of individuals. The reasons is that individuals rapidly reach the maximum amount of knowledge that they can barely learn over the course of their lives, and they cannot go any further because they have no resources left to further their knoweledge acquisiton. In other words, culture is a property of the extended phenotype of individuals and this phenotype is reached very rapidly and kept unchanged afterwards.

Second, we show that sustainable cultural accumulation, with bistable dynamics and phases of acceleration, is possible if culture is a genuine capital that affects the productivity of individuals. In this case, the cultural knowledge available to a given generation improves the ability of individuals to invest in new knowledge, eventually allowing them to go further than the previous generation.

These results are actually well explained by Dino Buzzati in his short story *The Eiffel Tower*. Buzzati imagines that, when his tower has reached the 325 metres planned by the government, Gustave Eiffel proposes to his workers to raise it higher, without limits. Workers accept and the tower grows taller and taller, but a practical problem eventually slows down its rise. To add metal beams to the top of the tower, every morning, workers have to walk up the hundreds of metres already built, and every night they have to walk down them again. Eventually, there comes a day when the tower is so high that, in their working day, workers have just enough time to climb it up and down and no time left to actually work. The tower cannot grow any higher.

Like Buzzati's workers over the course of a day, each person over the course of their life must learn, or at least take advantage, of all the cultural knowledge already available, and only then can they contribute to increasing this knowledge further. When the amount of knowledge becomes too high, the cost of acquiring it becomes so large that people simply do not have the time and resources available to create more. Like Buzzati's tower, cultural knowledge reaches a ceiling.

Things would be different, however, if the tower was not only a tower but a tool that would enable workers to be more efficient. If, for instance, workers also built an elevator, then they would have invested into a capital that would reduce (rather than increase) the cost of climbing up to the top. To accumulate significantly, knowledge must increase, not reduce the possibility of producing more knowledge, by reducing the cost of reaching the technological frontier and/or by increasing people's ability to innovate. In this case, then not only can cultural knowledge accumulate almost without limits, but its accumulation can also accelerate, rather than slow down.

This principle has two important consequences for cultural evolution. First, demography has little effect on the rate and extent of cultural accumulation. Adding more individuals to a population, all unable to innovate beyond existing knowledge, does not foster the accumulation of more knowledge. This helps understand, for instance, why the industrial revolution took place in relatively small but rich countries, rather than in the most densely populated but poorer ones (Baumard, 2018, Clark, 2008, McCloskey, 2016). Second, the respective rates of cultural evolution in different fields of knowledge all depend similarly on the time and resources that individuals have at their disposal to innovate. As a result, all these rates move in parallel, including in intellectually unrelated fields. This helps understand why independent areas of knowledge often flourish, stagnate, or regress together in the same historical periods.

Models and Results

Overview of the modelling approach. We build a microscopic model of cultural accumulation. Our objective is to describe the dynamics of the amount of knowledge – and more generally the dynamics of cumulative capital– as a macroscopic consequence of investments made by individuals during their growth. To simplify the analysis, we represent the amount of cumulative capital present in a population as a one-dimensional quantity, z. This approach is inspired by life history models in which all the dimensions of individ-

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ual growth are summarized into a single variable measuring the "amount of biological capital" of each individual (often called their body weight). This unidimensional simplification is also undertaken by several scholars in the field of cultural evolution (e.g. Enquist et al., 2008, Lehmann et al., 2013) as well as in endogenous growth models in economics (Romer, 1986).

The basic building block of our models consists in the description of the growth of individuals, from birth to death, as a succession of investments. During this growth, individuals invest in biological capital, by growing their soma. They also invest in capital outside their body, by improving their environment. And they invest in knowledge, both by acquiring knowledge already produced by others and also, potentially, by producing new knowledge themselves. We distinguish these various forms of capital according to a single property that we assume, for the sake of simplicity, binary: capital can be disposable or non-disposable (that is, cumulative). The former consist in all the investments whose value disappears upon the biological death of the individual, while the later consists in the investments that retain a value after the death of the individual.

At each age a of her life, an individual is characterized by the quantities $x(a)$ and $y(a)$ of disposable and non-disposable capital that she owns, respectively, at this age. With this capital, the individual produces a certain amount of resources that she can then decide to allocate to three possible activities. (1) First, she may invest in the growth of her disposable capital, $x(a)$. We will call this type of investment "Growth." (2) Second, she can invest in the production of new forms of non-disposable capital, $y(a)$, by producing new knowledge, or by improving the quality of her environment. We will call this type of investment "innovation" (even if it really covers a broader set of activities). (3) Third, she can invest in the growth of her cumulative capital, $y(a)$, not by producing new forms of cumulative capital by herself, but by converting the cumulative capital already produced by others into her own cumulative capital, typically by learning existing knowledge. We will call this third type of investment "learning" (even if, here too, it potentially covers a broader set of investments). Throughout the article we make the standard assumption that learning socially a certain amount of knowledge is always more efficient than producing this same knowledge from scratch.

Individuals are characterized by a production function $P(x,y)$ measuring the rate at which they produce resources, in function of their amounts of disposable and non-disposable capital, x and y. Throughout this article, as is often the case in economics, we will use the Cobb-Douglas production function

$$P(x,y) = x^{\alpha} y^{\beta} + P_0 \qquad \textbf{(1)}$$

where the parameters α and β, both strictly positive, represent so-called elasticities of production, that is the responsiveness of production to a change in either x or y. We will always consider the case where $\alpha + \beta \leq 1$, which means that total capital has diminishing returns (or at most a constant return). We will often use the variable $\kappa \equiv \frac{\beta}{\alpha} \in [0, +\infty]$, that represents the relative importance of non-disposable capital in an individual's production function. That is, κ represents the relative importance of cumulative capital (e.g. knowledge) in the "pyramid of needs" of individuals. The parameter P_0 represents essentially the resources obtained from parental care. In the course of the analyses we will often use the partial derivatives of this production function. Hence, we define $P_x(x,y) \equiv \frac{\partial P(x,y)}{\partial x}$ and $P_y(x,y) \equiv \frac{\partial P(x,y)}{\partial y}$.

We assume that individuals' allocation decisions have been shaped by natural selection so that they make "optimal" allocation decisions at each age. This hypothesis cannot be strictly valid in all circumstances, but it is useful at least as a first approximation. Standard result of optimal control theory show that the optimal allocation consists in making, at all times, the investment(s) with the greatest marginal effect on the production function (Iwasa and Roughgarden, 1984, Perrin, 1992, Perrin et al., 1993). This allows us to describe the series of investments made by an individual over the course of her life (see also Lehmann et al., 2013).

Our model is deterministic with discrete generations. We consider a Wright-Fisher population of constant size, in which all individuals are born at the same time, and grow in parallel. We assume that individuals have an exogeneously fixed time budget L for their growth, after which they stop growing and invest in reproduction.

Let us consider a population at the beginning of generation t, with an amount of cultural knowledge (or more generally an amount of cumulative capital) equal to z_t. Individuals of this generation develop by making optimal investment decisions over a period of time L. Among other things, they may learn socially the existing knowledge z_t (from the adults of the previous generation), and/or they may produce new knowledge on their own. At the end of this development, individuals reach a given level of disposable capital, $x(L)$, and a given level of knowledge, $y(L)$, which thus becomes the knowledge available for the next generation, that is $z_{t+1} = y(L)$. The objective of our model is to describe the dynamics of z_t from generation to generation.

A neutral model: when culture is not a capital. The objective of our first model is to characterize the dynamics of cultural evolution under the "null" assumption that culture does not affect the life history of individuals. That is, we assume that the growth rates of x and y do not depend on the individual's production function $P(x,y)$. The production function must therefore be seen here as a mere "target" function that individuals seek to maximize at all times. But it does not affect their growth rate. In this sense, culture cannot really be considered a capital in this first model. The growth of x and y depend only on the respective time an individual spends in each activity. Per unit of time invested in growth, the growth rate of x is γ. Per unit of time invested in learning and innovation, respectively, the growth rate of y is λ and η.

Consider a population of N individuals born with an initial level of $x = 0$ and $y = 0$, in a social environment in which they have a pre-existing amount of knowledge z. Under the

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Table 1. List of symbols used in main text

Symbol	Definition
a	Age of an individual
$x(a)$	Disposable capital of an individual of age a
$y(a)$	Cumulative capital of an individual of age a
N	Population size
z_t	Cumulative capital available in a population at the end of generation t
α	Exponent of x in the Cobb-Douglas production function
β	Exponent of y in the Cobb-Douglas production function
κ	β/α
P_0	Production independent of personal capital
$P(x,y)$	Production of an individual with capital x and y
$P_x(x,y)$	Marginal productivity of x for an individual with capital x and y
$P_y(x,y)$	Marginal productivity of y for an individual with capital x and y
$l(a)$	Fraction of resources invested in social learning at age a
$d(a)$	Fraction of resources invested in innovation at age a
γ	Rate of increase of x for each unit of resource invested in growth
λ	Rate of increase of y for each unit of resource invested in social learning
η	Rate of increase of y for each unit of resource invested in innovation
L	Total duration of development
$\tau_1(z)$	Duration of the first development phase when the available knowledge is z
$\tau_2(z)$	Duration of the second development phase when the available knowledge is z
$\tau(z)$	$\tau_1(z)+\tau_2(z)$

assumption that social learning is more efficient than innovation, the optimal allocation schedule consists in the three following phases (see Fig. 1, and Appendix A for more details).

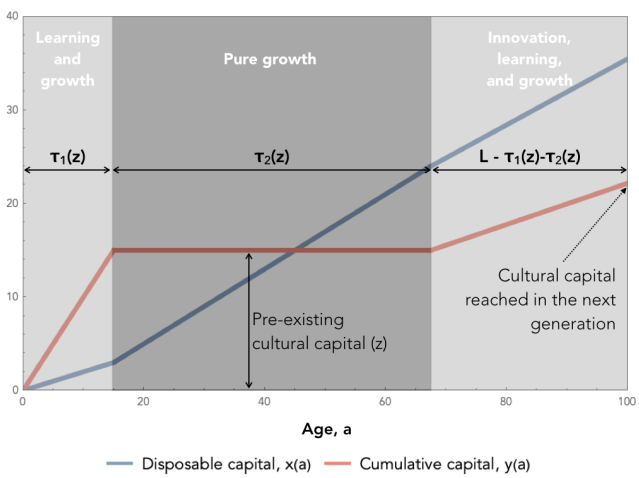

Fig. 1. Individual development in the neutral model. Variations of the two types of capital through the development of an individual when the amount of pre-existing cumulative capital is z. Here, parameters are chosen to make the figure as readable as possible: $\gamma = 0.4$, $\lambda = 2$, $\eta = 0.25$, $\alpha = 0.5$, $\beta = 0.5$, $N = 100$, $L = 100$, $z = 15$

Learning and growth toward the frontier. During the first phase of their lives, individuals invest in parallel in (i) the growth of their personal "capital" x and (ii) the learning of the available knowledge z (i.e. in the conversion of public capital z into personal capital y). The optimal allocation of time between these two activities consists in investing each unit of time where its return is the highest with respect to the target function $P(x,y)$, which implies keeping at all times the equality of returns $\lambda P_y(x,y) = \gamma P_x(x,y)$ and therefore investing exactly a fraction of the time $1/(1+\kappa)$ in growth and $\kappa/(1+\kappa)$ in learning. Consequently, during this first catch-up phase, y rises at a constant rate $\lambda\kappa/(1+\kappa)$ until all available knowledge has been learned, which takes a time

$$\tau_1(z) = \frac{z}{\lambda}\frac{\kappa+1}{\kappa} \tag{2}$$

At the end of this phase, we have $y = z$ and $x = x_1 = \frac{\gamma}{\lambda\kappa}z$.

Pure growth toward the frontier. Once z is fully socially learned, the "capital" y can potentially continue to increase if individuals invest in innovation. However, the efficiency of innovation is lower than the efficiency of social learning (i.e. $\eta < \lambda$), which implies $\eta P_y(x,y) < \lambda P_y(x,y)$. At the end of the first phase we had equal returns $\lambda P_y(x_1,z) = \gamma P_x(x_1,z)$. This implies $\eta P_y(x_1,z) < \gamma P_x(x_1,z)$. That is, at the end of Phase 1, investing in growth is necessarily more profitable than innovating. So individuals dot not start innovating right away. They first experience a phase during which they only invest in the growth of x at a constant rate γ. During this phase, the return of growth $\gamma P_x(x,y)$ decreases. Hence, it ceases when this return meets that of innovation, that is when $\gamma P_x(x,y) = \eta P_y(x,y)$, which implies $x = x_2 = \frac{\gamma}{\eta\kappa}z$, at which point individuals can start innovating (phase 3). This second catch-up phase therefore lasts for a duration

$$\tau_2(z) = \frac{\lambda-\eta}{\lambda\eta\kappa}z \tag{3}$$

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Hence, catching-up takes a total time $\tau(z) \equiv \tau_1(z) + \tau_2(z)$, which gives

$$\tau(z) = \frac{\lambda + \eta\kappa}{\lambda\eta\kappa} z \tag{4}$$

This allows us to define the average growth rate of individuals during the catch-up phase, $r_c \equiv \frac{z}{\tau(z)} = \frac{\lambda\eta\kappa}{\lambda+\eta\kappa}$.

Innovation at the frontier and cultural interference. Once the frontier is reached, individuals start investing in innovation. But they are not alone. Other individuals in the population also invest in innovation in parallel. Here we assume that individuals coordinate to share the innovation work. Each individual makes a fraction of the innovations at the frontier and learns the rest socially, since it is more efficient to learn something than to reinvent it by oneself. The difficulty then consists in calculating the speed at which a population of N individuals produces new knowledge.

To do this, let us assume that each individual invests a fraction of his time d in innovation, a fraction l in social learning, and a fraction $1-l-d$ in the growth of his personal capital x. Two conditions must be met by d and l.

1. Individuals must learn all innovations produced by others, which implies that l and d must follow the condition $\lambda l = \eta d(N-1)$.

2. Individuals must maintain the respective returns of innovation and growth equal, i.e. $\eta P_y(x,y) = \gamma P_x(x,y)$. This implies that they maintain the ratio $\frac{y}{x} = \frac{\eta}{\gamma}\kappa$. Therefore, l and d must also follow the condition $\frac{\lambda l + \eta d}{\gamma(1-d-l)} = \frac{\eta}{\gamma}\kappa$.

These two conditions can be solved. This gives us $l = \frac{\eta\kappa(N-1)}{\eta\kappa(N-1)+\lambda(\kappa+N)}$ and $d = \frac{\kappa\lambda}{\eta\kappa(N-1)+\lambda(\kappa+N)}$. The speed of cultural evolution during this third phase is therefore $r_i = \lambda l + \eta d = \eta d N$, which gives

$$r_i = \frac{\lambda\eta\kappa N}{\lambda(N+\kappa) + \eta\kappa(N-1)} \tag{5}$$

Hence population size, N, has a saturating effect on the rate of cultural evolution at the frontier. Population size has a quasi-linear effect when low, but the rate of cultural evolution asymptotically tends towards a maximum $\frac{\lambda\eta\kappa}{\lambda+\eta\kappa}$ for large population sizes. This is a consequence of the fact that individuals must spend time learning the innovations made by others, which forces them to divert resources away from their own innovations. In other words, if more heads means more ideas, it also implies more ideas to learn, and therefore less time available to create new ideas. In parallel with the notion of selective interference, which limits the speed of biological adaptation, we call this phenomenon "cultural interference."

Culture cannot be cumulative in large populations. If a population contains an amount of knowledge z_t in generation t, in the next generation it contains an amount $z_{t+1} = z_t + r_i(L - \tau(z))$, where $\tau(\cdot)$ and r_i are given by the equations 4 and 5 above, resulting in

$$z_{t+1} = \frac{\kappa(\eta\lambda L N + z_t(\lambda - \eta))}{\eta\kappa(N-1) + \lambda(\kappa+N)} \tag{6}$$

This linear recurrence equation can be solved analytically, which gives us the explicit dynamics of z over successive generations, when $z_0 = 0$

$$z_t = \frac{\lambda\eta\kappa}{\lambda+\eta\kappa} L \left(1 - \left(1 + \frac{\lambda+\eta\kappa}{\kappa(\lambda-\eta)} N\right)^{-t}\right) \tag{7}$$

This equation shows us two things.

(1) The level of knowledge contained in a population converges towards an equilibrium, a cultural "carrying capacity" independent of population size and given by

$$z_{\text{conv}} = \frac{\lambda\eta\kappa}{\lambda+\eta\kappa} L \tag{8}$$

In addition to the total time budget available (L), this equilibrium depends on two limiting factors: the learning rate λ and the effective innovation rate $\eta\kappa$ which depends both on the efficiency of investments into innovation (η) and on the relative importance of knowledge in the pyramid of needs of individuals (κ). Even if the cost of social learning is not limiting (for example because λ is very large), the equilibrium amout of culture in a population is still limited by the fact that people "waste" time investing in disposable capital. Every investment in (i) learning existing knowledge and (ii) growing disposable capital constitutes a loss for culture, as it must be re-made from scratch every generation.

(2) The rate of convergence towards equilibrium increases with population size (see Fig. 2). In fact, when population size is very large (that is, when $N \gg 1$), convergence towards the cultural equilibrium is almost instantaneous. The population reaches its cultural carrying capacity in almost a single generation, regardless of its starting point. This can also be observed from equation 6. When $N \gg 1$, this equation simply becomes $z_{t+1} \approx z_{\text{conv}}$. The level of knowledge in generation $t+1$ is approximately independent of the level of knowledge in generation t. That is, culture does not accumulate.

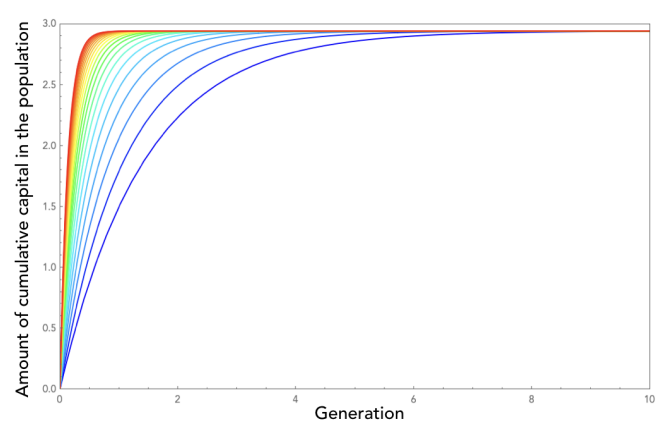

Fig. 2. Cultural dynamics in the neutral model. Dynamics of cumulative capital through generations, plotted for 20 different values of population size ranging from $N = 1$ (blue curve) to $N = 2200$ (red curve). Other parameters are as follows: $\gamma = 1$, $\lambda = 5$, $\eta = 0.1$, $P_0 = 0.1$, $\alpha = 0.45$, $\beta = 0.45$, $L = 30$.

This phenomenon can be intuitively understood by observing that, when $N \gg 1$, the rate of cultural evolution during the innovation phase is approximately equal to the mean rate

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of evolution during the catch-up phases ($r_i \approx r_c$; eq. 5). In a large population, the vast majority of knowledge acquired by an individual is acquired through social learning and not through innovation. Thanks to the division of the innovation labor, each individual needs to produce only a very small part of the knowledge by himself. It is therefore almost the same for an individual to grow up in a population in which there is already a quantity of information z produced by previous generations (and where the rate of cultural growth is therefore r_c), as to grow up in a large population that produces this information on the fly by innovation (and where the rate of cultural growth is therefore $r_i \approx r_c$). In contrast, in a small population, cultural evolution is significantly slower at the frontier than during catch-up because the cost of innovation is limiting.

This result is a consequence of the fact that social learning is an expensive activity in our model. Mesoudi (2011) already showed in simulations that the cost of social learning imposes a limit on the maximum amount of cultural knowledge that can be sustained in a population. However, our analytical model allows going further and demonstrating that culture is hardly cumulative at all in large populations.

Culture can be cumulative accelerating and bistable if it is a capital. Equation 6 shows that, in a large population, when knowledge has no effect on the life history individuals, the amount of knowledge z_{t+1} reached in generation $t+1$ does not depend on the amount of knowledge z_t present in the previous generation. The knowledge that a population is able to produce merely depends on the life history parameters of individuals and is achieved in a single generation.

But this same equation allows one to understand by which mechanisms the result could be different. If the life history of individuals in generation t (η, κ, λ and L in equation 6) depend, in one way or another, on the amount of knowledge z_t present in that generation, then z_t can indirectly affect z_{t+1}. This may happen, for example, if knowledge makes (i) individuals' life expectancy longer, (ii) their learning more efficient, (iii) their pyramid of needs more culture-oriented, or (iv) their investments in innovation more profitable. To characterize more precisely the mechanisms by which these effects are possible, it is necessary to consider explicitly how knowledge, and more generally how the two forms of capital (x and y) affect the life history parameters of individuals.

To this aim, we have built a second model, similar to the neutral model, but in which the productivity of individuals depends on their capital. As in the first model, individuals develop by accumulating two types of capital, x and y, and they are characterized at each moment of their lives by a production function given by equation 1. But here, unlike in the neutral model, this production is invested in the growth of x and y. If an individual of age a has amounts of capital $x(a)$ and $y(a)$, respectively, and invests a fraction $d(a)$ of his production in innovation, a fraction $l(a)$ in learning, and a fraction $1-d(a)-l(a)$ in growth, $x(a)$ and $y(a)$ experience instantaneous increases:

$$\frac{dx(a)}{da} = \gamma\,(1-d(a)-l(a)) \cdot P(x(a),y(a)) \qquad \textbf{(9)}$$

$$\frac{dy(a)}{da} = (\eta d(a) + \lambda l(a))) \cdot P(x(a),y(a)) \qquad \textbf{(10)}$$

Optimal growth schedule. As in the neutral model, we assume that individuals have a time L to develop (after which they reproduce) and we assume that they allocate their production optimally at all times to growth, learning and innovation, which implies that they always make the investment(s) that have the greatest marginal effect on production (see Appendix A.2). This optimal allocation consists of three phases, as in the neutral model. The only difference with the neutral model is that, here, the growth of individuals is not linear. This growth cannot be expressed analytically, hence we simulate it numerically (see Appendix A.2). As in the neutral model, but numerically here, we derive the level of knowledge reached by a population of N individuals at generation $t+1$ as a function of the level of knowledge at generation t.

Knowledge can accumulate. Unlike in the neutral case, knowledge (or more generally cumulative capital) can accumulate here from generation to generation (see Fig. 3). This occurs because knowledge allows individuals to be more efficient in the production of new knowledge. In result, knowledge first accumulates in an accelerating way. However, the time it takes to learn the existing knowledge keeps on increasing as knowledge accumulates. At some point therefore, individuals do not have enough time left to innovate. In result, the production of new knoweldge eventually decelerates, until knowledge finally reaches an equilibrium.

This model also allows us to explore more subtle effects of culture on individuals' life histories. In the following, we explore three biologically plausible effects and show that they often lead to bi-stable cultural dynamics and abrupt acceleration phases.

Investments in knowledge increase along the pyramid of needs. It is reasonable to assume that the most basic needs of individuals are purely personal and not cumulative. Individuals at the beginning of their growth invest mainly in their biological capital, that will be lost upon their death. It is only when they become richer, moving upward on their pyramid of needs, that they can begin to invest in forms of capital that are further away from biology, improving their environment at a larger scale, or investing in knowledge (see Baumard, 2018 for a review). Here, we capture this effect by assuming that the ratio κ is low when the amount of disposable capital, x, owned by an individual is below a threshold $\hat{x}$ and increases to a higher value when $x > \hat{x}$. Only sufficiently wealthy individuals in terms of personal capital can afford spending a large fraction of their resources into knowledge.

The consequences of this effect on cultural dynamics are shown in Figure 4. For reasonnable parameter values, culture can be bi-stable. On the one hand, a population starting initially without any cultural knowledge accumulates little culture and eventually remains stuck in a "poverty trap" (Azariadis and Stachurski, 2005), at a very low level of knowledge.

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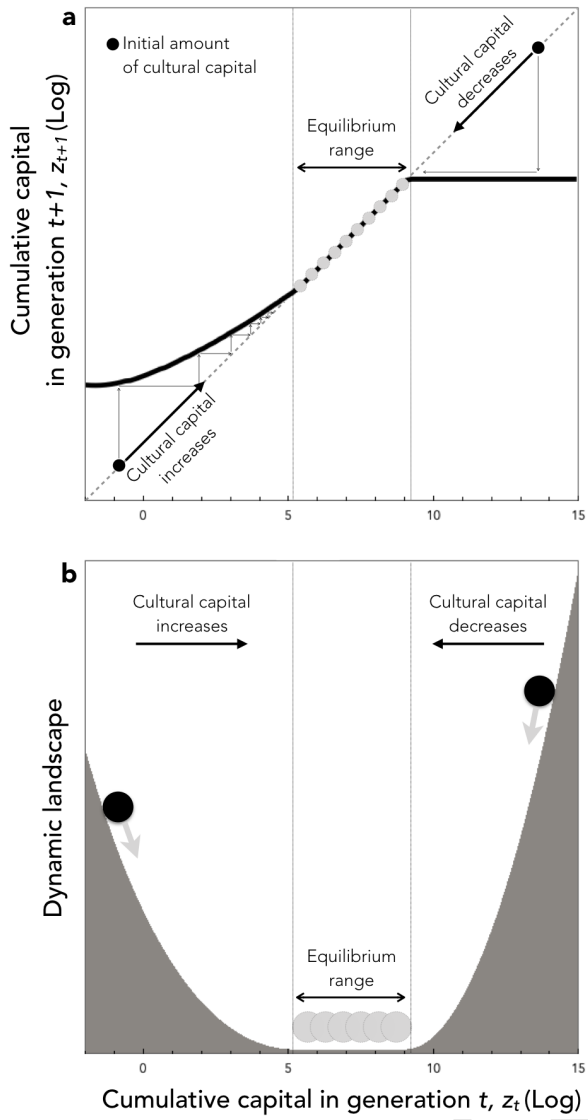

Fig. 3. Cultural dynamics in the non-neutral model. (a) Amount of cultural capital in generation $t+1$ plotted in function of cultural capital in generation t. This allows to trace the dynamics of culture and to find equilibria. (b) Landscape showing the dynamics of cultural capital. The steepness of the landscape in each point z_t is proportional to the change of cultural capital in one generation when starting from z_t. Parameters are as in figure 2, with population size $N = 1000$ and the time-step used in numerical simulations $\delta = 0.01$.

On the other hand, if the amount of cultural knowledge exceeds a threshold, for stochastic reasons for example or because of a change in the environment, then individuals reach a state where they can afford to invest a larger fraction of their resources in knowledge. They then manage to capitalize from generation to generation, which allows them to reach eventually a much higher level of cultural knowledge.

Parental care and age at first reproduction increase with the amount of cultural knowledge. The development of individuals depends, among other things, on two essential factors: the time during which they grow (that is, their age at maturity) and the amount of parental care they receive. Age at maturity is a life history decision of the offspring (Charnov, 1991, Stearns, 1977). Parental care is a life history decision of the parents who can choose either to produce a large number of offspring with few resources for everyone, or a small number of offspring with a lot of resources for each.

Empirical observations show that these two aspects of life history are plastic in humans, and depend in particular on the level of wealth of individuals (Nettle, 2010, Roser, 2017). For instance, in the case of parental care, during their economic development, human societies make a relatively abrupt transition, the demographic transition, from a strategy with many children, each with relatively little investment, to a strategy with a high investment per child (Blanc and Wacziarg, 2019, Cummins, 2013). And a similar phenomenon occurs regarding the age at first reproduction. Economic develoment and wealth leads people, on average, to delay their reproduction and invest longer in their studies while, conversely, poverty leads women to choose to reproduce early (Roser, 2017).

We have introduced these two types of plasticity into our model. Formally, the age at sexual maturity is captured by the parameter L, and parental care is captured by our parameter P_0 measuring the productiviy of individuals that is independent of their own capital. In both cases, for simplicity, we assume that they increase with the wealth of the parental generation, that is L and/or P_0 in generation $t+1$ increase with the amount of knowledge z_t available in the previous generation. Here we show results in the case where only L is plastic. We assume that $L(\cdot)$ is a sigmoid function, with a sudden change in strategy when z_t exceeds a threshold. This assumption leads, again, to bi-stable dynamics, with a sudden acceleration of cultural evolution when individuals' life history strategy changes (Fig. 5).

We also included the possibility that the change of life history involved in the demographic transition may be accompanied by a reduction of population size. In reality, it has only been accompanied by a slowdown in population growth (not by a reduction of population size). But the important point is that there is indeed a trade-off between population size and parental care (or duration of growth) per child. Since population size has a small effect on the dynamics of cultural accumulation, however, this effect did not counteract the positive effect of life history (not shown). Cultural accumulation is much more intense in a small population where each individual has a lot of parental care and a long growth than in a large population where each individual has little care and little time to grow.

Division of cognitive labor and the effective cost of learning. The efficiency of social learning itself can increase with the amount of cultural information available if, on average, the greater the amount of information produced in the past, the faster each unit of information is learned. This hypothesis is followed implicitly in many papers that assume the rate of social learning to be *proportional* to the amount of knowledge available (e.g. Aoki et al., 2012, Lehmann et al., 2013). This is a very strong assumption that has no reason to be true in general. However, it is conceivable that sometimes it may be true, particularly if new cultural knowledge partially replaces old ones. Arabic numerals, for example, have replaced Roman numerals, and they are more useful but not more expen-

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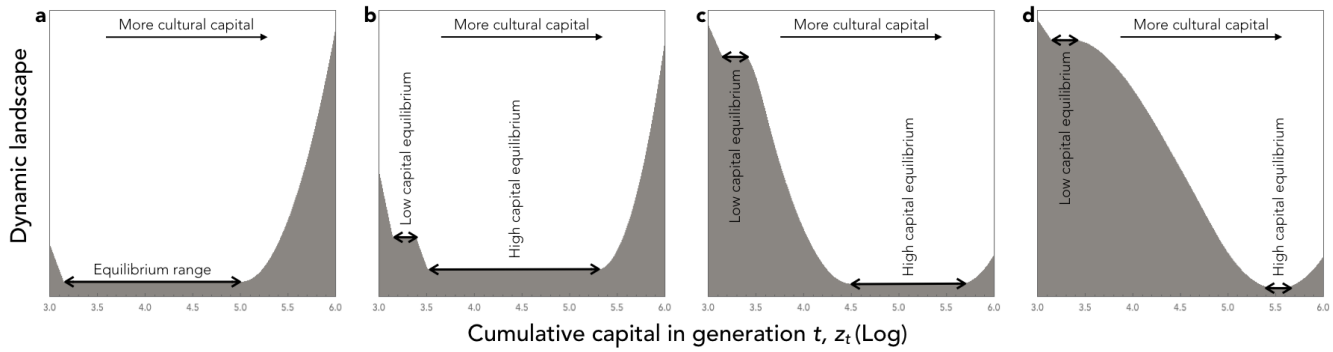

Fig. 4. Cultural dynamics when investments in knowledge increase along the pyramid of needs Parameters are as in figure 3, but with $\alpha = (1-c)\zeta$ and $\beta = c\zeta$, where $\zeta = 0.9$, and c is a hard threshold function of x: $c = c_{\text{low}}$ for $x \leq \hat{x}$, and $c = c_{\text{high}}$ for $x > \hat{x}$, with $\hat{x} = 3 \cdot 10^5$, $c_{\text{low}} = 0.05$, and $c_{\text{high}} = 0.05$ (**a**), $c_{\text{high}} = 0.1$ (**b**), $c_{\text{high}} = 0.5$ (**c**), or $c_{\text{high}} = 1$ (**d**)

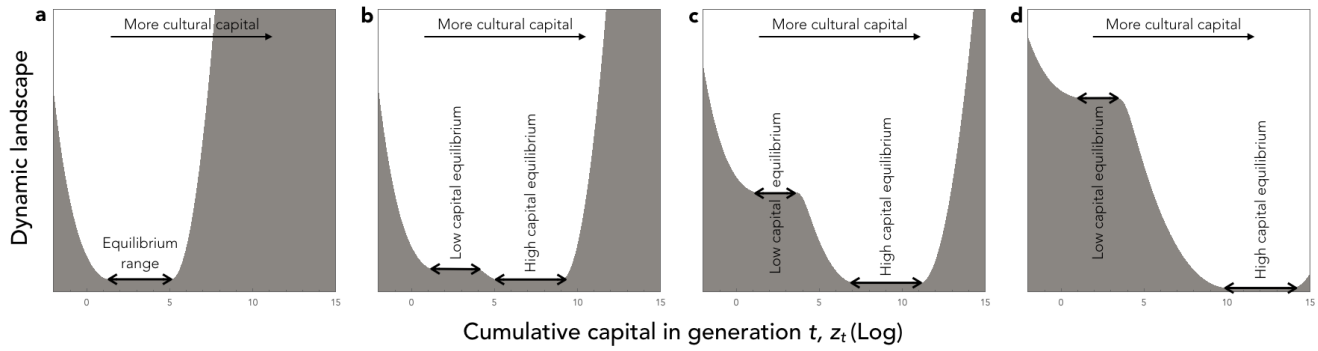

Fig. 5. Cultural dynamics when the age at maturity increases with cultural capital. Parameters are as in figure 3, but with the time available for growth, L, varying as a function of z according to a sigmoid function: $L(z) = L_{\text{low}} + (L_{\text{high}} - L_{\text{low}})z^2/(\hat{z}^2 + z^2)$, with $\hat{z} = 10^4$, $L_{\text{low}} = 10$, and $L_{\text{high}} = 10$ (**a**), $L_{\text{high}} = 30$ (**b**), $L_{\text{high}} = 50$ (**c**), or $L_{\text{high}} = 100$ (**d**).

sive to learn. The efficiency of social learning has therefore increased after the invention of Arabic numerals. More generally, people do not need to learn the whole history of science and technology, but simply to learn the latest state of the art. Thus the energy required to learn existing knowledge does not increase linearly with the energy required to produce it. In our model, this means that the return on investment of social learning, λ, could increase with z.

However, in fact, knowledge has a stronger and more general effect on the cost of learning through another mechanism. In practice, in any developed society with a large number of technologies, we acquire the benefits of the vast majority of cultural knowledge without having to learn it. For example, we benefit from our societies' technical knowledge on internal combustion engines without having to learn anything, or almost anything, about the functionning, let alone the making, of these engines. Only a very small fraction of people in our societies invest in the acquisition of this knowledge. All the others obtain the benefits of internal combustion engines by exchanging with these specialists.

Thus, the true cost of "learning" a technique is not really the cost of learning it but rather the cost of acquiring the benefits of that technique via an exchange with others. This cost is lower because only one individual pays the cost of learning and then passes it on to all its customers. Standard models of cultural evolution take into account the existence of a division of labour of *innovation*, which constitutes the major benefit of culture in these models. But to capture the full benefits of culture, we must also take into account another division of labour: the division of labour of *social learning*.

This principle has an essential consequence. As technological progress creates economies of scale, it paradoxically reduces the effective cost of learning (that is, the cost of acquiring technical goods). The higher the level of technical knowledge in a society about food production, for example, the more a small number of producers can supply a large number of consumers at low prices. Thus, even if the cost of learning to become a farmer increases with the amount of technical knowledge (it requires longer and longer studies), the price of food can actually *decrease*, because this cost is passed on to a larger and larger number of consumers.

In Appendix B, we formalize this principle with an approach inspired by micro-economic models of markets. The result of this analysis is illustrated in Figure 6. In a large population, we observe once again bi-stable dynamics, with a poverty trap at low technical level (and low division of labour) and a sudden acceleration beyond a threshold, towards a new equilibrium at high technical level (and high division of labor). Besides, we also observe an indirect effect of population size as it constitutes an upper limit on the division of labour (Fig. 6).

Discussion

In this article we have considered cultural knowledge as a capital in which individuals invest at a cost. To this end, following other models of cultural evolution, we have explicitly

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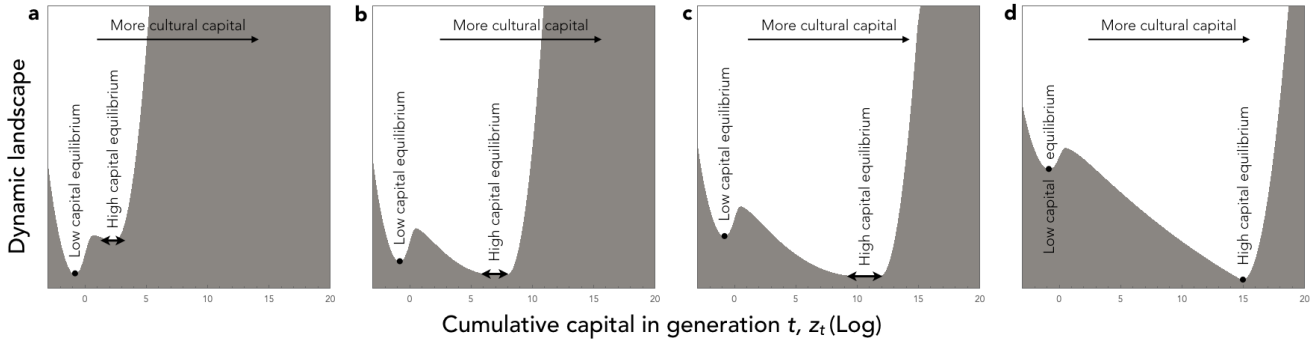

Fig. 6. Cultural dynamics with division of labor. Parameters are as in figure 3, but with $\alpha = \beta = 0.5$, and the division of labor model described in Appendix B with $\lambda_{\min=0.01}$, $\phi = z$, $u = 1$, and the exponent of the production cost varying in function of z according to eq. 38 with $a_{\text{high}} = 2$, $a_{\text{low}} = 1$, and $\sigma = 10$, and with population size $N = 10$ (**a**), $N = 50$ (**b**), $N = 100$ (**c**), or $N = 1000$ (**d**).

considered the investments made by individuals in culture as life history decisions. Our objective was to understand what then determines the dynamics of cultural accumulation.

We have shown that, if culture does not affect the life history of individuals then it cannot accumulate, or only very slightly. Culture can accumulate substantially only if it changes the life history of individuals by making their lives more efficient, because the knowledge available to a given generation improves the ability of the individuals of that generation to invest in new knowledge, generating a positive feedback loop.

We have explored several ways in which this positive feedback can occur. We have shown that it can occur if cultural knowledge merely increases people's productivity, allowing them more time to learn and/or innovate (Figs. 3 and 4). We have shown that the positive feedback is even stronger if cultural knowledge, and thus the wealth that results from increased productivity, leads individuals to modify their life history decisions through phenotypic plasticity, either by delaying their sexual maturity or by producing fewer offspring but investing more in each (Fig. 5). And finally, we have shown that the feedback is also enhanced if technical knowledge reduce the effective cost of their own acquisition via division of labour (Fig. 6). In general, the key point is that culture accumulates, and can experience phases of acceleration, if it increases the *cultural* productivity of individuals, either by increasing their *overall* productivity, or by increasing the *fraction* of their production that they allocate to knowledge.

These results have important consequences regarding our understanding of the dynamics of culture. Cultural evolution has periods of stagnations where the amount of knowledge is constant, periods of bursts where the amount of knowledge increases rapidly (see e.g. Enquist et al., 2008, Kolodny et al., 2015 and references therein), and also periods of decline, where the amount of knowledge decreases (Aiyar et al., 2008). So far, these dynamics have been explained in two ways: demography and interdependent discoveries.

(1) The demographic explanation is based on the combination of two mutually reinforcing effects (Aoki, 2015, Henrich, 2004). (i) If there is more knowledge in a population, then individuals are more productive, which increases the carrying capacity of the environment and leads to a denser population (Malthusian effect). (ii) This increased population density, in turn, allows individuals to produce more new knowledge because "more heads means more ideas" (Boseruptian effect). The combination of these two effects leads to a positive feedback loop that can cause an acceleration of cultural accumulation, concomitant with a population densification. Conversely, phases of cultural decline are caused by the two opposing effects, also reinforcing each other.

(2) The "interdependent discoveries" explanation, on the other hand, assumes that the phases of cultural acceleration are caused by key discoveries (e.g. calculus) that then facilitate the realization of a large number of lesser discoveries (Kolodny et al., 2015, 2016). Cultural evolution thus takes place in a punctuated manner, with phases of stagnations, and sudden bursts when a key discovery arises. In principle, the same effect can also explain cultural regressions. If some key knowledge is lost leading to the disappearance of a large number of more applied knowledge.

Both of these explanations have problems, however.

(1) The demographic explanation makes inadequate predictions regarding the times and places where cultural evolution should be the fastest. Historical observations (Allen, 2009, Clark, 2008) show that small populations (e.g. the UK) often created more innovations than larger ones (e.g. medieval China). Besides, in a given country, periods of cultural acceleration do not coincide with significant demographic rises (see for instance China during the 19th century). Demographic rises are mostly slow and minor, whereas cultural bursts are fast.

(2) The "interdependent discoveries" explanation predicts that cultural accelerations, or decline, should be domain-specific. For instance, knowledge in physics should accumulate fast after the dicovery of calculus but this should have no impact on biology or paintings. However, observations show that, on the contrary, the historical periods and areas of the world that were flourishing were flourishing in all domains, or in a large number of domains at the same time, including in completely unrelated areas (physics, biology, gastronomy, paintings, music, etc.). Classical Greece, Abbasid Irak, Song China or Renaissance Italy naturally come to mind.

Several scholars have already put forward the general im-

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portance of creativity in determining the pace of cultural evolution (Fogarty et al., 2015, and see also Kobayashi and Aoki, 2012), and others have even suggested that cultural acceleration could result from the fact that, for a reason or another, cultural knowledge itself increases either creativity (Enquist et al., 2008, Mesoudi, 2011) or the efficiency of social learning (Mesoudi, 2011). But these scholars did not propose a specific reason why this last effect should occur. In this paper, we propose a straightforward explanation of this effect. We propose that cultural knowledge simply creates wealth, and that wealth incites individuals to invest more into knowledge, generating a positive feedback. We show that this simple mechanism explains that the rate of cultural evolution (i) is largely independently of demography, and (ii) changes through historical time in independent areas of knowledge in parallel.

Our article has, however, a number of methodological limitations that are worth noting. The first concerns the extent of phenotypic plasticity. We have assumed that individuals are always optimal in their decisions about resource allocation. This implies that they are endowed with *perfect* phenotypic plasticity. In reality, especially in environments that have been profoundly modified by culture, individuals probably make mistakes in their allocation decisions, under-investing for example in innovations (or the other way around) and it would be important to characterize these mistakes and take them into account in further models.

Second, and most importantly, our model is deterministic. We do not consider the stochastic aspects of cultural evolution. This limitation has three dimensions. First, we consider innovations and learning as deterministic growth processes when in reality they have a stochastic component. Second, we consider a mean-field model in which all individuals are identical. In reality, individuals always differ at least slightly from each other, so that exceptionally creative individuals may appear sporadically in populations. Finally, we model culture as a single quantitative dimension, whereas a more realistic model should explicitly consider different cultural items, which would allow capturing the fact that key discoveries can suddenly accelerate the emergence of other discoveries (Kolodny et al., 2015, 2016). These three types of stochastic mechanisms are likely to cause shocks in cultural evolution. They could play an important role in the dynamics of culture and explain some of the variability in the trajectories of different populations.

Finally, we began this article by arguing that cultural knowledge should be considered as part of the *non-disposable* capital produced by individuals, this form of capital differing from *disposable* capital in that it retains its value after the death of its producer. We would like to conclude by suggesting that it could be useful to broaden the definition of culture to include in fact *all* forms of non-disposable capital, including those that are not knowledge. The knowledge and skills of a population (i) can accumulate, (ii) have lasting effects over time and on a large number of individuals and (iii) partly explain the differences between human societies. But other properties of the environment, also resulting from the efforts of past human beings, have exactly the same effects. An area that has been deforested around a village, a temple or church built by ancestors, a reduced density of dangerous predators, an efficient railway system, a trustworthy political institution, etc.; all these human productions have a lasting influence on people's development and behaviour, can accumulate, and explain a part of human variability, just as knowledge does. Hence, the culture of a society, we think, has no reason to be restricted to knowledge and skills but should be seen, more broadly, as a capital produced by past generations that affects the lives of present generations.

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Appendix

A. Evolutionarily stable schedule

A.1. Neutral model. The neutral model is essentially intended to play the role of a point of comparison with the non-neutral one. In this model, the production function is merely seen as a "target" function that individuals seek to maximize when they invest time in different compartements of their capital, but this model deliberately neglects the fact that this function in turn determines the amount of resources that can be invested per unit of time in different forms of capital. It is assumed that, whatever the amount of capital available to an individual, per unit of time invested in growth, the growth of x is always γ; per unit of time invested in learning the growth of y is always λ and per unit of time invested in innovation, the growth of y is always η. This is a deliberately false approximation but it serves as a point of comparison with the non-neutral model.

In the neutral model (as in the non-neutral one), natural selection favours the strategy that consists for individuals to invest at all times in the activity (growth, learning, or innovation) that has the greatest marginal impact on the production function (see Iwasa and Roughgarden, 1984, Perrin, 1992, Perrin et al., 1993). From the production function given by the equation 1 of main text, the marginal production of x and y, respectively, are given by

$$P_x(x,y) \equiv \frac{\partial P(x,y)}{\partial x} = \alpha x^{\alpha-1} y^{\beta}$$
$$P_y(x,y) \equiv \frac{\partial P(x,y)}{\partial y} = \beta x^{\alpha} y^{\beta-1}$$

So the marginal return of investing a unit of time in growth is $\gamma P_x(x,y)$, the marginal return of investing a unit of time in learning is $\lambda P_y(x,y)$ and the marginal return of investing a unit of time in innovation is $\eta P_y(x,y)$ with $\eta < \lambda$.

We consider a population of N individuals developping in parallel in an environment in which an amount z of knowledge is already available from the previous generation.

A.1.1. Phase 1: Learning and growth. As long as individuals have not learned all the cultural information already available (that is, as long as $y < z_0$) then the return on innovation is always lower than the return on social learning, and individuals thus only arbitrate between (i) growth and (ii) social learning. During this phase, if $\gamma P_x(x,y) > \lambda P_y(x,y)$ then individuals prefer to invest all their time in growth, while if $\gamma P_x(x,y) < \lambda P_y(x,y)$ then they prefer to invest all their time in social learning. Natural selection therefore favours a strategy that consists of investing a fraction of the time in growth and a fraction in learning in order to maintain at all times $\gamma P_x(x,y) = \lambda P_y(x,y)$, which implies maintaining a ratio

$$\frac{y}{x} = \frac{\lambda\beta}{\gamma\alpha} = \frac{\lambda}{\gamma}\kappa$$

where $\kappa \equiv \beta/\alpha$. To maintain this ratio, individuals invest a fraction of their time l in social learning and a fraction $1-l$ in growth, with

$$l = \frac{\beta}{\alpha+\beta} = \frac{\kappa}{1+\kappa}$$

The growth rate of x during this phase is therefore $\gamma(1-l)$ while the growth rate of y is λl. This phase lasts until all available knowledge has been learned, so until $y = z$.

A.1.2. Phase 2: Pure growth. Once $y = z$, individuals cannot improve y through social learning. They only have the choice between innovating or growing. However, since the efficiency of innovation is lower than the efficiency of social learning at the end of Phase 1 (i.e. $\eta < \lambda$), investing in growth is necessarily more profitable than innovating. So individuals experience a second phase during which they only invest in the growth of x at a constant rate γ (see main text for details).

A.1.3. Phase 3: Innovation, learning and growth, at the frontier. At the end of phase 2, the marginal return on investment in growth is exactly equal to the return on investment in innovation $\gamma P_x(x,y) = \eta P_y(x,y)$. Since social learning is always more efficient than innovating ($\lambda > \eta$) this means that social learning is still the most profitable activity. So, as soon as an individual in the population produces an innovation, then all the other individuals prefer to invest in learning this innovation rather than in any other activity. In other words, during this third phase, individuals do not only invest in innovation and growth, they always keep a fraction (sometimes very large in fact) of their time to invest in the social learning of *all* the innovations produced by others (see main text for details).

A.2. Non-neutral model. In the non-neutral model, it is explicitly considered that the production function determines the amount of resources available per unit of time, that individuals can then allocate to their different activities. This model is therefore a problem of optimal control in which individuals can invest in two organs (here x and y). As long as the production function is concave (which is the case here since we have assumed $\alpha < 1$ and $\beta < 1$), standard results of optimal control theory (see Iwasa and Roughgarden, 1984,

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Perrin, 1992, Perrin et al., 1993) tell us that the optimal allocation strategy for individuals is to make, at each instant, the investment(s) with the strongest marginal effect on productivity. This simple result allows us to simulate the development of individuals.

The problem is that, in the non-neutral model, the growth rate of individuals is not constant (unlike the neutral model) but given by the production function and the development of individuals is therefore not analytically solvable. We therefore simulate numerically step by step this development in a social environment in which they initially have an amount z of available knowledge from the previous generation. These simulations are performed by choosing a time step δ, the smallest possible (ideally infinitely small). At each time step we numerically calculate the marginal return, $P_x(x,y)$ and $P_y(x,y)$, of each type of capital and we calculate the growth of individuals during this time step as follows:

(1) When $y < z$ (that is, individuals still have things to learn socially). (i) If $\lambda P_y(x,y) < \gamma P_x(x,y)$ individuals invest all their production in growth and therefore x increases by $\gamma P(x,y)\delta$ while y remains constant. (ii) If $\lambda P_y(x,y) > \gamma P_x(x,y)$ individuals invest all their production in social learning and therefore y increases by $\lambda P(x,y)\delta$ while x remains constant.

(2) When $y \geq z$ (that is, individuals no longer have anything to learn socially from the previous generation). (i) If $\eta P_y(x,y) < \gamma P_x(x,y)$ individuals invest all their production in growth and therefore x increases by $\gamma P(x,y)\delta$ while y remains constant. (ii) If $\eta P_y(x,y) > \gamma P_x(x,y)$ individuals invest all their production in both (i) innovating and (ii) learning the innovations made by others. In this case, y increases by $\frac{\eta\lambda N}{\lambda+\eta(N-1)}P(x,y)\delta$ while x remains constant.

With these simulations, by considering a population of N individuals with a quantity of knowledge z_t available in generation t, we can simulate the development of individuals and thereby obtain the quantity of knowledge that they reach at the end of their development, which gives us z_{t+1}, the quantity of knowledge available for the next generation. Eventually, performing the same simulations for different values of z_t allows us to plot z_{t+1} in function of z_t (Figs. 3, 4, 5, and 6 of main text).

In the particular case where the pyramid of needs depends on the capital of individuals (section of main text), we assume that the two exponents, α and β , of the production function (Eq. 1 of main text) depend on disposable capital, via two functions $\alpha(x) = (1-c(x))\zeta$ and $\beta(x) = c(x)\zeta$, with $\zeta \in [0.1]$ and $c(\cdot)$ an increasing monotonic mapping from $[0.+\infty]$ to $[0.1]$. The model is then exactly the same except that the marginal productivities of x and y are given by

$$P_x(x,y) = \delta x^{\zeta(1-c(x))-1} y^{\zeta c(x)} \left(-xc'(x)\ln\left(\frac{x}{y}\right) - c(x) + 1\right)$$
$$P_y(x,y) = \zeta c(x) x^{\zeta(1-c(x))} y^{\zeta c(x)-1}$$

A.3. Optimal control theory with two types of capital and constant mortality. In this section we simply recall the essential results of optimal control theory in the case of an individual who has a choice between three possible investments: investing in two types of capital, x or y, or reproducing. Individuals are characterized, at any age t, by the size of their two types of capital $x(t)$ and $y(t)$. These affect the amount of resources that the individual produces per unit of time, through the productivity function $P(\cdot)$. We assume that the mortality rate is a constant m, i.e. mortality is not affected by the level of capital.

An individual's strategy consists in choosing, at each instant of her life, how she allocates the resources she produces at that moment. She can invest these resources in three activities: reproduction, growth or learning. Formally, an individual's strategy is therefore (i) an allocation function $u(\cdot) \in [0.1]$ that indicates the fraction of her resources that she allocates to x at each age, (i) an allocation function $v(\cdot) \in [0.1]$ that gives the fraction of her resources that she allocates to y at each age, the rest $(1-u(t)-v(t))$ being allocated to reproduction. It is therefore on the two functions $u(\cdot)$ and $v(\cdot)$ that natural selection acts. The aim of optimal control theory is to characterize the nature of these functions at an evolutionary equilibrium.

To do this, we consider a population at its demographic equilibrium, subject to density-dependent regulation via fertility, in which natural selection maximizes the "lifetime reproductive success" of individuals (Dańko et al., 2018). In other words, selection favours the allocation functions that maximizes the total amount of "reproductive investments" made by the individual over her lifetime.

Let us consider an individual of age t. This individual is characterized by three variables: his capital $x(t)$ and $y(t)$ and his probability of still being alive $l(t)$. The following system of differential equations gives us the dynamics of these variables along the individual's life:

$$\frac{dx(t)}{dt} = \gamma u(t) P\left(x(t), y(t)\right) \quad \textbf{(11)}$$
$$\frac{dy(t)}{dt} = \lambda v(t) P\left(x(t), y(t)\right) \quad \textbf{(12)}$$
$$\frac{dl(t)}{dt} = -ml(t) \quad \textbf{(13)}$$

where γ and λ represent the growth rate of x and y per unit of resources invested in these two types of capital respectively. In the following, for the sake of simplicity of exposition, we sometimes omit the explicit dependence on time in $x(t)$ and $y(t)$. A function called the Hamiltonian is then defined:

$$\begin{aligned} H(t) \equiv & \gamma u(t) P(x,y)\chi(t) \\ & + \lambda v(t) P(x,y)\xi(t) \\ & - l(t) m V(t) \\ & + \left(1-u(t)-v(t)\right) P(x,y) l(t) \end{aligned} \quad \textbf{(14)}$$

An intuitive way to understand this function is to see it as the "marginal value" of the instant t. In other words, $H(t)dt$ represents how much the infinitesimal duration dt has contributed to total fitness. To do this, the marginal changes in the three variables x, y and l at time t are weighted by a measure of their respective "value" in terms of reproduction.

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1. The investment into capital x and y is weighted by $\chi(t)$ and $\xi(t)$ which represent respectively the marginal value of x and y at time t.
2. The investment in survival is weighted by $V(t)$ which is the reproductive value of an individual of age t.
3. The investment in reproduction is weighted by $l(t) = e^{-mt}$ which represents the probability that the individual is still alive at age t.

The maximum principle states that the optimal allocation function consists in always investing, at each instant, so as to maximize $H(t)$. For instace, if $\gamma\chi(t) > \lambda\xi(t)$ and $\gamma\chi(t) > l(t)$, then the individual should invest all the resources produced at time t into capital x only. On the other hand if two compartments have the same marginal value then the inividual should invest in both, e.g. if $\gamma\chi(t) = \lambda\xi(t)$ the individual should invest both into x and y.

To determine the evolutionarily stable allocation function we must therefore calculate the three functions $\chi(t)$, $\xi(t)$ and $V(t)$. For this purpose, we use the canonical equations of optimal control:

$$\frac{d\chi(t)}{dt} = -\frac{\partial H(t)}{\partial x(t)} \tag{15}$$

$$\frac{d\xi(t)}{dt} = -\frac{\partial H(t)}{\partial y(t)} \tag{16}$$

$$\frac{dV(t)}{dt} = -\frac{\partial H(t)}{\partial l(t)} \tag{17}$$

For an intuitive understanding of these equations, we recommend Iwasa and Roughgarden (1984).

A.3.1. Optimal schedule. Consider the following strategy. (1) At birth, the individual starts by investing all her resources in both types of capital, leaving nothing for reproduction, in such a proportion that she always maintains $\gamma P_x(x,y) = \lambda P_y(x,y)$, i.e. always maintaining the ratio $\frac{y}{x} = \frac{\lambda\beta}{\gamma\alpha}$. (2) From a certain age t_a, called the switching age, the individual stops investing entirely in both types of capital and only invests in reproduction until he dies. Here we will assume that an individual follows this schedule and infer the consequences regarding the dynamics of the marginal values of the two types of capital. We will then show that this schedule is indeed optimal (see also Iwasa and Roughgarden, 1984).

A.3.2. Pure reproduction phase and derivation of the switching time. For simplicity, we call $x_a \equiv x(t_a)$, and $y_a \equiv y(t_a)$ the capital of adults, that is individuals in the pure reproduction phase. During this phase we have $u(t) = v(t) = 0$ and thus the hamiltonian is

$$H(t) = -l(t)mV(t) + P(x_a, y_a)l(t)$$

We also have the canonical equation for χ and ξ:

$$\frac{d\chi(t)}{dt} = -\frac{\partial H(t)}{\partial x(t)} = -P_x(x_a, y_a)l(t) \tag{18}$$

$$\frac{d\xi(t)}{dt} = -\frac{\partial H(t)}{\partial y(t)} = -P_y(x_a, y_a)l(t) \tag{19}$$

where we recall that $l(t) = e^{-mt}$. Under the constraint that $\chi(t)$ and $\xi(t)$ must tend toward zero at infinity because the probability that the individual is still alive to benefit from her capital tends toward 0, equations 18 can be integrated into

$$\chi(t) = \frac{1}{m}P_x(x_a, y_a)e^{-mt} \tag{20}$$

$$\xi(t) = \frac{1}{m}P_y(x_a, y_a)e^{-mt} \tag{21}$$

Assuming the individual does follow the optimal schedule, we have $\gamma P_x(x_a, y_a) = \lambda P_y(x_a, y_a)$. Hence, during the reproduction period we also have $\gamma\chi(t) = \lambda\xi(t)$ at all times $t \geq t_a$. Since we know, from equation 14 and the maximum principle, that the switching age t_a must obey the condition $\gamma\chi(t_a) = \lambda\xi(t_a) = l(t_a) = e^{-mt_a}$, this gives us the necessary and sufficient conditions for t_a to be the switching age:

$$\gamma P_x(x_a, y_a) = \lambda P_y(x_a, y_a) = m \tag{22}$$

In other words, the organism stops investing in her capital at the precise moment where the marginal productivity of capital is exactly equal to mortality rate (see Kozlowski, 1996, Kozłowski and Wiegert, 1987, Kozlowski and Weiner, 1997, Perrin, 1992, Perrin et al., 1993). From this equation and taking into account the fact that $\frac{y}{x} = \frac{\lambda\beta}{\gamma\alpha}$, we can find the levels of capital at the switching age

$$x_a = \left(\frac{(\beta\lambda)^{\beta}(\alpha\gamma)^{1-\beta}}{m}\right)^{\frac{1}{1-\alpha-\beta}} \tag{23}$$

$$y_a = \frac{\beta\lambda}{\alpha\gamma}x_a \tag{24}$$

The equations 20 and 22 tell us that $\gamma\chi(t) = \lambda\xi(t) = e^{-mt} = l(t)$ during the entire reproduction phase. So once reproduction has begun, the marginal value of capital will never exceed the value of reproduction. So it will never be optimal for the individual to start investing in capital again after the switching age.

A.3.3. Pure growth phase. During this phase, we have $u(t) + v(t) = 1$, and the Hamiltonian is thus:

$$H(t) = [\gamma u(t)\chi(t) + \lambda v(t)\xi(t)]\, P(x,y) - l(t)mV(t)$$

With the canonical equation for $\chi(\cdot)$ and $\xi(\cdot)$

$$\frac{d\chi(t)}{dt} = -\frac{\partial H(t)}{\partial x(t)} = -[\gamma u(t)\chi(t) + \lambda v(t)\xi(t)]\, P_x(x,y) \tag{25}$$

$$\frac{d\xi(t)}{dt} = -\frac{\partial H(t)}{\partial y(t)} = -[\gamma u(t)\chi(t) + \lambda v(t)\xi(t)]\, P_y(x,y) \tag{26}$$

Suppose we have $\gamma\chi(t_0) = \lambda\xi(t_0)$ at a certain time t_0 and suppose that the individual follows the optimal schedule, i. e. she always maintains her levels of capital so that $\gamma P_x(x,y) = \lambda P_y(x,y)$. Hence, the equation 25 tells us that in this case we

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have $\gamma\dot{\chi}(t) = \lambda\dot{\xi}(t)$ for all $t \geq t_0$, so the equality of marginal values is maintained at all times in the future i.e. for all $t \geq t_0$, we have $\gamma\chi(t) = \lambda\xi(t)$ (see Iwasa and Roughgarden, 1984 for the same reasoning in a more general context). Therefore, it remains optimal for the individual to continue to invest in both types of capital in parallel.

The optimal allocation strategy is therefore as described above. Individuals first invest in the growth of their two types of capital in parallel and then stop both investments at the same time to start reproducing.

In the present article, however, we are interested in a slightly more complex case where the growth of the second type of capital (y) can be done in two ways depending on the value of y. When y is lower than a threshiold z, individuals grow their y by so-called "learning", whereas when $y \geq z$, individuals cannot use learning anymore and have to rely on innovation which is less efficient. In this more complex case, it is straightforward to show that the same principle holds, namely that individuals must invest at all times in the activity with the largest marginal effect on production. This leads to the optimal development schedule shown in the main text.

According to optimal control analysis, the duration of the development period should depend on the productivity parameters of both forms of capital as well as on the level of mortality (see Eq. 23). However, in our article, for the sake of simplicity, we chose to control the duration of development exogeneously by directly setting this duration as a parameter L .

B. Division of labour

Here we consider a model in which individuals share the work of learning and producing cultural goods. We assume that they do so in a cooperative manner by seeking the most efficient division of labour possible. When the size of the population and the discrete nature of individuals does not constrain the division of labour, then the result under this assumption is identical to the long-term equilibrium of a competitive market (see Mas-Colell et al., 1995, chapter 10).

We consider a population of N individuals and we consider to simplify a good for which the demand is constant. The good has a benefit b and each of the N individuals in the population needs exactly one and only one token of this good. Among the N individuals in the population, n are producers of the good (and also consumers like everyone else). The ratio N/n therefore measures the extent of the division of labour. The higher it is, the more the more extensive is division of labour.

The cost of producing the goods is two fold. First, being a producer entails a "fixed cost", ϕ, that is independent of the amount of goods actually produced, and represents the cost of acquiring the knowledge and skills to make the good, and more generaly all the fixed costs necessary to become a producer. Second, being a producer entails a "production cost", $\pi(q)$, that depends on the number q of goods produced. Typically, the producion cost function should be convex, at least at some point, such that it becomes too costly to produce more goods (see Mas-Colell et al., 1995, chapter 10). Here, we consider a standard production cost

$$\pi(q) = uq^a \tag{27}$$

where u is the cost of producing one unit of the good and $a > 1$ measures the convexity of the production cost.

Let us first assume that there are exactly n producers of the good in the population. Every producer will have to produce exactly N/n goods that they sell at a price p. In this case, non-producing consumers earn a payoff $b-p$. And producers earn a payoff $g(p,n)$ given by

$$g(p,n) = p\frac{N}{n} - \left(\phi + \pi\left(\frac{N}{n}\right)\right) + b - p \tag{28}$$

We assume that the number of producers, n, and the price of the good p are (i) in equilibrium and (ii) efficient. They must therefore comply with two conditions.

(1) Equilibrium condition: The price of the good is such that producers and consumers earn the same payoff. Otherwise some consumers would prefer becoming producers, or vice versa (Mas-Colell et al., 1995, chapter 10.F), and n would therefore not be in equilibrium. This implies the condition $p\frac{N}{n} = \phi + \pi\left(\frac{N}{n}\right)$, which gives us the equilibrium price $\hat{p}(n)$ at which the good is sold when there are n producers:

$$\hat{p}(n) = \frac{n}{N}\left(\phi + \pi\left(\frac{N}{n}\right)\right) \tag{29}$$

When the good is sold at the equilibrium price $\hat{p}(n)$, individuals share the cost of producing the goods in such a way that everyone earns the same payoff given by $b - \hat{p}(n)$.

(2) Efficiency condition. The number of producers n should be such that the average payoff of individuals is maximized when the good is sold at the equilibrium price $\hat{p}(n)$. In combination with the condition 29 above, this implies that the $\hat{p}(n)$ is minimized. So this gives us

$$\hat{n} = \arg\min_n \left(\frac{n}{N}\left(\phi + \pi\left(\frac{N}{n}\right)\right)\right) \tag{30}$$

From these two conditions, and with the production cost given by equation 27, we obtain the optimal number of producers $\hat{n}$ given by

$$\hat{n} = \frac{N}{\hat{s}} \text{ if } \hat{s} \in [1, N] \tag{31}$$

$$\hat{n} = N \text{ if } \hat{s} \leq 1 \tag{32}$$

$$\hat{n} = 1 \text{ if } \hat{s} \geq N \tag{33}$$

with

$$\hat{s} = \left(\frac{\phi}{(a-1)u}\right)^{1/a} \tag{34}$$

In other words, $\hat{s}$ corresponds to the optimal division of labour in the absence of constraints (i.e. when the size of the population and the discrete nature of individuals are not limiting). $\hat{s}$ increases with the fixed cost ϕ and decreases with a and u which is expected since production techniques are less efficient. The actual division of labour is, however,

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constrained by (i) population size (at most all individuals will be producers) and above all by (ii) the discrete nature of the individuals (at least there must be 1 producer).

At the optimum division of labour, the price of the good is thus given by

$$\hat{p} = a \cdot u \left(\frac{l}{(a-1)u} \right)^{\frac{a-1}{a}} \text{ if } \hat{s} \in [1, N] \tag{35}$$

$$\hat{p} = u + \phi \text{ if } \hat{s} \leq 1 \tag{36}$$

$$\hat{p} = \frac{uN^a + \phi}{N} \text{ if } \hat{s} \geq N \tag{37}$$

This prize is then integrated into the cultural evolution model as follows.

First, the fixed cost of becoming a producer, ϕ, represents the amount of cultural information needed to become a producer. We assume that this cost is simply given by $\phi = z$. Second, we assume that the greater the amount of information, z, available in the previous generation, the more efficient are the techniques for producing goods. This is modelled by assuming that the convexity of the production cost function (eq. 27) is a decreasing function of the technical complexity z, equal to a_{high} when $z = 0$, and asymptotically reaching a_{low} when z tends toward infinity:

$$a(z) = a_{\text{high}} - z(a_{\text{high}} - a_{\text{low}}) \frac{\sigma}{a_{\text{high}} - a_{\text{low}} + z\sigma} \tag{38}$$

During the catch-up phase, when individuals still have less knowledge than the amount of knowledge available in the previous generation ($y < z$), the effective learning rate is given by $\lambda(z) = \lambda_{\min} \cdot \max(1, \frac{z}{p(z)})$. At worst, when the price of cultural goods is very high, the learning rate is $\lambda_{\min}$. When z increases, the efficiency of production techniques improves so that the division of labour is greater (the number of producers decreases), the price of goods decreases ($p(z) < z$), and thus the effective learning rate increases (i.e. $\lambda(z) > \lambda_{\min}$). When individuals are innovating at the frontier, however, then we assume that their learning rate is constant, and given by $\lambda_{\min}$.

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