POPULATION, TECHNOLOGICAL PROGRESS AND THE EVOLUTION OF INNOVATIVE POTENTIAL

by

Jason Collins
Business School
University of Western Australia

and

Boris Baer
Centre for Integrative Bee Research (CIBER)
ARC CoE in Plant Energy Biology
University of Western Australia

and

Ernst Juerg Weber
Business School
University of Western Australia

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We present an evolutionary theory of long-term economic growth in which technological progress and population growth are driven by the population size and the innovative potential of the people in the population. We expand on current theory proposing that population growth is proportional to population size due to greater production of ideas, and submit that technological progress and population growth are also driven by the accelerating evolution of people with a higher innovative potential. As a larger population implies a larger number of mutations, population growth will increase the rate at which innovation-enhancing traits may emerge. Heritable traits that increase idea development or productivity increase the fitness of the bearer, increase in frequency in the population and drive technological progress. This dual-driver model of economic growth has a sharper acceleration in population growth and greater robustness to technological shocks than a model without human evolution. We also show that as the population size increases, increases in population size become a relatively more important driver of the acceleration of technological progress than further increases in innovative potential.

**Key words:** technological progress, human evolution, population growth, innovation

Corresponding author: Jason Collins - jason@jasoncollins.org
1. Introduction

In his seminal paper on population growth and technological change, Kremer (1993) proposed that the growth of population over most of human history is proportional to its level. As more people generate more ideas (Kuznets, 1960; Simon, 1998), larger populations generate technological progress that can ease the Malthusian constraints on further population growth.

We propose that a complementary driver of technological progress is evolution of the human potential to innovate. As a larger population generates more mutations (Fisher, 1930), population growth will increase the rate at which new traits may emerge. If mutations that increase innovative potential raise the fitness of the host, these genes will spread in the population, enhance technological progress and provide an economic basis for further population growth. Larger populations would thus be expected to grow faster than smaller populations through evolution-driven technological progress.

In this paper we explore the effect of evolutionary dynamics on population and technological growth. We demonstrate that the higher number of mutations in larger populations, and hence a faster rate of evolutionary change, can provide an explanation for the greater than exponential population growth that Kremer (1993) has documented for one million years of human history.¹ Our evolutionary model of population growth is more robust to technological shocks than a model in which the innovative potential of the population is not evolving, with successively faster recovery from each shock. We also show that as the population increases, population size becomes a relatively more

¹ Homo sapiens did not emerge as a distinct species until approximately 200,000 years ago. However, for ease of terminology, we will refer to the agents evolving over the last one million years, including various hominid precursors to modern humans, as “humans” or “people”.

important driver of the acceleration of technological progress than further increases in innovative potential.

In the following sections, we develop a model of population growth and technological progress in which the model agents’ innovative potential evolves endogenously. We examine the model under a number of specifications and incorporate evolution of the productivity of the agents in using the new technology. We then test the response of the model population to technological shocks and investigate the evolutionary dynamics where there is a delay in the spread of mutations. We close our analysis with an agent-based model that allows us to endogenise factors such as the relative fitness of more innovative agents and the rate of spread of mutations through the population.

2. Background

Until recently, the global annual population growth rate was positively correlated with population size, implying faster than exponential population growth. Figure 1 shows the relationship between global population size and population growth for the last one million years. The first data point indicates a global population of 125,000 and a population growth rate of 0.0003 per cent. The last data point represents the global population of close to seven billion people and a growth rate of 1.1 per cent in 2009. The population growth rate increased with population size until the global population increased above three billion people in the mid-twentieth century, but then the positive relationship between population size and population growth broke down. The recent reduction in the population growth rate coincided with many populations undergoing a demographic transition to lower fertility rates.
Kremer (1993) proposed to explain this demographic pattern with a model in which a larger population leads to faster technological progress through a larger population generating more ideas. Adopting the Malthusian assumption that population size is limited by technology, the effect of population size on technological progress creates a positive feedback loop between population size and population growth. Kremer’s model predicts that the growth rate of the population is proportional to its level, as is observed in the historical data until approximately 1950. Generalising the model, he further suggested that there is a point where the rate of technological progress increases beyond that which population can grow, leading to an increase in per capita income. If people reduce fertility in response to income, a fertility reduction will then occur, allowing for a demographic transition to lower population growth. This provides scope for the model to match the rise in the population growth rate before 1950, as well as the recent attenuation of population growth.
While Kremer characterises the driver of technological change as the total human population, humans have also undergone significant evolutionary change over the time that he examines. Evolutionary change is evident in the increase in brain size, which may affect innovative potential. The cranial capacity of *Homo erectus* skulls from one million years ago are typically around 900 cubic centimetres (Lee and Wolpoff, 2003; Rightmire, 2004; Ruff et al., 1997). A significant increase in brain size then occurred, with that increase concentrated between 600 thousand and 150 thousand years ago (Ruff et al., 1997). Cranial capacity peaked at over 1,500 cubic centimetres approximately 30,000 years ago in the late upper Palaeolithic, although it has since declined to around 1,350 cubic centimetres (Henneberg, 1988).

Changes in skull capacity and brain size are reflected in the emergence of what are termed behaviourally modern humans, at the earliest, 200,000 years ago (Henshilwood and Marean, 2003; Mcbrearty and Brooks, 2000). Some estimates put behavioural modernity within the last 50,000 years (Klein, 2000). While there was evidence of technological progress before behaviourally modern humans, such as increases in the quality of hand axes and other stone tools around 600,000 years ago (Klein and Edgar, 2002), technological progress was slow (and from the archaeological record, often undetectable) until behaviourally modern humans emerged.

The observed correlation between brain and population size that occurs over this time has been proposed to be a causative relationship. For example, Bailey and Geary (2009) examined three major hypotheses for larger brain evolution: climate change, ecological

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2 One million years ago, *Homo sapiens* did not exist as a species, with *Homo erectus* found in Africa, Asia and Europe (Rightmire, 1998). Subsequently, a number of hominid species proposed as the ancestors of *Homo sapiens* emerged, including *Homo antecessor* (Carbonell et al., 2008) and *Homo heidelbergensis* (Rightmire, 1998). Further, genomic evidence has revealed that *Homo sapiens* cross bred with *Homo neanderthalensis* in Europe (Green et al., 2010) and Denisova hominins in Asia (Rasmussen et al., 2011) within the last hundred thousand years.
pressure and social competition. While all three pressures were relevant, they found that competition within large cooperative groups for control of social dynamics comprised the major contribution. By comparing 175 hominid crania dating from between 1.9 million to 10 thousand years ago with a proxy for population density, Bailey and Geary found that cranial size increased consistently with population density, and by inference social competition, before declining slightly at the highest densities.

Brain size, together with any other trait that may influence innovative potential, is also affected by population size through the link between population and mutation rates. Fisher (1930) observed the greater potential for mutation in larger populations and proposed that larger populations should experience more evolutionary change. More people mean more mutations. Whether a mutation will be successful, driving out the original allele (variant of a gene) and reaching fixation, depends on the fitness advantage of the mutation. In a larger population, the mutation is more likely to reoccur in subsequent generations if previously eliminated by genetic drift (Reed and Aquadro, 2006). Further, in a growing population, the number of beneficial mutations moving to fixation increases because a mutation is less likely to be eliminated by genetic drift.

Fisher’s observation of the higher potential for mutations in a larger population has received empirical support from examinations of genomic data. Genomic evidence suggests that human evolution has accelerated over the last 40,000 years, with genomic

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3 Let $s$ be the selective advantage of a mutation. Then, a mutation has an approximate probability of $2s$ of moving to fixation (Haldane, 1927). More generally, the probability of fixation is $1 - e^{-2s} / 1 - e^{-4N_e s}$, where $N_e$ is the effective population size (Kimura, 1957). Where $N_e$ is large and $s$ is small, this approximates to $2s$.

4 In that case, the probability of the mutation driving out the original allele is approximately $2(s + r)$, where $r$ is the population growth rate (Otto and Whitlock, 1997). Beneficial mutations move to fixation at a rate of $1 + rs$ times greater than in a population of constant size.
surveys identifying significant selection (Hawks et al., 2007). Voight et al. (2006) documented widespread signals of recent selection in East Asian, Western European and African populations.

One striking finding of rapid evolution was by Mekel-Brobov et al. (2005), who found that the ASPM allele that arose approximately 5,800 years ago (95% confidence interval 500 to 14,000 years), which is associated with brain size regulation, has since swept to high frequencies under strong positive selection. Similarly, Evans et al. (2005) discovered a variant of the gene Microcephalin, associated with brain size regulation, that arose approximately 37,000 years ago and also spread rapidly under strong positive selection.

3. Related literature

The connection between human evolution and economic growth is the subject of an increasing literature. The link proposed by Hansson and Stuart (1990) was first examined in depth by Galor and Moav (2002), who developed a unified growth model in which parents have a genetically determined preference for quantity or quality of children. In the Malthusian state, those who invest a greater amount in educating their children have higher fitness, allowing them to increase in prevalence in the population, thereby increasing the average level of education. As education leads to technological progress, and technological progress increases the returns to human capital, a virtuous circle develops until the broader population starts to educate their children. This leads to a take-off in economic growth and subsequent demographic transition to lower population growth. Galor and Michalopoulos (2012) applied a similar framework to the evolution of entrepreneurial spirit, and Collins et al. (2013) provided a quantitative analysis of the Galor and Moav model.
Clark (2007) proposed that genetic change was a factor in the Industrial Revolution. Clark proposed that as the wealthy in England had more children than those with fewer resources, their industrious traits spread through the population, which triggered the take-off in economic growth. Zak and Park (2002) suggested that sexual selection that affects the ability to attract mates may play a role in economic growth.

Research incorporating genetic data has also been used to examine the evolutionary determinants of economic development. Spolaore and Wacziarg (2009) showed that genetic distance between populations was linked to regional economic development. They suggested that this was because genetic distance is a summary statistic for a range of beliefs, customs, habits and biases that are transmitted across generations and that can act as a barrier to technological transfer between populations. Ashraf and Galor (2013) established a humped-shaped relationship between genetic diversity and economic development. They proposed that this relationship was due to genetic diversity expanding production possibilities through complementarities in knowledge production, but reducing the efficiency of production processes due to lower levels of trust and coordination.

4. The basic model

This section describes a model of population growth and technological progress in the style of the base model contained in Kremer (1993). The model incorporates an additional element in the form of the innovative potential of the population, with that potential subject to evolutionary change. A more innovative population produces more ideas, strengthening the effect of population growth on technological progress in the Kremer model.
The model comprises a population of $N$ people who live for one generation. The members of the population are of innovative potential $q$, which is genetically determined and passed from parent to child. Mutation, however, provides a basis by which innovative potential may change between generations.

Total output $Y$ is:

$$Y = AN^\alpha X^{1-\alpha} \quad (1)$$

$A$ is the level of technology and $X$ is the amount of a fixed input factor, such as land or the environment, which is normalised to one. The parameter $\alpha$ is the elasticity of output with respect to labour input. Then, the level of per person income is:

$$y = AN^{\alpha^{-1}} \quad (2)$$

In a Malthusian environment, population will increase above a subsistence level of per person income, and decrease below it. This is a consequence of increasing fertility and decreasing mortality as income increases. If the subsistence level of income where population is constant is $\bar{y}$, equation (2) can be solved for the level of population, as shown in equation (3). Population instantaneously adjusts to the Malthusian equilibrium, which is a reasonable approximation on a millennial timescale (Richerson et al., 2001).

$$N = \left( \frac{\bar{y}}{A} \right)^{\frac{1}{\alpha^{-1}}} \quad (3)$$

The quantity and innovative potential of humans spur technological change as they increase the number of inventors and their production of ideas. If research productivity of each person is independent of population size and increases linearly with the level of

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technology $A$, the technological growth rate $g(A) \equiv (1/A)(dA/dt)$ is proportional to the population:

$$g(A) = \delta qN$$

(4)

$\delta$ is research productivity per innovative unit of people.

Similarly, the number of beneficial mutations emerging in the population and accordingly, the evolution of the population’s innovative potential, is proportional to the population. The growth rate in innovative potential $g(q) \equiv (1/q)(dq/dt)$ is:

$$g(q) = 2vN$$

(5)

$v$ is the genome wide mutation rate for the emergence of beneficial mutations.\(^5\) As for technological progress, we assume that the effect of new mutations builds upon previous mutations, which provides for increasing returns to mutation. We relax this assumption in the Appendix.

For traits associated with innovative potential to spread through the population, innovative individuals must have higher fitness. However, as we define innovative potential as the ability or propensity to develop ideas that increase technological progress, innovative potential itself will not lead to higher fitness if ideas are non-excludable and available to anyone regardless of their innovative potential. Therefore, to enable the spread of innovation-enhancing mutations independently of drift, we assume that innovative individuals accrue a fitness advantage. This assumption might be supported by temporary excludability of ideas in the form of trade secrets and – in

\(^5\) Due to the manner in which the genome wide mutation rate is implemented in this model, $v$ can also be interpreted as the increase in innovative potential arising due to mutations. We multiply the rate by two as humans are diploid.
modern times – patent laws, higher productivity of innovative individuals, or prestige attached to the generation of new ideas (Henrich and Gil-White, 2001). A direct productivity component to innovative potential is explicitly included in the model section 5.

We can derive the growth rate of the population $g(N) \equiv (1/N)(dN/dt)$ by taking the log of equation (3) and differentiating with respect to time:$^6$

$$g(N) = \frac{1}{1-\alpha} g(A) \quad (6)$$

Substituting equation (4) into equation (6) gives:

$$g(N) = \frac{\delta}{1-\alpha} qN \quad (7)$$

Equation (7) predicts that the growth rate of a population is proportional to the size of population and the innovative potential of the population. This leads to a prediction of stronger population growth than would be made under a model with constant innovative potential for a similar value of $\delta$. The contribution of increasing innovative potential to population growth can be seen in Figure 2, which compares numerical simulations of a population with and without the evolution of innovative potential.

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$^6$ Take the logarithm of equation (3): $\ln N = \frac{1}{\alpha - 1} (\ln N - \ln A)$. Then, $\frac{d\ln N}{dt} = \frac{1}{1 - \alpha} \frac{1}{A} \frac{dA}{dt} = \frac{1}{1 - \alpha} g(A)$.
Figure 3 shows the evolution of innovative potential during this period. Around the time of the population explosion at approximately year 350,000 of the simulation, innovative potential growth sharply accelerates.

The results in Figures 2 and 3 are generated by iterating equations (3), (4) and (5), with 1,000 years per iteration. The simulation parameters were $A_0 = 1$, $N_0 = 1$, $\alpha = 0.5$, $\bar{y} = 1$, $\delta = 0.001$ and $\nu = 0.0005$. Population growth accelerates faster with the evolution of
innovative potential (maintaining other parameters the same), with the increased population quantity and innovative potential creating a positive feedback loop and an increasing gap between the two scenarios.

As both models seek to explain the same trajectory of human history, the appropriate interpretation of Figure 2 is that a model incorporating evolution of innovative potential requires a lower value of $\delta$ to generate similar acceleration in population growth to a model without evolution. However, if there is a time where the population size for each model is the same, the population growth rate in the evolutionary scenario will accelerate faster from that point. Accordingly, while we use the simulation of the scenario without evolution of innovative potential for illustrative purposes in figures, this is to provide a reference point for interpreting the simulations, rather than providing a direct comparison of two alternative models of population growth.

This stronger population growth rate is apparent if we look at the acceleration in the growth of the population, $a(N)$. Taking the log and first derivatives of equation (7) gives:

$$a(N) = g(q) + g(N)$$

$$= g(q) + \frac{1}{1-\alpha} g(A)$$

$$= \left(2\nu + \frac{\delta}{1-\alpha} q\right)N$$

The acceleration in population growth is driven by the growth in innovative potential and the growth in population size, with the term $2\nu$ being the additional acceleration in growth in the evolutionary model over a model with no evolution of innovative potential.
We can apportion the relative contribution to the acceleration of population growth between increase in innovative potential and growth in population size. The proportion of population growth attributable to increasing innovative potential is obtained by dividing the first term of equation (8) by the whole equation.

\[
\pi(q) = \frac{2v}{2v + \frac{\delta}{1-\alpha} q}
\]  

(9)

As population growth is directly a function of technological progress, this equation can also be thought of apportioning the acceleration of population growth between growth in innovative potential and growth in technology.

Equation (9) shows that the contribution to the acceleration of population growth by increasing innovative potential grows weaker as innovative potential increases. As population members become increasingly innovative, increasing their numbers has more effect on innovation than where innovative potential is low. Figure 4 plots the proportion of the acceleration in population growth that can be attributed to increasing innovative potential for the simulation shown in Figure 2. The panel on the left-hand side shows the negative relationship between innovative potential and its contribution to the acceleration of population growth. The panel on the right-hand side depicts the contribution of innovative potential to the acceleration of population growth over time. Initially, improvements in innovative potential are a significant factor in accelerating population growth, with one third of the acceleration attributable to increasing innovative potential, but this effect fades as innovative potential increases. As innovative potential growth accelerates rapidly at year 370,000 of the simulation, the contribution of increasing innovative potential to accelerating population growth plunges to near zero at that time. However, the level of innovative potential of the population remains an important factor in the rate of technological progress.
Adjustment of the mutation rate and innovation rate can shift the relative contribution of innovative potential to the acceleration of population growth to values other than those simulated. However, the general pattern of declining contribution by innovative potential as innovative potential increases and the population takes off remains. The results in this section do not materially change if we use a more general version of equation (4) for technological progress that allows for technological progress to vary with the level of technology, such as where there are positive spillovers from earlier inventions to new ones, or where research productivity varies with population, such as from network effects. Similarly, a more general version of equation (5) that allows for spillovers between mutations does not much change the results. The effects of the more general functional forms of these equations are explored in the Appendix.

5. The evolution of productivity

In the preceding model, innovative potential affects the production of ideas, and not the productivity of the population in using them. In this section, we add an additional component to the production function so that innovative people are more productive in
using ideas in addition to producing more ideas. This assumption is intuitively sensible, as those developing new technologies are likely to be better able to understand and use them. The addition of a productivity component provides a basis for more innovative individuals to have a fitness advantage even where no personal advantage can be accrued through the production of ideas.

Total output $Y$ depends on innovative potential $q$:

$$Y = A(qN)^\alpha X^{1-\alpha} \quad (10)$$

As for the first model, $X$, the amount of land, is normalised to one for the remainder of the analysis. Then, the level of per capita income is:

$$y = Aq^\alpha N^{\alpha-1} \quad (11)$$

The unique level of population $N$ for the subsistence level of income $\bar{y}$ is:

$$N = \left( \frac{\bar{y}}{Aq^\alpha} \right)^{\frac{1}{\alpha-1}} \quad (12)$$

The growth rate in technology and innovative potential is as presented in equations (4) and (5).

We can derive the growth rate of the population by taking the log of equation (12) and differentiating with respect to time:

$$g(N) = \frac{1}{1-\alpha} \left( g(A) + \alpha g(q) \right) \quad (13)$$

Equation (13) identifies two major drivers of population growth: the technological growth rate $g(A)$ which captures the production of ideas by a population of a given size
and innovative potential, and the increasing productivity of the population (represented by $a_g(q)$). Substituting equations (4) and (5) into equation (13) gives:

$$g(N) = \frac{1}{1-\alpha} \left( \delta q + 2\nu \alpha \right) N$$  \hspace{1cm} (14)

As for equation (7), equation (14) predicts that the growth rate of a population is proportional to population size. The new term $2\nu \alpha$ leads to a prediction of stronger population growth than would be made under a model with constant labour productivity.

Taking the log and total derivative of equation (14) gives the acceleration in the growth of population:

$$a(N) = g \left( q + \frac{2\nu \alpha}{\delta} \right) + g(N)$$

$$= \left( \frac{q}{q + 2\nu \alpha \delta} + \frac{\alpha}{1-\alpha} \right) g(q) + \frac{1}{1-\alpha} g(A)$$

$$= \left( \left( \frac{q}{q + 2\nu \alpha \delta} + \frac{\alpha}{1-\alpha} \right) 2\nu + \frac{\delta}{1-\alpha} q \right) N$$  \hspace{1cm} (15)

Comparing with equation (8), where productivity is not affected by increasing innovative potential, the acceleration in population growth is higher for a given innovative potential and quantity unless $q/(q + 2\nu \alpha /\delta) + \alpha/(1-\alpha) < 1$. As $2\nu \alpha /\delta$ becomes smaller relative to $q$ as $q$ increases and $\alpha$ lies in the range of 0.4 to 0.6, it is unlikely that this condition would be satisfied unless innovative potential is very low. Further, if the condition were satisfied, the higher population enabled by higher population productivity would likely result in the lower acceleration in population growth being from a higher base level of population growth.
Figures 5 and 6 show a simulation of the population and its innovative potential where innovative people are more productive. Relative to a simulation where evolution of innovative potential only affects the production of ideas, this model results in a steeper acceleration of population growth and innovative potential. The stronger population growth in the simulation that includes productivity growth suggests that we could explain the observed historical record by lower levels of idea generation ($\delta$) or mutation ($\nu$) for a given level of innovative potential than is required in the absence of productivity enhancing evolution.

**Figure 5: Population size with evolution of productivity**

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7 The simulation is generated by iterating equations (3), (4) and (12), with 1,000 years per iteration. The simulation parameters were $A_0 = 1, N_0 = 1, \alpha = 0.5, \bar{y} = 1, \delta = 0.001$ and $\nu = 0.0005$. 
For this model, it is not possible to apportion the acceleration of population growth between increasing innovative potential and population size as innovative potential growth is now part of population growth in equation (13). However, we can apportion the relative contribution to accelerating population growth between increasing innovative potential and technological progress by dividing the first term of equation (15) by the whole equation.\(^8\)

\[
\pi(q) = \frac{\frac{q}{q+2\nu\alpha} + \frac{\alpha}{1-\alpha}}{2\nu + \frac{\delta}{1-\alpha}}
\]

Equation (16) shows that the contribution to the acceleration of population growth of increasing innovative potential decreases as innovative potential increases. Population growth is driven increasingly by the innovations of the growing number of innovative people rather than further increases in the genetically determined innovative potential.

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\(^8\) This is effectively what was done in the earlier apportioning exercises as population growth was purely a function of technological progress.
Figure 7 illustrates the decline in the relative importance of increases in innovative potential as a determinant of acceleration of population growth. At the start of the simulation, innovative potential accounts for 42 per cent of the acceleration in population growth. This is more than in the basic model as innovative potential contributes to population growth through both increased innovation and productivity, but as for the basic model, the surge in innovative potential that occurs in the simulation precipitates a plunge in the future contribution of evolution driven population growth.

**Figure 7: Relative contribution of increase in innovative potential to acceleration of population growth**

6. Population dynamics

The above analysis is predicated on a steadily increasing population. However, human evolutionary history comprises non-linear features, including population cycles and bottlenecks. For example, genetic evidence suggests that human populations experienced a bottleneck (or multiple bottlenecks) within the last 100,000 years that reduced the human population to around 10,000 individuals (Harpending et al., 1993).

Under a model with no evolution, a sudden decline in population would constitute a significant setback to technological progress. The decline in population would result in
a commensurate decline in idea production, and technological progress would revert to the level experienced when the population was last of that size. If the decline in population was caused by a technological shock, or if the population decline reduced the level of technology available to the population through the loss of people holding ideas, the population recovery would be no faster than the rate of population growth when the population was last of that size. Therefore, a population suffering frequent exogenous shocks may never escape the Malthusian state.

In a model incorporating the evolution of innovative potential, a population decline due to a technological shock is still a setback, but technological progress and population growth is higher than when population was last of that size as the innovative potential of the population is now higher. This results in a faster recovery in population size and allows for continuing acceleration of technological progress. If an evolving population is subject to successive technological shocks, there will be successively faster recovery from each shock, as the population will have increasingly greater innovative potential.

Figure 8 shows a simulation of four scenarios over a period of 500,000 years: a base case for the population model without evolution, a base case for the model incorporating human evolution, and those two scenarios being subject to exogenous environmental shocks.\(^9\) The shock may represent a change in environmental or climatic conditions that reduces the effective level of technology. For the two scenarios in which exogenous technology shocks are applied, a shock at year 200,000 reduces the level of technology to what it was at the start of the simulation \((A_{200,000} = 1)\). We first assume that innovative potential does not affect productivity, before relaxing that assumption in later simulations.

\(^9\) The simulations in Figure 11 are generated by iterating equations (3), (4) and (5), with 1,000 years per iteration. The parameters were \(A_0 = 1, N_0 = 1, \alpha = 0.5, \bar{y} = 1, \delta = 0.001\) and \(v = 0.0005\). At \(t = 200,000\), a shock is applied such that \(A_{200,000} = 1\).
After the application of the technological shock, the population declines from around 1.7 in the base case without evolution and 1.8 in the base case with evolution to one in both scenarios. The rebound in population following the shock is faster in the scenario with human evolution. Without evolution, the shock effectively winds the clock back to the start of the simulation. Population growth during the next 200,000 years mirrors that for the previous 200,000 years, resulting in recovery from the shock taking that full period. However, where innovative potential can evolve, the population recovers faster. It takes 157,000 years for the population in the base case simulation with human evolution to recover to the level it was at the time of the shock, compared to the 200,000 years it took to initially reach that level. The later the shock and the higher the innovative potential of the people at the time of the shock, the faster the population will recover.

**Figure 8: Population size with environmental shocks**

The recovery from shocks is even stronger where evolving innovative potential also affects productivity. Due to the increasing productivity of the population, a higher population is maintained at the time of the shock than in the base case model. The population does not decrease to one because the more productive population can make
better use of the available technology. This is shown in Figure 9, in which a shock reducing technology to the initial level is applied at year 200,000. In response to the shock, the population size declines from 2.9 to 1.4. It then takes only 96,000 years for the population to recover to the size it was before the shock. The robustness of the productivity scenario to exogenous technology shocks is further demonstrated by applying an additional shock in year 350,000. Even though 75 per cent of the population is eliminated by this shock, the recovery in population is rapid. It takes only 64,000 years for the population to recover to its pre-shock level.

**Figure 9: Population with environmental shocks and evolving productivity**

7. A model with spread of mutations

An important assumption of these models is that beneficial mutations spread immediately through the population once they arise. In reality, mutations take time to spread through the population, and require many generations to go to fixation. The results in Figure 12 are generated by iterating equations (12), (4) and (5), with 1,000 years per iteration. The simulation parameters were $A_0 = 1$, $N_0 = 1$, $a = 0.5$, $\bar{y} = 1$, $\delta = 0.001$ and $v = 0.0005$. At $t = 200,000$, a technology shock is applied such that $A_{200,000} = 1$. A second shock is applied at $t = 350,000$ such that $A_{350,000} = 1$. 

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10 The results in Figure 12 are generated by iterating equations (12), (4) and (5), with 1,000 years per iteration. The simulation parameters were $A_0 = 1$, $N_0 = 1$, $a = 0.5$, $\bar{y} = 1$, $\delta = 0.001$ and $v = 0.0005$. At $t = 200,000$, a technology shock is applied such that $A_{200,000} = 1$. A second shock is applied at $t = 350,000$ such that $A_{350,000} = 1$. 

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delay in the spread of beneficial mutations may have significant effects on the model outcomes, particularly for larger populations where population growth and associated technological progress is rapid. In such cases, new mutations may initially have a weaker effect due to their low frequency in the population. In this section, we explore the consequences of easing the assumption of instantaneous spread of beneficial mutations.

The time for a new mutation to spread to fixation is a function of the relative fitness of those carrying the mutation and the size of the population. Where the mutation has a selective advantage, the time from the emergence of a mutation to fixation can be approximated as (Stephan et al., 1992):\(^{11}\)

\[
d = \frac{2}{s} \ln(2N)
\]  

(17)

\(s\) is the selective advantage of the mutation. As an example, a mutation with a 5 per cent fitness advantage \((s = 0.05)\) in a population of one million individuals would take approximately 580 generations or 11,600 years to spread to fixation. However, much of this time would be related to periods where the mutation is at very low or very high frequency along an \(s\)-shaped path. That same mutation would take only 95 generations or 1,900 years to spread from a prevalence of one per cent to 99 per cent. Due to the time to fixation being proportional to the log of \(2N\), population size has a smaller effect on the time to fixation than the strength of selection.

\(^{11}\) Letting the frequency of the mutation be \(\omega_t\), the change in frequency over \(d\) generations is given by:

\[
\frac{\omega_{t+d}}{\omega_t} = \frac{\omega_t (1 + s)^d}{\omega_t (1 + s)^d + (1 - \omega_t)}
\]

Setting \(\omega_t = 1/2N\), \(\omega_{t+d} = 1-1/2N\) and using \(\ln(1+s) \approx s\), we can solve for \(d\) as in equation (17).
Despite a mutation taking \( d \) generations to spread to fixation, the effects of the new mutation are felt through the population as soon as it arises, and it is of increasing importance as a greater proportion of the population carries it. Letting \( \omega_t \) be the prevalence of the mutation in the population at time \( t \) and \( \Delta q_t \) an incremental change in innovative potential due to a mutation, the contribution to technological progress from the appearance of the mutation at time \( t = m \) to fixation at time \( t = d \) is:

\[
\Delta A_t = \delta \Delta q_t \int_m^d \omega_t N_t dt
\]

(18)

If the spread of the mutation is symmetric on either side of 50 per cent, \(^{12}\) then equation (18) can be approximated as:

\[
\Delta A_t \approx \delta \Delta q_t \frac{1}{2} d N_t \cdot d/2
\]

(19)

While this approximation underestimates the contribution of the mutation if the population is growing, and will overstate or understate the contribution if the mutation is recessive or dominant, it provides an approximate basis to incorporate the delay of the mutation spreading through the population. We assume that any new mutation has no effect on innovative potential until \( d/2 \) generations after it arises, and full effect thereafter, as in this modified version of equation (5).

\[
g_t(q) = 2\nu N_t \cdot d/2
\]

(20)

\(^{12}\) In a haploid population, the spread of mutations would be approximately symmetric. A recessive mutation in a diploid population (e.g. humans) increases from 50 per cent to 100 per cent more quickly than it increases from 0 per cent to 50 per cent, while dominant mutations spread more quickly from 0 per cent to 50 per cent of the population than it will from 50 per cent to fixation.
Substituting equations (7) and (20) into equation (8), the acceleration in population growth is given by:

\[
\alpha_t(N_t) = g_t(q_t) + g_t(N_t) = 2\nu N_t - d/2 + \frac{\delta}{1 - \alpha} q_t N_t
\]

(21)

The effect of a slow spread of mutations is seen in the simulation results charted in Figure 10. The selective advantage of the mutation is 0.001. The population growth is marginally lower than would be in a simulation without the delay, and the gap between the simulations with and without delay grows as \(N_t - d/2\) lags further behind \(N_t\) in size. However, the gap is relatively minor until population size grows large, as the delay in the spread of mutations is relatively small in small populations.

**Figure 10: Population size with delay in mutation moving to fixation**

While the gap in population growth appears small, the delay prevents a sudden increase in innovative potential at the time of the population explosion. As shown in Figure 11,

---

13 The results in Figures 10 and 11 are generated by iterating equations (3), (4) and (20), with 1,000 years per iteration. The simulation parameters were \(A_0 = 1, N_0 = 1, \alpha = 0.5, \gamma = 1, \delta = 0.001, \nu = 0.0005\) and \(s = 0.001\).
after 300,000 years innovative potential has increased to 1.7 in the model without delay, and to 1.6 where there is delay in the spread of mutations. By year 350,000 the gap has grown to 2.3 against 1.9; by year 365,000 to 3.8 against 2.0; and by year 368,000 when population size is exploding to 147 against 2.0. In the model with delay, innovative potential growth reflects the mutations that arose when the population was much smaller, with the new mutations in the much larger population plentiful but at low prevalence as they have not had time to spread.

**Figure 11: Innovative potential with delay in mutation moving to fixation**

The role of innovative potential growth in accelerating population growth, represented by the first part of equation (21) and shown in Figure 12, drops rapidly with increasing innovative potential when there is a delay in the spread of mutations. The panel on the left-hand side shows the relationship between innovative potential and its contribution to the acceleration of population growth, and the panel on the right is a time series representation. As innovative potential does not take off when the population booms, there is no diminishing effect of innovative potential on the acceleration of population growth. Therefore, most of the decline in the role of innovative potential is due to increases in population growth rather than the growth of population innovative
potential. Conducting the simulations with a delay in the spread of mutations for the model that incorporates a productivity component in the production function produces a similar pattern.

**Figure 12: Relative contribution of increase in innovative potential to acceleration of population growth**

8. **An agent-based model**

In this section, we implement the productivity-enhancing model in an agent-based framework. In contrast to the homogeneous agents of the above models, in this agent-based model each agent has his or her own specific level of innovative potential and interacts with the environment as an autonomous agent.

Due to the homogeneity of the agents in the earlier models, we assumed that more innovative people have higher fitness and that mutations spread to all agents at the same moment. The use of an agent-based framework allows us to relax these assumptions by endogenously incorporating these features into the model. When an agent experiences a mutation, the spread of the mutation depends on the fitness of that agent relative to other agents. Their fitness advantage is the result of their level of innovative potential relative to the innovative potential of the other agents in the population. The population
at any point may comprise agents of multiple levels of innovative potential, with various mutations simultaneously spreading through the population as a result of the reproductive success of those carrying the mutations.

The population in generation $t$ comprises $N_t$ agents who live for one generation, with each agent $i$ ($i \in 1, 2, \ldots, N_t$) having innovative potential $q^i_t$. The innovative potential of each agent affects their rate of idea production and the productivity with which they utilise the available technology.

In each generation the heterogeneous agents work, producing total output $Y_t$.

$$Y_t = A_t \left( \sum_{i=1}^{N_t} q^i_t \right)^\alpha X^{1-\alpha}$$

$$= A_t \left( \bar{q}_t N_t \right)^\alpha X^{1-\alpha}$$

(22)

$A_t$ is the level of technology available to generation $t$ and $\bar{q}_t$ is the average innovative potential of the agents in the population. $X$ is the amount of land, which is normalised to one. The parameter $\alpha$ is the elasticity of output with respect to labour input. The level of per capita income is:

$$y_t = A_t \bar{q}_t^\alpha N_t^{\alpha-1}$$

(23)

Technological progress is a function of the number and innovative potential of people generating ideas:

$$A_{t+1} = A_t \left( 1 + g(A) \right)$$

$$= A_t \left( 1 + \delta \bar{q}_t N_t \right)$$

(24)

$\delta$ is research productivity per innovation units of people.
As we assume that there is no ownership of or return to land, the wage per unit of innovative potential is:

\[ w_i = \lambda_i \left( q_i N_i \right)^{\alpha - 1} \]  

(25)

Therefore, the income of person \( i \) is:

\[ z_i^i = w_i q_i^i \]

\[ = \lambda_i (q_i N_i)^{\alpha - 1} q_i^i \]  

(26)

Taking the level of per capita income where population is constant as \( \bar{y} \), the population will tend towards the population size that can survive off that level of income (the Malthusian population), \( \bar{N}_t \):

\[ \bar{N}_t = \left[ \frac{\bar{y}}{A \bar{q}_t^\alpha} \right]^{\frac{1}{\alpha - 1}} \]  

(27)

The expected number of children of agent \( i \) is proportional to agent \( i \)'s share of total income and the Malthusian population level for that level of total income. The realised number of children follows a Poisson distribution.\(^{14}\)

\[ n_i^i \sim \text{Pois} \left( \bar{N}_t \frac{z_i^i}{\bar{Y}_t} \right) \]  

(28)

\(^{14}\) A Poisson distribution has regularly been used in the examination of the spread of beneficial mutations (Otto and Whitlock, 1997). There is some evidence that a negative binomial distribution may be more appropriate for human populations as the observed variance tends to be greater than the mean (Kojima and Kelleher, 1962), but that distribution may under-predict the number of childless agents (Waller et al., 1973). Regardless, the choice of distribution has limited effect on the simulation results.
Thus, the probability that \( n_t^i \) is equal to \( \mu \) (\( \mu \in \{0, 1, 2, \ldots \} \)) is:

\[
\Pr\left(n_t^i = \mu\right) = \frac{\left(\frac{\bar{N}_t z_t^i}{Y_t}\right)^\mu e^{-\frac{\bar{N}_t z_t^i}{Y_t}}}{\mu!}
\]

(29)

The higher productivity and income of more innovative agents gives them a greater expected number of children than less innovative agents and therefore, a fitness advantage.\(^{15}\)

The innovative potential of an agent \( j \) may differ from that of his or her parent \( i \) due to mutation. A child inherits their parent’s level of innovative potential, plus or minus the effect of any mutations. Mutation occurs at the rate \( 2v \), with equal probability that the mutation is positive or negative:

\[
P\left(m_{i+1}^j = 1\right) = v \quad P\left(m_{i+1}^j = -1\right) = v
\]

(30)

\[
P\left(m_{i+1}^j = 0\right) = 1 - 2v
\]

\(^{15}\) An alternative specification for the number of children of each agent is based on a surplus of resources over a personal level of subsistence.

\[
n_t^i \sim \Pr_{\text{out}}\left(\bar{N}_t \left(\frac{z_t^i}{Y_t} - \bar{c}\right)\right)
\]

\( \bar{c} \) is the proportion of income that agents must allocate to their own survival before allocating any resources to the production of children. Given the rapid spread of the mutations in the agent-based simulations, this specification has limited effect on the model outcomes beyond increasing the probability that a new mutation will survive past its initial appearance.
When an agent experiences a mutation, the mutation increases or decreases innovative potential by a factor of $1 + \rho$. Thus, the innovative potential of a new agent $j$ in period $t+1$ is:

$$q_{t+1}^j = q_t^j \left(1 + m_{t+1}^j \rho\right)$$  \hspace{1cm} (31)

### 8.1. Simulation results

The agent-based simulations were developed in NetLogo (Wilensky, 1999), with the agents run through the following model protocol:\(^{16}\)

- Each agent $i$ works and generates income $z_t^i$ (equation (26)).
- The agents’ activity generates technological progress, which sets the level of technology available to the agents in the next generation (equation (24)).
- Each agent $i$ has $n_t^i$ children (equation (28)).
- The innovative potential of each child $j$ is determined (equation (31)).
- The agents from generation $t$ die.

The parameters for the simulations are given in Table 1. All agents start at the same level of innovative potential. The values of $\delta$ and $v$ are lower than used in simulations earlier in this paper, as these are rates per generation compared to rates per thousand years used previously.

---

\(^{16}\) The code for the agent-based model is contained in the Appendix. The full NetLogo model is available for download from [http://www.jasoncollins.org/downloads](http://www.jasoncollins.org/downloads).
Table 1: Model parameters

<table>
<thead>
<tr>
<th>Parameters</th>
<th>Description</th>
<th>Base case value</th>
<th>Range explored</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\alpha$</td>
<td>Output elasticity of labour</td>
<td>0.5</td>
<td></td>
</tr>
<tr>
<td>$\delta$</td>
<td>Rate of innovation</td>
<td>$10^{-8}$</td>
<td>$10^{-9}$ to $10^{-7}$</td>
</tr>
<tr>
<td>$\nu$</td>
<td>Mutation rate</td>
<td>$10^{-6}$</td>
<td>$10^{-2}$ to $10^{-5}$</td>
</tr>
<tr>
<td>$\rho$</td>
<td>Mutation increment</td>
<td>0.1</td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Initial values</th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>$N_0$</td>
<td>Population</td>
<td>1000</td>
<td></td>
</tr>
<tr>
<td>$\bar{N}_0$</td>
<td>Malthusian population</td>
<td>1000</td>
<td></td>
</tr>
<tr>
<td>$A_0$</td>
<td>Level of technology</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>$q$</td>
<td>Agent innovative potential</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>$X$</td>
<td>Land</td>
<td>1</td>
<td></td>
</tr>
</tbody>
</table>

Figures 13 and 14 show the time paths of the population size and average innovative potential of the population for 10 runs of the base case model. To compare the simulation runs between the two figures, we kept the same colour code for each of the 10 runs. There is significant variation in the rate of population and innovative potential growth despite the same parameters being used in each model run, with the timing of chance innovative potential mutations the major determinant of the timing of the take-off. Even where mutations occur, many mutations are eliminated at low frequencies due to the number of children of an agent being a Poisson distribution. The number of children of an agent may be zero even if the mutant has a higher than average expected number of children. For example, the model runs represented by the blue and black lines had several mutations within the first 5,000 generations, leading to an early increase in the level of idea production per person and population size that then drives further increases. In contrast, there were no innovation-enhancing mutations in the model run represented by the dark green line for over 15,000 generations. This significantly reduced the positive feedback loop between population size and innovative potential relative to those model runs with numerous early mutations, resulting in population differences greater than an order of magnitude at specific points. If a version of the model were developed that relied on individual chance inventions, rather than the
steady accumulation of ideas as in the current implementation, the variation in the rate of population growth between simulation runs would be even larger.

**Figure 13: Population size in agent-based simulation**

The step-wise nature of innovative potential growth in Figure 14 is indicative of the rapid spread of fitness enhancing mutations when they arise and spread through the population. As for the model in which there is a delay to the spread in mutations, the increase in innovative potential does not match the explosive population growth at the end of the simulation run, although it has accelerated materially.
The parameter values for the rate of innovation (δ) and mutation (ν) determine the effect on the rate of population growth, the growth in innovative potential of the agents, and of the contribution of innovative potential growth to population growth. Tables 2 and 3 show the results of sensitivity testing in which we increase and decrease these rates by a factor of 10 in each direction from the base case. This represents exploration of a compound relative change by a factor of 10,000 (δ = 10^{-9} and ν = 10^{-5} through to δ = 10^{-7} and ν = 10^{-7}). For each pair of parameters, we report the average result of 10 model runs. Table 2 reports the number of generations it takes for the population to increase by a factor of 100, from 1,000 to 100,000, while Table 3 reports the innovative potential of the agents at that point.
Table 2: Sensitivity testing - Generations to 100,000 population.

<table>
<thead>
<tr>
<th>Rate of innovation (δ)</th>
<th>10⁰</th>
<th>5×10⁻⁹</th>
<th>10⁻⁸</th>
<th>5×10⁻⁸</th>
<th>10⁻⁷</th>
</tr>
</thead>
<tbody>
<tr>
<td>10⁻⁷</td>
<td>204,409</td>
<td>74,039</td>
<td>43,844</td>
<td>9,407</td>
<td>4,885</td>
</tr>
<tr>
<td></td>
<td>(35,859)</td>
<td>(13,214)</td>
<td>(3,633)</td>
<td>(631)</td>
<td>(182)</td>
</tr>
<tr>
<td>5×10⁻⁷</td>
<td>90,674</td>
<td>44,632</td>
<td>29,729</td>
<td>8,575</td>
<td>4,573</td>
</tr>
<tr>
<td></td>
<td>(17,616)</td>
<td>(7,010)</td>
<td>(3,056)</td>
<td>(681)</td>
<td>(243)</td>
</tr>
<tr>
<td>10⁻⁶</td>
<td>47,518</td>
<td>33,702</td>
<td>21,457</td>
<td>7,879</td>
<td>4,555</td>
</tr>
<tr>
<td></td>
<td>(12,261)</td>
<td>(7,172)</td>
<td>(3,656)</td>
<td>(750)</td>
<td>(341)</td>
</tr>
<tr>
<td>5×10⁻⁶</td>
<td>13,418</td>
<td>10,872</td>
<td>9,767</td>
<td>4,402</td>
<td>3,268</td>
</tr>
<tr>
<td></td>
<td>(1,821)</td>
<td>(2,619)</td>
<td>(1,781)</td>
<td>(502)</td>
<td>(317)</td>
</tr>
<tr>
<td>10⁻⁵</td>
<td>7,689</td>
<td>6,799</td>
<td>5,992</td>
<td>3,600</td>
<td>2,563</td>
</tr>
<tr>
<td></td>
<td>(1,478)</td>
<td>(716)</td>
<td>(1,088)</td>
<td>(451)</td>
<td>(288)</td>
</tr>
</tbody>
</table>

Note: Mean and standard deviation (in brackets) of 10 model runs.

Table 3: Sensitivity testing - Average innovative potential at 100,000 population.

<table>
<thead>
<tr>
<th>Rate of innovation (δ)</th>
<th>10⁰</th>
<th>5×10⁻⁹</th>
<th>10⁻⁸</th>
<th>5×10⁻⁸</th>
<th>10⁻⁷</th>
</tr>
</thead>
<tbody>
<tr>
<td>10⁻⁷</td>
<td>3.83</td>
<td>1.70</td>
<td>1.32</td>
<td>1.09</td>
<td>1.02</td>
</tr>
<tr>
<td></td>
<td>(0.59)</td>
<td>(0.27)</td>
<td>(0.12)</td>
<td>(0.08)</td>
<td>(0.04)</td>
</tr>
<tr>
<td>5×10⁻⁷</td>
<td>8.90</td>
<td>3.58</td>
<td>2.36</td>
<td>1.29</td>
<td>1.19</td>
</tr>
<tr>
<td></td>
<td>(0.85)</td>
<td>(0.64)</td>
<td>(0.23)</td>
<td>(0.10)</td>
<td>(0.10)</td>
</tr>
<tr>
<td>10⁻⁶</td>
<td>12.75</td>
<td>4.51</td>
<td>3.17</td>
<td>1.58</td>
<td>1.26</td>
</tr>
<tr>
<td></td>
<td>(1.01)</td>
<td>(0.54)</td>
<td>(0.40)</td>
<td>(0.19)</td>
<td>(0.10)</td>
</tr>
<tr>
<td>5×10⁻⁶</td>
<td>23.00</td>
<td>9.46</td>
<td>6.58</td>
<td>2.60</td>
<td>1.85</td>
</tr>
<tr>
<td></td>
<td>(0.85)</td>
<td>(0.79)</td>
<td>(0.50)</td>
<td>(0.30)</td>
<td>(0.12)</td>
</tr>
<tr>
<td>10⁻⁵</td>
<td>26.45</td>
<td>12.32</td>
<td>8.03</td>
<td>3.36</td>
<td>2.24</td>
</tr>
<tr>
<td></td>
<td>(1.33)</td>
<td>(0.83)</td>
<td>(0.25)</td>
<td>(0.27)</td>
<td>(0.18)</td>
</tr>
</tbody>
</table>

Note: Mean and standard deviation (in brackets) of 10 model runs.

The adjustment of these parameters materially affects the rate of growth and the contribution of innovative potential to that growth. Taking a generation to be approximately 20 years, the parameters explored can generate a 100-fold increase in population size in 50,000 years (lower-right cell of Table 2) to four million years (upper-left cell). Innovative potential may play almost no part in population growth (upper-right cell of Table 3), or may increase by over 20 times (lower-left cell) being the major driver of population growth.
The rate of population and innovative potential growth also varies where we use a more general form of the equations for technological progress and the evolution of innovative potential in which ideas or mutations may be “fished out”. However, the level of variation is significantly below that where the rates of innovation or mutation are adjusted. The results of sensitivity testing of more general functional forms of these equations in the agent-based framework are contained in the Appendix.

9. Discussion

In this paper, we propose that evolutionary changes in human innovative potential can be a complementary driver of long-term technological progress and population growth. The concurrent increase in this potential and population growth increases the sharpness of the take-off in technological progress and population relative to population growth driven solely by increasing population size. The model provides scope for technological progress to accelerate in the absence of population growth if population size is constrained. This is particularly important where the population is subject to setbacks that hamper long-term growth in population size, as has occurred repeatedly in human evolutionary history. The evolution of more innovative people provides robustness to technological shocks. Further, if human evolution selects for individuals with higher productivity, a larger population can be maintained after a technological shock.

We also show that as the population increases in its ability to produce and use ideas, increases in population size become a more important driver of accelerating population growth than continued evolutionary change. This is particularly the case if there is a delay to the spread of mutations. Increasing population size is particularly effective where the population is already innovative, as population size has the potential to change more quickly than mutations can spread. Indeed, the global population has doubled over last 50 years, but any genetically based human innovative potential has
almost certainly not changed materially during that period. However, we did not extend this model beyond the demographic transition and the decline in fertility of the last 200 years.

Where population size is the major driver of technological progress, there may be potential for small populations to shrink and experience technological regress, such as that experienced by Tasmanian aboriginals after Tasmania was isolated from the rest of Australia by sea level rise (Diamond, 1993; Kremer, 1993). A similar possibility arises with the evolution of the innovative potential. In a smaller population, the low level of fitness enhancing mutation and the increased potential for the loss of beneficial mutations through drift may reduce the ability to generate new ideas. However, the historical presence of population bottlenecks where the human population was likely small (in the order of 10,000 individuals) suggests that human populations have often recovered from population shocks.

One feature of the evolution of innovative potential in this paper is that the evolution occurs along the dimension of production of ideas, and not in relation to human ability to transmit the ideas to other people in the population. The concept that technological growth increases when more people create more ideas is premised on the ability of ideas to be spread and shared between population members. While some non-human species are recognised as engaging in learning and communication that allows the transmission of ideas, it is limited compared to humans (Cavalli-Sforza, 1986) as they lack mechanisms such as complex languages. Further, it is suggested that observational learning is not a by-product of intelligence and requires specific psychological mechanism (Boyd and Richerson, 2005). This raises the question of how and when the human ability for the transmission of ideas evolved to allow the ideas generated by a person to systematically spread and be used across the population. If an idea is kept by
and dies with an individual, or is used by only a small sub-population of humans, a larger population will not, on average, generate more technological progress.

On that basis, the slow technological change before the emergence of behaviourally modern humans may be partially attributable to the failure to transmit ideas across the population. Rather than the increase in innovative potential and population size driving increasing technological change, there may have been a step where the accumulation of the ideas became possible, finally allowing the feedback between population, innovation and technology to occur as humans developed the cognition and tools of cultural learning. Before that time, the increase in population and spread to fill new ecological niches would effectively be the result of increasing productivity, which can capture population-supporting changes that are not the result of the spread of ideas. As such, it is possible to develop a two-step evolutionary model with population growth initially driven only by productivity changes. Following the evolution of a trait allowing transmission of ideas, population size and increased innovative potential eventually become the drivers of technological progress.

Data constraints make empirical tests of this model challenging. First, empirical tests would require some measure of human innovation potential. A proxy such as cranial capacity or brain size may serve this purpose, but would be a crude proxy at best. More problematic is the degree of resolution for population data between 1 million BCE and the present. The Deevey (1960) data used in Figure 1 contains only three data points between one million BCE and 25,000 BCE, yet population data points would be required for each brain size data point. Further, higher resolution population data would likely expose the non-linear population dynamics of the human population, including population bottlenecks. These would render a simple regression analysis of population and innovative potential across time inappropriate. One empirical prediction of the
model, however, is that there would be successively faster recovery from population shocks. For a population of the same size, an inherently more innovative population is more resilient because it produces more ideas, with continuing evolution of that innovative potential through time.

References


Appendix

(For online publication only)

I. General function forms of innovation and mutation equations

A more general version of equation (4) for technological progress is given in equation (32) (derived from Jones (1995)). This equation allows for technological progress to vary with the level of technology, such as where there are positive spillovers from earlier inventions to new ones, and for research productivity to vary with population, such as from network effects.

\[ g(A) = \delta (qN)^{\lambda} A^\phi - 1 \] (32)

Technological progress (in absolute terms) accelerates when there are positive spillovers in the creation of new ideas ($\phi > 0$) and it falls when there is a ‘fishing out’ of ideas ($\phi < 0$). Where $\lambda > 1$, the network effects are significant and groups are more productive than individuals, while $\lambda < 1$ represents a situation where there is duplication of effort as the number of researchers increases. Equation (4) has the implicit assumption of $\phi = 1$ and $\lambda = 1$; that is, there are positive spillovers in research.

Substituting equation (32) into equation (6) to derive equation (33), we can determine the growth rate of the population. The positive relationship between population growth and the size and innovative potential of the population persists using this more general functional form. The strength of the effect of innovative potential and population size on population growth is changed by the degree to which network effects are negative or positive, while less than linear returns to technology decrease the growth effect of both innovative potential and the population size in model simulations. This result reflects the findings of Kremer (1993), who also found that the more general equation for
technological progress did not substantially change the prediction of increasing population growth with population size.

\[
g(N) = \frac{\delta}{1-\alpha} (qN)^{\lambda} A^{\phi-1}
\]  

(33)

Similarly, equation (5), which describes the evolution of the innovative potential of the population, can be generalised, allowing for spillovers between mutations. There is the possibility that the rate of “new” mutations is a function of the existing level of mutations, as one critical mutation may provide the environment for another mutation to have a fitness advantage, and there is the potential for depletion of certain mutations. For example, the ability to digest lactose past childhood evolved in at least three locations through different mutations (Ingram et al., 2008; Tishkoff et al., 2006). Once the ability to digest lactose had evolved, new mutations that cause this trait may not have a selective advantage relative to the existing allele.

A more general form of equation (5) where the mutation rate varies with the existing level of innovative potential is:

\[
g'(q) = 2\nu q^{\theta-1} N
\]  

(34)

There are positive returns (in absolute terms) to the existing number of fitness-enhancing mutations when \(\theta > 0\) and decreasing when \(\theta < 0\). This contrasts with the implicit assumption in equation (5) that there are positive returns to mutations \((\theta = 1)\). Changing the functional form for mutations does not change equation (33).

Values of \(\phi\) that vary from one are of interest as time series evidence from industrialised economies suggests that the value of \(\phi\) is less than one (Jones, 1995). While there is no equivalent evidence that bears directly on the value of \(\theta\), it is plausible that it may also be less than one.
Figures 15 and 16 show a simulation of the population with the more general functional forms for technological progress and mutation, with $\phi = 0.4$ (consistent with one estimate of $\phi$ provided by Kremer (1993)), $\theta = 0.5$ and $\lambda = 1$. Relative to the simulation in Figure 2, population growth is slower as ideas and mutations are depleted. However, the acceleration of growth remains robust and population size increases at a greater than exponential rate.

**Figure 15: Population size with general functional forms**

---

17 The simulation is generated by iterating equations (3), (32) and (34), with 1,000 years per iteration. The simulation parameters were $A_0 = 1$, $N_0 = 1$, $\alpha = 0.5$, $\bar{y} = 1$, $\delta = 0.001$, $v = 0.0005$, $\phi = 0.4$, $\theta = 0.5$ and $\lambda = 1$. 
To determine the acceleration in population growth, we substitute equation (34) into equation (8).

\[
\dot{a}(N) = \dot{\lambda}g(q) + \dot{\lambda}g(N) - (1-\phi)g(A)
\]

\[
= \lambda \left( 2q^\alpha N + \frac{\delta}{1-\alpha} (qN)^\lambda A^\rho - 1 \right) - (1-\phi)\delta (qN)^\lambda A^\rho - 1
\]

The acceleration in population growth is now mitigated or enhanced depending on whether there are negative or positive network effects to innovation, and whether there is depletion of mutations. Diminishing returns to innovation lower the acceleration in population growth.

We can apportion the source of the acceleration of population growth between innovative potential growth and population growth. Dividing the first term of equation (35) by the full equation, the proportion of the acceleration in growth attributable to increasing innovative potential is:
From equation (37), the relative contribution to the acceleration of population growth by increasing innovative potential declines with innovative potential unless $\lambda < (1-\phi)(1-\alpha)$, which is unlikely to be the case. Equation (38) shows that the relative contribution of increasing innovative potential to the acceleration of population growth declines with population size under the same condition.

Figure 17 illustrates the change in the contribution of increasing innovative potential to the acceleration of population growth for the simulation shown in Figure 15. The panel on the left-hand side shows the underlying relationship between innovative potential and its contribution to the acceleration of population growth, and the panel on the right provides a time series representation. As innovative potential increases, growth in size of the more innovative population becomes more important than continued improvement in innovative potential.
As was the case for the simulation of the less general functional forms, innovative potential undergoes a rapid take-off (around year 470,000 in this case), at which point the relative contribution of increasing innovative potential to population growth drops to near zero.
II. Sensitivity testing of more general functional forms in agent-based framework

Setting the equations for technology and innovative potential growth as in equations (39) and (40), there are less than linear returns to ideas or mutations where \( \phi \) or \( \theta \) are below one (which is the effective value of each in the base case simulation) and declining returns where \( \phi \) or \( \theta \) are below zero.

\[
A_{t+1} = A_t + \delta q_t N A_t^\phi
\]  
\[ (39) \]

\[
q_{t+1} = q_t^i + m_{t+1}^i \left(q_t^i\right)^\theta
\]  
\[ (40) \]

In Tables 4 and 5 we report the results of sensitivity testing for these parameters. We calculate the number of generations for population to increase 100 fold and the innovative potential at that point. Each result is the average of 10 model runs. Table 4 shows the number of generations for the population to increase by a factor of 100, from 1000 to 100,000, while Table 5 reports the innovative potential of the agents at that point. These simulations show that adjusting the parameters for a more generalised form of the technological progress and mutation equations has limited effect on the rate at which the population grows compared to adjustment of the rates of innovation or mutation. In the range tested, the time taken for the population to reach 100,000 varies by less than a factor of two, while the final average agent innovative potential varies by less than a factor of three.
Table 4: Sensitivity testing of more general forms - Generations to 100,000 population.

<table>
<thead>
<tr>
<th>Innovation productivity parameter (ϕ)</th>
<th>-0.25</th>
<th>0</th>
<th>0.25</th>
<th>0.5</th>
<th>0.75</th>
<th>1</th>
</tr>
</thead>
<tbody>
<tr>
<td>-0.25</td>
<td>40.255</td>
<td>40.544</td>
<td>32.778</td>
<td>31.215</td>
<td>30.414</td>
<td>29.044</td>
</tr>
<tr>
<td></td>
<td>(3,858)</td>
<td>(3,468)</td>
<td>(3,188)</td>
<td>(3,874)</td>
<td>(4,187)</td>
<td>(2,371)</td>
</tr>
<tr>
<td>0</td>
<td>36.837</td>
<td>35.099</td>
<td>32.342</td>
<td>30.615</td>
<td>29.620</td>
<td>27.353</td>
</tr>
<tr>
<td></td>
<td>(5,024)</td>
<td>(3,924)</td>
<td>(3,082)</td>
<td>(6,029)</td>
<td>(4,193)</td>
<td>(3,654)</td>
</tr>
<tr>
<td>0.25</td>
<td>36.350</td>
<td>32.373</td>
<td>30.554</td>
<td>30.524</td>
<td>27.285</td>
<td>26.201</td>
</tr>
<tr>
<td></td>
<td>(5,242)</td>
<td>(5,650)</td>
<td>(3,565)</td>
<td>(4,343)</td>
<td>(3,757)</td>
<td>(2,892)</td>
</tr>
<tr>
<td>0.5</td>
<td>35.734</td>
<td>31.585</td>
<td>28.878</td>
<td>28.952</td>
<td>26.102</td>
<td>27.410</td>
</tr>
<tr>
<td></td>
<td>(6,980)</td>
<td>(4,927)</td>
<td>(4,636)</td>
<td>(3,195)</td>
<td>(3,712)</td>
<td>(2,861)</td>
</tr>
<tr>
<td>0.75</td>
<td>29.907</td>
<td>27.553</td>
<td>27.847</td>
<td>28.020</td>
<td>24.824</td>
<td>24.006</td>
</tr>
<tr>
<td></td>
<td>(3,807)</td>
<td>(3,866)</td>
<td>(2,903)</td>
<td>(5,912)</td>
<td>(4,686)</td>
<td>(5,266)</td>
</tr>
<tr>
<td></td>
<td>(3,737)</td>
<td>(4,204)</td>
<td>(7,571)</td>
<td>(4,177)</td>
<td>(4,266)</td>
<td>(4,706)</td>
</tr>
</tbody>
</table>

Note: Mean and standard deviation (in brackets) of 10 model runs.

Table 5: Sensitivity testing of more general forms - Average innovative potential at 100,000 population.

<table>
<thead>
<tr>
<th>Innovation productivity parameter (ϕ)</th>
<th>-0.25</th>
<th>0</th>
<th>0.25</th>
<th>0.5</th>
<th>0.75</th>
<th>1</th>
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<tr>
<td>-0.25</td>
<td>2.67</td>
<td>2.51</td>
<td>2.36</td>
<td>2.18</td>
<td>2.08</td>
<td>1.88</td>
</tr>
<tr>
<td></td>
<td>(0.10)</td>
<td>(0.13)</td>
<td>(0.10)</td>
<td>(0.10)</td>
<td>(0.11)</td>
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<tr>
<td>0</td>
<td>3.04</td>
<td>2.77</td>
<td>2.58</td>
<td>2.35</td>
<td>2.22</td>
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</tr>
<tr>
<td></td>
<td>(0.14)</td>
<td>(0.12)</td>
<td>(0.24)</td>
<td>(0.11)</td>
<td>(0.13)</td>
<td>(0.11)</td>
</tr>
<tr>
<td>0.25</td>
<td>3.25</td>
<td>3.13</td>
<td>2.85</td>
<td>2.46</td>
<td>2.45</td>
<td>2.30</td>
</tr>
<tr>
<td></td>
<td>(0.12)</td>
<td>(0.22)</td>
<td>(0.16)</td>
<td>(0.09)</td>
<td>(0.14)</td>
<td>(0.13)</td>
</tr>
<tr>
<td>0.5</td>
<td>3.69</td>
<td>3.32</td>
<td>3.18</td>
<td>2.90</td>
<td>2.77</td>
<td>2.43</td>
</tr>
<tr>
<td></td>
<td>(0.27)</td>
<td>(0.25)</td>
<td>(0.23)</td>
<td>(0.20)</td>
<td>(0.11)</td>
<td>(0.27)</td>
</tr>
<tr>
<td>0.75</td>
<td>4.61</td>
<td>4.17</td>
<td>3.88</td>
<td>3.28</td>
<td>3.13</td>
<td>2.80</td>
</tr>
<tr>
<td></td>
<td>(0.31)</td>
<td>(0.30)</td>
<td>(0.30)</td>
<td>(0.39)</td>
<td>(0.45)</td>
<td>(0.34)</td>
</tr>
<tr>
<td>1</td>
<td>5.27</td>
<td>4.81</td>
<td>4.50</td>
<td>4.00</td>
<td>3.42</td>
<td>3.36</td>
</tr>
<tr>
<td></td>
<td>(0.64)</td>
<td>(0.38)</td>
<td>(0.78)</td>
<td>(0.44)</td>
<td>(0.47)</td>
<td>(0.42)</td>
</tr>
</tbody>
</table>

Note: Mean and standard deviation (in brackets) of 10 model runs.
III. Agent-based model code

The simulations in this paper were conducted using NetLogo (Wilensky, 1999), a multi-agent programmable modelling environment. The full NetLogo model is available for download from http://www.jasoncollins.org/downloads. Figure 18 shows a screenshot of the NetLogo interface.

Figure 18: NetLogo interface

Program code for the agent-based simulation:

```plaintext
globals [ 
  A ;; technology
  A-old
  A-growth
  N ;; population
  average-q
  average-q-old
  average-q-growth
  w ;; wage
  Y ;; total income
  Y-old
  Y-growth
  average-z ;; average income
  malthusian-limit ;; population at equilibrium for a given level of technology
  subsistence ;; subsistence income at the Malthusian limit
  c ;; proportion of subsistence income that must be used on
     ;; self (rest available for children)
  alpha
  gamma
```
v ;; mutation rate - set by slider mutation-rate
m ;; mutation increment - set by slider mutation-increment
pheta
phi
lambda
]
turtles-own [
q ;; turtle innovative potential
z ;; turtle income
children ;; expected number of children for a turtle
age ;; use for mechanism to kill off turtles after one generation
]
to setup
clear-all
setup-turtles
set alpha labour-share
set gamma innovation-rate
set v mutation-rate
set m mutation-increment
set pheta fishing-out-mutations
set phi fishing-out-A
set lambda network-effects
set A 1
set average-z number ^ (alpha - 1) ;; to give non-zero initial value for plot
set Y average-z * number
set average-q 1 ;; to give non-zero initial value for plot
set subsistence number ^ (alpha - 1) ;; to set subsistence such that users can
; ; select any initial number of turtles
set c subsistence-self
reset-ticks
end
to setup-turtles
create-turtles number
ask turtles [
    setxy random-xcor random-ycor
    set q 1
]
end
to go
if N >= 100000 [
    stop ;; control to stop population getting too large
]
if ticks >= number-of-ticks [
    stop ;; stop after a certain number of ticks
]
work
innovate
reproduce
tick
end

to work
  set average-q-old average-q
  set average-q mean [q] of turtles
  set average-q-growth average-q / average-q-old - 1
  set N count turtles
  ifelse productivity?
    [set w A * ((average-q * N) ^ (alpha - 1))
     set malthusian-limit (subsistence / (A * average-q ^ alpha)) ^ (1 / (alpha - 1))]
    [set w A * (N ^ (alpha - 1))
     set malthusian-limit (subsistence / A) ^ (1 / (alpha - 1))]
  ask turtles [    ;; age turtles so can kill off at end of generation
    ifelse productivity?
      [set z q * w]
      [set z w]
    set age 1
  ]
  set Y-old Y
  set Y sum [z] of turtles
  set Y-growth Y / Y-old - 1
  set average-z Y / N
end

to innovate
  set A-old A
  set A A + (A ^ phi) * (gamma * (average-q * N) ^ lambda)
  set A-growth A / A-old - 1
end

to reproduce
  ask turtles [    ;; ability to turn off evolution to allow
    set children malthusian-limit * (z - c * subsistence) / (Y - c * subsistence * N)
    hatch random-poisson children [    ;; simulation of Kremer model
      set age 0
      setxy random-xcor random-ycor
      if evolution? [
        if (2 * v * 1000000000) > random 1000000000 [    ;; set q of next generation, mutation rate 2v
          ifelse 1 = random 2    ;; one in two chance that mutation is either positive or negative
            [set q q + (m * q ^ pheta)]
            [set q q - (m * q ^ pheta)]
        ]
      ]
    ]
    if age = 1 [die]    ;; kills off turtles from the last generation
    if q <= 0 [die]    ;; kills turtles where innovative potential has mutated to zero
    ;; or below in no productivity simulation
  ]
end
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