The Neolithic Revolution and Contemporary Variations in Life Expectancy *

Oded Galor and Omer Moav[†]

August 28, 2007

Abstract

This research advances an evolutionary theory and provides empirical evidence that shed new light on the origins of contemporary differences in life expectancy across countries. The theory suggests that social, economic and environmental changes that were associated with the Neolithic Revolution affected the nature of the environmental hazards confronted by the human population, triggering an evolutionary process that had a significant impact on human longevity. The empirical analysis shows that a significant portion of contemporary variations in life expectancy across countries can be traced to the differences in the time passed since the ancestors of the population of each country experienced the Neolithic Revolution.

Keywords: Life Expectancy, Growth, Technological Progress, Evolution, Natural Selection, Malthusian Stagnation.

JEL classification Numbers: I12, J13, N3, O10.

---

[*] The authors are especially grateful to Yona Rubinsiten for numerous discussion and comments. In addition, they wish to thank Josh Angrist, Roland Benabou, Herbert Ginitis, Moshe Hazan, Peter Howitt, David Laibson, Victor Lavy, Alex Levkov, Rodrigo Soares, Richard Steckel, Neil Wallace, David Weil, Jorgen Weibull, and seminar participants at BU, Copenhagen, Harvard, Hebrew University, LSE, Penn State, Rome, Royal Holloway, Tel-Aviv, NES, and conference participants at DEGIT X, Mexico 2005, and "Biological Welfare and Inequality in Pre-Industrial Times", Yale 2005, NBER Summer Institute, 2006, and "Health, Human Development Potential and the Quality of Life" IADB and PAHO, 2007, for helpful discussion and comments, and Tamar Roth for excellent research assistantship.

[†] Galor: Brown University, and CEPR; Moav: Hebrew University, University of London Royal Holloway, Shalem Center, and CEPR

1 Introduction

This research advances an evolutionary theory and provides empirical evidence that shed new light on the origins of contemporary differences in life expectancy across countries. The theory suggests that social, economic and environmental changes, that were associated with the transition from hunter-gatherer tribes to sedentary agricultural communities, affected the nature of the environmental hazards confronted by the human population, triggering an evolutionary process that had a significant impact on human longevity.

The rise in population density, the domestication of animals, and the increase in work effort in the course of the Neolithic Revolution increased the exposure and the vulnerability of humans to environmental hazards, such as infectious diseases, and led to the decline in life expectancy during that period, as depicted in Figure 1 and detailed in Table A1.[1] The theory suggests, however, that in light of the fundamental trade-off between current and future reproduction, the Neolithic transition altered the evolutionary optimal allocation of resources towards somatic investment, repairs, and maintenance (e.g., enhanced immune system, DNA repairs, accurate gene regulation, tumor suppression, and antioxidants).[2] The rise in the extrinsic mortality risk (i.e., risk associated with external environmental factors, as opposed to internal biochemical decay) in the course of the Neolithic Revolution generated an evolutionary advantage to individuals who were genetically pre-disposed towards higher somatic investment, increasing their representation in the population, and leading to the observed increase in life expectancy in the post-Neolithic period, as depicted in Figure 1.[3]

The theory predicts that the interaction between the rise in the extrinsic mortality risk and the evolutionary process manifests itself in the observed non-monotonic time path of life

---

[1] For the effect of the Neolithic Revolution on the exposure and the vulnerability of humans to environmental hazards such as infectious diseases see Diamond (1997), Hibbs and Olson (2004) and Weisdorf (2006). Most comparisons between hunter-gatherers and farmers (e.g., Cohen (1989)) suggest that, in the same locale, farmers suffered higher rates of infection due to the increase in human settlements in size and permanence, poorer nutrition due to reduced meat intake and greater interference with mineral absorption by the cereal-based diet. Consequently, Neolithic farmers were shorter and had a lower life expectancy relative to Mesolithic hunter-gatherers. Although it is difficult to draw reliable conclusions about relative life expectancy in these periods, because skeletal samples are often distorted and incomplete, available evidence suggests that prehistoric hunter-gatherers often fared relatively well in comparison to later populations, particularly with reference to the survival of children. The Illinois Valley provides life tables for hunter-gatherers which confirm the assessment that their life expectancies matched or exceeded those of later groups. Additional evidence mostly from the Old World, are provided in Table 1, and are depicted in Figure 1.

[2] For the effect of somatic maintenance on longevity see Kirkwood (1998).

[3] The eventual trend of increasing life expectancy was accompanied by regional fluctuations, reflecting local environmental and climatic conditions. For instance, life expectancy fluctuated in the Malthusian epoch, ranging from 24 in Egypt in the time period 33 - 258 AD, to 42 in England in the end 16th century.

expectancy. In the short run – while the composition of the population remains nearly stationary – a rise in the mortality risk reduces life expectancy. However, the evolutionary process that is triggered by the environmental change generates an evolutionary advantage for individuals characterized by higher life expectancy, increasing their representation in the population. As the composition of the population shifts sufficiently in favor of individuals with higher life expectancy, the population's life expectancy increases and ultimately it could reach a higher level than the one existed prior to the increase in the mortality risk.

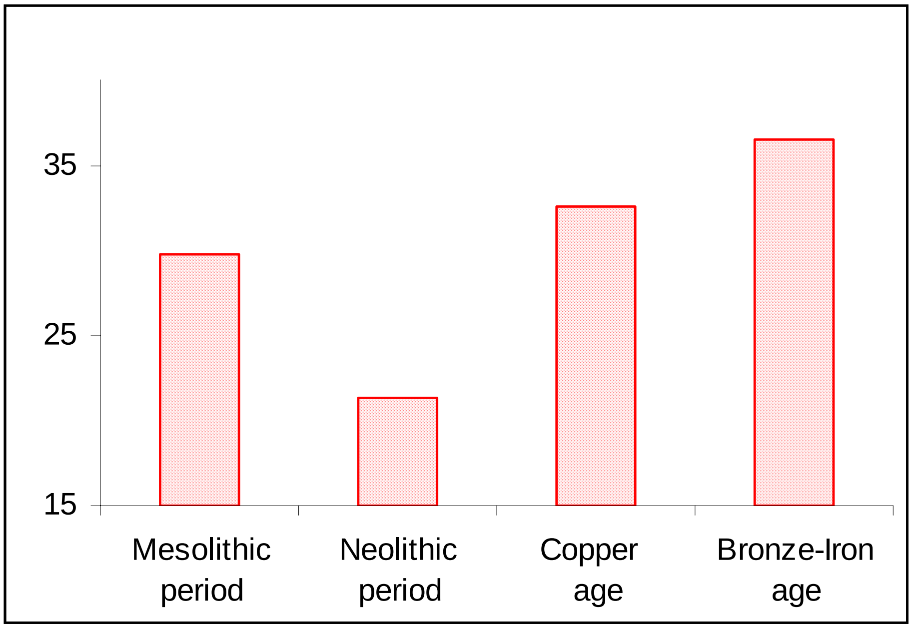

Figure 1: The Non-Monotonic Evolution of Life Expectancy (at birth) in the course of the Agricultural Revolution

The evolutionary process that was triggered by the transition to sedentary agriculture was maintained and, possibly reinforced, by the gradual increase in population size and density that accompanied the process of development since the Agricultural Revolution, prior to the emergence of significant improvements in health infrastructure.[4] Evidence suggest that the process of development since the Neolithic Revolution was indeed accompanied by an increase in the extrinsic mortality risk. For instance, skeletal remains from the pre-Colombian America, analyzed by Steckel (2004), demonstrate a decline in the health environment over the time period 6,000

---

[4] As argued by Mokyr (1998), significant improvements in health infrastructure did not occur prior to the middle of the 19th century.

BCE until 1500 CE.[5] Moreover, the process of urbanization suggests that the rise in population density further contributed to the increase in the extrinsic mortality risk, as reflected by the rise in the prevalence of major epidemics, such as the Black Death in Europe in the middle of the 14th century (e.g., McNeil (1998)), and a significant decline in life expectancy in some European countries in the 16th and the 17th centuries.[6] Furthermore, evidence suggests that changes in the environment may generate significant evolutionary processes in the composition of existing genetic traits within a time period that corresponds to the one required by the proposed theory.[7] Voight et al. (2006) detected about 700 regions of the human genome where genes appear to have been reshaped by natural selection within the last 5,000 to 15,000 years. In addition, Mekel-Bobrov et. al (2005) report that a variant of the gene ASPM (a specific regulator of brain size in the lineage leading to Homo sapiens) arose in humans about 5800 years ago and has since swept to high frequency under strong positive selection.

Importantly, differences in the timing of the Neolithic Revolution across regions generated significant variations in the genetic composition of the contemporary human population. For instance, lactose tolerance was developed among European and Near Easterners since the domestication of dairy animals in the course of the Agricultural Revolution, whereas in regions that were exposed to dairy animals in later stages a larger proportion of the adult population suffers from lactose intolerance. Furthermore, genetic immunity to malaria, associated with the sickle

---

[5] Steckel (2004) constructs a health index based on skeletal infections (inflammatory responses to bacterial invasion), iron deficiency anemia (nutritional deprivation, low body weight, chronic diarrhea, parasite infections), dental health, degenerative joint disease (mechanical wear and tear on the joints of the skeleton due to physical activity), enamel hypoplasias (enamel deficiency commonly found in the teeth of people whose early childhood was biologically stressful), and trauma. The health index declined by an average of 2.5 percentage points per millennium, from 6,000 BCE until 1500 CE.

[6] In particular, during the initial process of European urbanization in which the percentage of the urban population increased six-fold from about 3% in 1520 to nearly 18% in 1750 [de Vries (1984) and Bairoch (1988)], life expectancy at birth fell in England from about 40 at the end of the 16th century to about 33 in the beginning of the 18th century while mortality rates increased by nearly 50% (Wrigley and Schofield, 1981). Furthermore, Clark and Hamilton (2003) find that in England during the early part of the 17th century, the average number of surviving offspring was nearly 50% higher among rural families in comparison to urban families, controlling for literacy.

[7] There are numerous examples of rapid evolutionary changes among various species that were triggered by significant changes in the environment. The color change that peppered moths underwent during the 19th century is a classic example of evolution in nature [See Kettlewell 1973]. Before the Industrial Revolution light-colored English peppered moths blended with the lichen-covered bark of trees. By the end of the 19th century a black variant of the moth, first recorded in 1848, became far more prevalent than the lighter varieties in areas in which industrial carbon removed the lichen and changed the background color. Hence, a significant evolutionary change occurred within a time period that correspond to only hundreds of generations. Moreover, evidence from Daphne Major in the Galapagos suggests that significant evolutionary changes in the distribution of traits among Darwin's Finches occurred within few generations due to a major drought [Grant and Grant 1989]. Other evidence, including the dramatic changes in the color patterns of guppies within 15 generations due to changes in the population of predators, are surveyed by Endler [1986].

cell trait, is prevalent among descendents of Africans whose engagement in agriculture improved the breeding ground for mosquitoes and thereby raised the incidence of malaria, whereas this trait is absent among descendents of nearby populations that have not made the transition to agriculture.[8]

In this research we explore the evolution of the distribution of life-history profiles (i.e., the life cycle of somatic investment and its effect on life expectancy)[9] in light of the fundamental trade-off that exists in nature between investments in somatic maintenance (and thus longevity and future reproduction) and the resources available for current reproduction. Evidence shows that the evolved capacity of somatic cells to carry out effective maintenance and repairs (e.g., DNA repairs, accurate gene regulation, tumor suppression, and antioxidants), governs the time taken for damage to accumulate thereby regulating longevity.[10] Experiments and observation in non-human species indicate that this trade-off exists.[11] Moreover, using an historical data set from the British aristocracy, Westendorp and Kirkwood (1998) argue that human life histories involve a trade-off between longevity and reproduction.

The analysis focuses on the evolutionary process with respect to the trade-off between parental somatic investment in each offspring and the number of offspring that can be supported.[12] Resources that are channeled towards higher somatic investment in each offspring generate higher life expectancy, but limit the number of offspring that can be raised.[13] "*Increased bearing is bound to be paid for by less efficient caring*" [Dawkins 1989, p. 116]. Thus, there is an evolutionary trade-off, regarding reproduction success, between the life expectancy of each offspring and the

---

[8] See Livingston [1958], Weisenfeld [1967] and Durham [1982].

[9] See Stearns (1992).

[10] Evidence at the molecular and cellular levels suggest that longevity is correlated with effort devoted to repair and cellular maintenance. A positive correlation is found among captive mammals between longevity and DNA repair capacity, genomic integrity, and mitochondrial ROS production. Furthermore, cell resistance to external stress is larger among long-lived species. Moreover, it should be noted that long-run adaptations that reduce extrinsic mortality (e.g., larger brains) are generally linked to increased longevity. [Kirkwood (1998)]. These long-run adaptations, however, are not the focus of the current study.

[11] See the survey of this evidence by Williams and Day (2003).

[12] As is well established in the evolutionary biology literature since the seminal work of Lack [1954], the allocation of resources between offspring 'caring' and 'bearing' is subjected to evolutionary changes. Lack (1954) suggests that clutch sizes (e.g., number of eggs per nest), among owls and other predatory vole-eating birds, for instance, are positively related to food abundance. He argues that the clutch size is selected such that under any feeding conditions fertility rates ensure the maximal reproductive success. Furthermore, Cody [1966] documents the existence of significant differences between clutch sizes of the same bird species on islands and nearby mainland localities of the same latitude. In temperate regions where food is more abundant in the mainland than on islands, the average clutch size is smaller on the islands. For instance, *Cyanoramphus novaezelandeae*, the average mainland clutch is 6.5 whereas the average in the island is 4.

[13] For instance, variations in somatic investment may manifest themselves in genetically pre-determined variations in the length of childhood and therefore in the amount of parental resources that are devoted to each offspring.

number of offspring that can be supported.[14] Similar insights would be obtained if one would have alternatively focused on the evolutionary process with respect to the trade-off between the resources allocated to current parental own somatic investments (and thus life expectancy and future reproduction success) and the resources invested in current parental reproduction.

The probability that an individual would survive to a reproduction age is affected positively by the genetically pre-determined somatic investment, and negatively by the extrinsic mortality risk that is associated with socio-environmental characteristics, which were altered by the Neolithic Revolution. A rise in mortality risk triggers a process of natural selection that alters the distribution of types within the population. Nature selects the level of somatic investment and thereby life expectancy that maximizes reproduction success in any given environment, and the distribution of these hereditary life-history traits evolves over time due to changes in the environment. As long as the adverse effect of population density on the survival probability is lower for individuals who are genetically pre-disposed for higher somatic investment, the evolutionary optimal level of somatic investment is an increasing function of the extrinsic mortality risk.

Thus, the rise in the extrinsic mortality risk in the course of the Neolithic Revolution shifted the evolutionary advantage towards individuals with higher somatic investment and thus higher life expectancy. Furthermore, the rise in the extrinsic mortality risk and its interaction with the forces of natural selection induced a non-monotonic time path of life expectancy. During the Neolithic Revolution life expectancy declined, as long as the extrinsic mortality risked increased and the distribution of types in the population did not evolve considerably. However, the onset of the evolutionary process increased the prevalence of individuals with higher somatic investment in the population and ultimately generated a rise in life expectancy.[15]

The theory suggests therefore that regions that experienced an earlier transition to agricultural communities, begun earlier the evolutionary process that increased the representation of individuals who are genetically pre-disposed towards higher somatic investment and higher life expectancy. The onset of the occurrence of the Neolithic Revolution, only 10,500 years ago, sug-

---

[14] Consistent with the existence of this trade-off, recent molecular and behavioral genetic research across historical and modern data from the United States and Europe suggests that fertility behavior has a significant hereditary component [Rodgers et al. 2001a]. For instance, as established recently by Kohler et al. [1999] and Rodgers et al. [2001b] based on the comparison of fertility rates among identical and fraternal twins born in Denmark during the periods 1870-1910 and 1953-1964, slightly more than one-quarter of the variance in completed fertility is attributable to genetic influence. These findings are consistent with those of Rodgers and Doughty [2000] based on kinship data from the United States.

[15] In the long-run the decline in the extrinsic mortality risk due to the improvements in medical technology and health infrastructure may reverse the evolutionary process outlined in this research.

gest that this evolutionary process has not been completed, and thus differences in the timing of the Neolithic Revolution across regions should be reflected in variations in the genetic component of life expectancy in the contemporary human population. In particular, the theory predicts that descendants of regions that experienced the Neolithic Revolution earlier would have a higher life expectancy today in comparison to others who live in similar socioeconomic conditions.

The prediction of the theory regarding the effect of the time passed since of the Neolithic Revolution on life expectancy is examined empirically. The empirical analysis demonstrates that a significant portion of contemporary variations in life expectancy across countries can be traced to the weighted average of the time passed since the ancestors of the population of each country experienced the Neolithic Revolution. In particular, controlling for geographical and continental characteristics of each country, as well as income, education and health expenditure per capita, every 1000 years of earlier Neolithic transition contributes to life expectancy 1.6-1.9 years. Thus, for instance, the European population that experienced the Neolithic Revolution on average 3160 years earlier than the African population would be expected to live 5 years longer, even if the gap in the socioeconomic conditions between these continents will be eliminated. Alternatively, Americans from European decent would be expected to live five years longer than Americans from African decent with similar socioeconomic background.

2 Related Literature

Evolutionary biologists suggest two complementary theories for the evolution of senescence (i.e., persistent decline in the somatic function of an organism with age) and thus of life expectancy.[16] The *mutation accumulation theory of aging* [Medawar, 1946] suggests that late-acting deleterious mutations have a smaller negative effect on the survival of the genes and aging therefore is an inevitable outcome of the declining force of natural selection in older age. *The antagonistic pleiotropy theory* [Williams, 1957] suggests that late-activating deleterious genes may be favored by natural selection and may be actively accumulated in population if they have a beneficial reproductive effects in early stages of life. In particular, *the disposable soma theory* [Kirkwood, 1977] examines the optimal allocation of metabolic resources between reproduction and maintenance.

Our theory advances the disposable soma theory, exploring the implications of the process

---

[16] An earlier theory that is widely considered among biologists as inconsistent with the evidence is the *theory of programmed death* (Weismann, 1882). It suggests that aging is beneficial and even necessary at the species level in order to free resources for the younger generation.

of economic development on the evolution of the distribution of life-history profiles (i.e., the life cycle of somatic investment and maintenance) within the human species since the onset of the Neolithic Revolution. The proposed theory demonstrates that if the effect of a *rise* in the extrinsic mortality risk on the survival probability can be mitigated by an increase in somatic investment, then it would necessarily generate an increase in the (evolutionary optimal) level of somatic investment and may thereby prolong longevity.[17]

The implications of the interaction between the process of economic development and human evolution have been explored in recent years.[18] Galor and Moav (2002) suggest that during the epoch of Malthusian stagnation traits that are complementary to the process of development, in particular higher valuation for offspring quality, generated an evolutionary advantage and their representation in the population gradually increased. This selection process and its effect on investment in human capital stimulated technological progress and ultimately triggered a reinforcing interaction between investment in human capital and technological progress that brought about the Industrial Revolution, a demographic transition and a shift to the modern regime of sustained economic growth.[19] Ofek (2001) and Saint Paul (2003) examine the effect of the emergence of markets on the evolution of heterogeneity in the human population. Lagerlof (2007) examines the evolution of human body size in the process of development, and Borghans, Borghans and ter-Weel (2004) analyze the effect of human cooperation on the evolution of Major Histocompatibility Complex (MHC).[20]

Robson and Kaplan (2003) examine the evolutionary optimal human brain size and life

---

[17] Most of the literature in evolutionary biology focused on the effect of a rise in the extrinsic mortality rate that cannot be mitigated by an increase somatic investment, arguing therefore that in this type of environment an increase in the extrinsic mortality rate would generate a decline in somatic investment and thereby a decline in life expectancy. Recently, however, in light of a wide range of compelling evidence, it has been recognized that the adverse effect of a rise in extrinsic mortality risk can be counteracted by an increase in somatic investment [Williams and Day (2003)]. In particular, Reznick et al. (2004) demonstrates that guppies that were exposed to higher extrinsic mortality risk had lower intrinsic mortality rate.

[18] The evolution of a wide range of attributes such as time preference, risk aversion, and altruism, in a *given* economic environment, has been extensively explored in the economic literature, as surveyed by Bowles (1998) and Robson (2001). The dynamics of evolutionary processes is explored as well (e.g., Benaim and Weibull (2003)).

[19] The theory is applicable for either social or genetic intergenerational transmission of traits. A cultural transmission is likely to be more rapid and may govern some of the observed differences in fertility rates across regions. The interaction between cultural and genetic evolution is explored by Boyd and Richardson (1985) and Cavalli-Sforza and Feldman (1981), and a cultural transmission of preferences is examined by Bisin and Verdier (2000). Clark and Hamilton (2006) provides evidence from England in the 1630s, supporting the view that the number of surviving offspring increases with wealth and education.

[20] The Darwinian methodology has been employed in the study of human behavior within the sociobiology literature (e.g., Wilson [1975]) and in a sequence of studies about the evolution of preferences surveyed by Bowles [1998] and Robson [2001], within the economics literature. The focus of these models is fundamentally different. They are primarily designed to explain the determination of preference (e.g., Becker [1976], and Hansson and Stuart [1990]).

expectancy in the context of hunter-gatherer societies that were prevalent during the two million years that preceded the Agricultural Revolution.[21] They argue that a *decrease* in the extrinsic mortality risk that was faced by the human population led to an increase in somatic investment leading to larger brain size and higher life expectancy. In contrast to the basic premise of Robson and Kaplan (2003) that the extrinsic mortality risk decreased in the course of human existence, evidence about the rise of population density and the lack of significant improvements in technology prior to the Mesolithic period, suggests in fact that extrinsic mortality risk increased in this era, consistently with the findings of Steckel (2004). For instance, the transition from the Paleolithic period to the Mesolithic hunter-gatherer economies corresponded to the disappearance of large game animals and the consequent adoption of broad spectrum foraging patterns aimed at a wider array of small animals, seeds, and aquatic foods resulting in a decline in nutrition and thus human health [Cohen (1989), and Acsa'di and Nemeskeri (1970, p. 169)]. Thus, our theory and empirical analyzes suggests, in contrast, that an *increase* in the extrinsic mortality risk led in fact to higher somatic investment, that mitigated the negative effect of the external environment, and eventually led to higher life expectancy. Moreover, the theory offers an explanation for the observed non-monotonic evolution of life expectancy in the context of the Agricultural Revolution, despite the apparent increase in the extrinsic mortality risk during these periods of increased population density.

Finally, in contrast to our evolutionary approach to the understanding of the time-path of life expectancy in the last 10,000 year, existing economic theories have focused on the contribution of the advancement of health infrastructure, medical technology and education to the rise in life expectancy in recent centuries, as documented by Fogel (1994) and Mokyr (1998), and explored by Erlich and Lui (1991), Galor and Weil (1999), Boucekkine, de la Croix and Licandro (2003), Cervellati and Sunde (2005), Lagerlof (2003), Hazan and Zoabi (2006), Weisdorf (2004), Weil (2005), Soares (2005), Iyigun (2005) and Strulik (2007).

3 The Basic Structure of the Model

Consider an economy that consists of individuals that are distinguished genetically by the resources that they allocate to somatic investment, repair and maintenance, and thereby by their

---

[21] Similarly, abstracting from the process of economic development, Lee (2003) examines the evolution of life expectancy in light of the effect of Intergenerational transfers, during the post fertility period, on offspring's quality.

life expectancy. Resources that are channeled towards higher somatic investment of each offspring generate higher life expectancy, but limit the number of offspring that can be raised. Thus, there is an evolutionary trade-off, regarding reproduction success, between the life expectancy of each offspring and the number of offspring that can be supported.

A rise in mortality risk triggers a process of natural selection that alters the distribution of types within the population. Nature selects the life-history profile (i.e., the life cycle of somatic investment) and thereby life expectancy that maximizes reproduction success, in any given environment and the distribution of these hereditary life-history traits evolves over time due to changes in the environment that are induced by increases in population density. Thus, the evolutionary process within the human population may lead to a reduction in mortality rates and an increase in life expectancy, despite the increase in extrinsic mortality risk that is associated with the rise in population density.

The economy is implicitly characterized by a Malthusian environment in which the growth of income per capita is constrained by the increase in the size of the population, whereas population size is constrained by the availability of resources as well as by the technological level.[22]

3.1 Individuals

Individuals are ex-ante identical except for their genetic disposition towards somatic investment and thus life expectancy. Individuals may live for either one period (childhood) or two periods (childhood and adulthood), i.e., children are subjected to a mortality risk that may prevent them from reaching adulthood. In their childhood, individuals consume part of their parental income. Those who survive and reach adulthood, work and allocate their income to consumption and child rearing. Reproduction is a-sexual and each individual is therefore born to a single parent.[23]

3.1.1 Somatic Investment, Extrinsic Mortality, and Life Expectancy

The survival probability of individuals depends upon their somatic investment and the extrinsic mortality risk that characterizes the environment in which they live. Individuals are distinguished by the resources that they allocate to somatic investment, repair, and maintenance, and thereby by their life expectancy. Individuals that are characterized by a higher, genetically predetermined,

---

[22] Consistently with the Malthusian theory, Clark and Hamilton (2006) and Botticini and Siow (2005) provide evidence that in pre-industrial society wealthier families had more surviving children, and Kelly (2004) provides evidence at the macro level regarding the effect of wages on population growth.

[23] The modeling of sexual reproduction would clutter the analysis, but would not alter the basic hypothesis.

somatic investment generate higher life expectancy. Somatic investment during childhood, μ, varies across individuals.[24] This genetic trait is transmitted imperfectly from parent to offspring, maintaining the variation in the population.

The survival probability of each type of individual depends upon the extrinsic mortality risk that is associated with the environment and the individual's genetically pre-determined somatic investment. The extrinsic mortality risk, x, is affected by the socioeconomic environment, population density and the level of health infrastructure.[25]

The probability, P, that an individual would survive to adulthood is affected positively by the genetically pre-determined somatic investment in childhood, μ, and negatively by the extrinsic mortality risk, x;

$$P = P(\mu, x). \tag{1}$$

Thus, life expectancy of individual $E = 1 + P$, is affected positively by the genetically pre-determined somatic investment in childhood, μ, and negatively by the extrinsic mortality risk, x;

$$E = E(P(\mu, x)). \tag{2}$$

The biological upper bound on life expectancy for individual of type i, $E^{\max}$, is reached when the extrinsic mortality risk is equal to zero, i.e.,

$$E^{\max} = E(P(\mu, 0)). \tag{3}$$

It is assumed that individuals whose genetically determined somatic investment is below a threshold $\bar{\mu}(x)$ would not survive and their type would become extinct. That is,

$$P = P(\mu, x) \begin{cases} > 0 \quad if \quad \mu > \bar{\mu}(x) \\ = 0 \quad if \quad \mu \leq \bar{\mu}(x), \end{cases} \tag{4}$$

---

[24] Variations in somatic investment may manifest themselves in genetically pre-determined variations in the length of childhood and therefore in the amount of parental resources that are devoted to each offspring. Clearly, the level of somatic investment of a given type may reflect a rigid component that is unaffected by the environment, as well as a flexible one that may react to the existing environment and individual choice. Although the model abstracts from the existence of flexible components, as would become apparent the qualitative analysis would not be affected if a flexible component would be integrated into the analysis.

[25] Variations in socioeconomic organizations (e.g., hunter-gatherers, agricultural society, urban society) may alter the relationship between population size and "effective" population density. In particular, the transitions from a hunter gatherer society to an agricultural one and from a rural society to an urban one increase the effective population density (for a given population size) and thus the extrinsic mortality risk

where for all x, $\bar{\mu}(x) > 0$. Moreover, for $\mu > \bar{\mu}(x)$, $P_{\mu}(\mu, x) > 0$, $P_{\mu\mu}(\mu, x) < 0$, $P_x(\mu, x) \leq 0$ and (a) the threshold level of somatic investment below which individuals do not survive, $\bar{\mu}(x)$, increases with the harshness of the environment, i.e.,

$$\bar{\mu}'(x) > 0; \tag{A1}$$

(b) the adverse effect of population density on the survival probability is (weakly) lower for individuals who are genetically pre-disposed for higher somatic investment and somatic investment increases the probability of survival in decreasing rates, i.e.,

$$P_{x\mu}(\mu, x) \geq 0 \qquad \text{for } \mu > \bar{\mu}(x). \tag{A2}$$

3.1.2 Fertility Across Types

Parental income, y, is allocated between consumption and child rearing. In particular, parents divide their income, y, between consumption, c, and the cost associated with raising n children, μn, where μ is the somatic investment of each child.[26] Thus, the individual resource constraint is

$$\mu n + c \leq y. \tag{5}$$

In a Malthusian environment in which population growth is affected positively by the level of income per capita, a fraction, β, of parental resources are devoted to childrearing and a fraction $1 - \beta$ to consumption.[27] Hence, the number of children of each parent is a function of their children's genetically predisposed somatic investment, μ [28]

$$n = \beta y / \mu. \tag{6}$$

Thus, consistent with the fundamental features of the Malthusian environment - the economic environment that is at the center of the proposed theory - the number of children is an increasing function of parental income.[29] In addition, parents whose children's somatic investment is higher would have fewer children.

---

[26] If some non-surviving children will parish in the beginning of the childhood period, rather than in the end, as it is currently assumed, no qualitative change will occur. The cost of those non-surviving children will be zero, and therefore, n_t^i will stand for the number of surviving children that completed their childhood period. Furthermore, the incorporation of time as well as real resources as inputs in the production of offspring would not affect the analysis qualitatively, as shown in the next footnote.

[27] This allocation of parental resources could be devided from a utility maximization. In particular, if preferences are homothetic, the fraction of parental resources that will be devoted to childrearing will be β.

[28] For simplicity it is assumed that β is identical across individuals.

[29] See for instance, Boyer (1989) and Clark and Hamilton (2006). The positive effect of the parental income on

3.2 Evolutionary Optimal Level of Life Expectancy

This section examines the evolutionary optimal level of somatic investment in a given environment, x (i.e., the level of somatic investment that generate the largest number of surviving offspring). Individuals who posses this genetic predisposition will dominate the population in the long run.

Let, μ^*, be the genetically determined level of somatic investment that, given the individual allocation of resource to child rearing (6), will generate the largest number of surviving offspring, $P(\mu, x)n$, and let $E^* = E(P(\mu^*, x))$ be the evolutionary optimal level of life expectancy. It follows that

$$\begin{array}{rl} \mu^* \quad = & \arg\max P(\mu, x)n \\ \text{s.t.} & n = \beta y/\mu \end{array} \tag{7}$$

Lemma 1 *The genetically determined level of somatic investment,* μ^**, that generates the largest number of surviving offspring, is a unique single-valued function of the environment,* x :

$$\mu^* = \mu^*(x) > \bar{\mu}(x),$$

and the evolutionary optimal level of life expectancy, E^**, is therefore*

$$E^* = E(P(\mu^*(x), x))$$

Proof. Since $P = P(\mu, x) = 0$ for $\mu \leq \bar{\mu}(x)$, it follows that $\mu^*(x) > \bar{\mu}(x)$. Further, as follows from the first order conditions for the maximization problem (7), for $\mu^*(x) > \bar{\mu}(x)$,

$$F(\mu^*, x) \equiv P_\mu(\mu^*, x)\mu^* - P(\mu^*, x) = 0. \tag{8}$$

Hence, since $F_\mu(\mu^*, x) = P_{\mu\mu}(\mu^*, x)\mu^* \neq 0$, the lemma follows from the *Implicit Function Theorem* and the definition of life expectancy. □

As follows from (8), the evolutionary optimal level of somatic investment, $\mu^*(x)$, depicted in Figure 2, is given by the unique tangency point between the function $P(\mu, x)$ and a ray from

---

the number of children, regardless of the level of income, reflects the assumption that child rearing is associated with a real cost, without any time cost. If a time cost would be added, it would generate the Malthusian structure in low levels of income but fertility rates will be bounded in a higher level of income. In particular, let τ be the time cost associated with an offspring. Individuals' budget constraint would become $n(y\tau + \mu) + c \leq y$ and the optimization would imply that $n = \beta y/(\tau y + \mu)$. Hence, as in the formulation without a time cost, the number of children is an increasing function of income and a decreasing function of somatic investment. However, under this specification, the number of children is a strictly concave function of income, bounded from above by β/τ.

the origin. Thus, at the optimum, reproductive success is maximized if the marginal return from an increase in somatic investment, $P_\mu(\mu^*, x)$, (i.e., the marginal return in reproductive success to an increase in child "quality") is equal to the marginal return in reproductive success due to an increase in the investment in number of children (i.e., to investment in child "quantity"). The latter generates an increase of $(1/\mu^*)$ in the number of children, resulting in an increase of $P(\mu^*, x)/\mu^*$ in the number of surviving children.

Proposition 1 *As depicted in Figure 2,*

- *Under A1 and A2, the evolutionary optimal level of somatic investment is an increasing function of the extrinsic mortality risk, i.e.,*

$$\mu^*(x) > 0.$$

- *Under A1 and A2, the evolutionary optimal biological upper bound of life expectancy is an increasing function of the extrinsic mortality risk, i.e.,*

$$\frac{dE(P(\mu^*(x), 0))}{dx} > 0.$$

Proof. See Appendix. □

The evolutionary optimal level of somatic investment is an increasing function of the extrinsic mortality risk since the threshold level of somatic investment that permits survival is an increasing function of the extrinsic mortality risk (Figure 2). As long as the adverse effect of population density on the survival probability is (weakly) lower for individuals who are genetically pre-disposed for higher somatic investment (i.e., as long as (A2) is satisfied), the increase in the minimal somatic investment, $\bar{\mu}(x)$, that is associated with a transition to a harsher environment, implies that the evolutionary optimal investment in each offspring is larger (i.e., the tangency between the function $P(\mu, x)$ and a ray from the origin in Figure 2, would necessarily occur at a higher level of μ).[30]

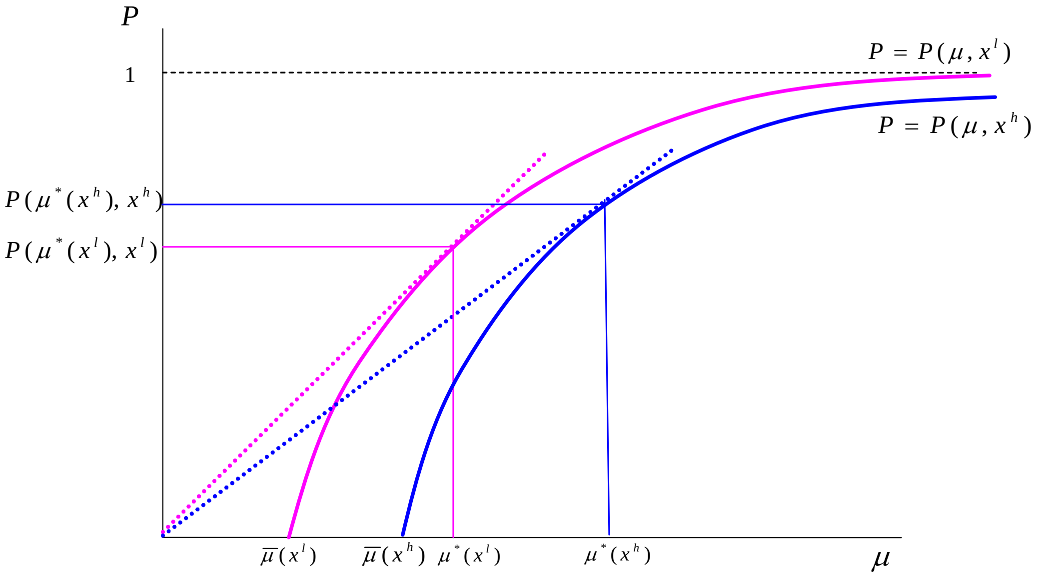

Figure 2. Evolutionary optimal levels of somatic investment and survival probability for different levels of extrinsic mortality risk: $x^h > x^l$

It follows from Lemma 1 and Proposition 1 that a permanent increase in the extrinsic mortality risk will initially generate a reduction life expectancy, but the process of natural selection that it will trigger will gradually increase somatic investment, life expectancy and the biological upper bound of life expectancy.

Despite the permanent rise in the extrinsic mortality risk, life expectancy will ultimately increase beyond its initial level, prior to the increase in the extrinsic mortality risk, if it is further assumed that the elasticity, $\eta_{P_\mu,\mu}$, of the marginal effect of somatic investment on the survival probability, $P_\mu(\mu, x)$, with respect to somatic investment, μ, is smaller than one in absolute value:

$$\eta_{P_\mu,\mu} \equiv \left| \frac{P_{\mu\mu}(\mu, x)\mu}{P_\mu(\mu, x)} \right| < 1 \qquad \text{for } \mu > \bar{\mu}(x), \tag{A3}$$

i.e., an increase in somatic investment, μ generates less than a proportional decrease in the marginal effect of somatic investment on the survival probability, $P_\mu(\mu, x)$.[31]

Proposition 2 *Under A1-A3,*[32] *the evolutionary optimal level of life expectancy is an increasing function of the extrinsic mortality risk, i.e.,*

$$\frac{dE(P(\mu^*(x), x))}{dx} > 0.$$

---

[30] For instance, if in contrast to (A2), the extrinsic component of the survival rate is independent of somatic investment then the optimal somatic investment may be negatively affected by the extrinsic mortality risk. For instance if the survival probability to adulthood $P(\mu, x) = p(\mu)(1 - x)$ then $P_{\mu x} = -p_\mu < 0$.

[31] That is, for $\mu > \bar{\mu}(L)$, the survival probability $P(\mu, L)$ is only "moderately" strictly concave function of μ.

[32] (A3) is a sufficient but not a necessary condition.

Proof. See Appendix.[33] □

Thus, the permanent rise in the extrinsic mortality risk in the course of the Neolithic Revolution initially generates a reduction in life expectancy, but due to the process of natural selection life expectancy gradually increased. Moreover, the biological upper bound of longevity increased, generating the biological infrastructure for the recent prolongation of life expectancy that was brought about by the decline in the extrinsic mortality risk due to improvements in the heath infrastructure.

4 Empirical Specifications and Findings

The theory suggests that regions that experienced an earlier transition to agricultural communities, were exposed to a longer period of evolutionary pressure that increased the representation of individuals who are genetically pre-disposed towards higher life expectancy. Since its earliest occurrence in the Middle East nearly 10,500 years ago, the average onset of the Neolithic Revolution in Asia was about 6900 years ago, 6300 years ago in Europe, 3800 in South America, 2900 in Africa, and in North America it occurred only 2300 years ago. From an evolutionary viewpoint, these are short time periods, suggesting that variations in the timing of the Neolithic Revolution across regions should be reflected in variations in the genetic component of contemporary life expectancy. In particular, the theory predicts that in a given socioeconomic environment descendants of people from regions that experienced the Neolithic Revolution earlier would have a higher life expectancy in comparison to descendants of people from regions that experienced the Neolithic Revolution later.

The prediction of the theory regarding the positive effect of the time passed since of the Neolithic Revolution on life expectancy is examined empirically. We exploit variations in the average time passed since the ancestors of the population of each country today experienced the Neolithic Revolution, as well as contemporary differences in life expectancy across countries, to identify the impact of the time passed since the Neolithic Revolution on life expectancy. Moreover,

---

[33] For instance, if

$$P(\mu, x) \begin{cases} 0 & \text{for} \quad \mu \leq x \\ (\mu - x)^{1/2} & \text{for} \quad \mu \in (x, x+1) \\ 1 & \text{for} \quad \mu > x+1 \end{cases}$$

for $x \in (0,1)$, then

$$\begin{array}{l} \mu^*(x) = 2x \\ P^* = x^{1/2}, \end{array}$$

and $\mu^{*\prime}(x) > 0$ and $dP(\mu^*(x), x)/dx > 0$.

we attempt to isolate the genetic effect on life expectancy, by controlling for plausible alternative routes for the relationship between the timing of the Neolithic Revolution and contemporary life expectancy.

The empirical analysis demonstrates that the time passed since the Neolithic transition has a positive and highly significant effect on life expectancy in the year 2000, controlling for a variety of geographical and socio-economic characteristics. Moreover, the findings lend credence to the hypothesis that one of the underlying mechanisms that contributed to contemporary life expectancy is the change in the composition of genetic traits triggered by the Neolithic Revolution.

The weighted average of the time passed since the ancestors of the population of each country today experienced the Neolithic Revolution is positively and significantly correlated with life expectancy in the year 2000, as shown in column 1 of Table 1.[34] Nevertheless, although contemporary life expectancy had no effect on the timing of the Neolithic Revolution, it does not necessarily imply that an earlier onset of the Neolithic Revolution contributed to contemporary life expectancy. In particular, one has to account for the possibility that a third factor (i.e., geographical attributes) that may be conducive for longer life expectancy today, may have permitted an earlier onset of the Neolithic Revolution.

Moreover, even if a causal effect of an earlier onset of the Neolithic Revolution on contemporary life expectancy could be established, it does not necessarily confirm the proposed genetic channel. An earlier onset of the Neolithic Revolution generated a socio-economic process that may had an impact on contemporary living standards and thereby on contemporary life expectancy, irrespective of potential changes in the composition of genetic traits.

Thus, the main empirical challenges are to account for the contribution of geographical attributes and socio-economic factors to the observed cross country correlation between the weighted timing of the Neolithic Revolution and contemporary life expectancy, and to demonstrate that the timing of the Neolithic Revolution has a significant additional effect on life expectancy that could be plausibly attributed to changes in the genetic composition of the human population.

These challenges are confronted in several ways. First we demonstrate that once we control

---

[34] The weighted average of the timing in which the population of each country experienced the Neolithic Revolution is computed based on the recently compiled data set on the timing of the Neolithic Revolution across different regions of the world (Putterman, 2006), as well as the data on post-1500 migratory patterns across the globe (Putterman, 2007).

for major geographical attributes (i.e., latitude, percentage of arable land, and continental dummies) that may have influenced the timing of Neolithic transition and possibility contemporary life expectancy, the effect of the timing of the Neolithic Revolution remains highly significant and powerful in explaining contemporary variations in life expectancy. Thus, we plausibly preclude the possibility that a third (geographical) factor governs the entire observed correlation between these two variables, establishing a causal effect of the time passed since the Neolithic Revolution on contemporary life expectancy.

Table 1 presents the analysis of the effect of the time passed since the Neolithic Revolution on life expectancy in the year 2000, accounting for variations in geographical characteristics across countries that may have jointly influenced the timing of the Neolithic Revolution and contemporary life expectancy. The results are based on linear OLS regressions, using a sample of 139 countries.[35] Regression 1 shows that in the absence of any controls, the coefficient of the time passed since the Neolithic Revolution is 4.23 years of life expectancy for every 1000 years of earlier Neolithic transition, and it is highly significant. Regression 2 incorporates exogenous geographical controls for absolute latitude and the percentage of arable land. These geographical variables, as elaborated above, are likely to have an effect on the timing of the Neolithic Revolution and could be expected to directly affect life expectancy today via climate, population density, and the level of income. The inclusion of these geographical controls suggests that the effect of the time passed since the Neolithic Revolution remains highly significant and the coefficient of the time passed since the Neolithic Revolution is 3.3 years of life expectancy for every 1000 years of earlier Neolithic transition. Furthermore, it is reassuring to note that the effects of the geographical factors on contemporary life expectancy are as one would have predicted. In particular, (a) absolute latitude (i.e. distance from the equator), that captures higher income per-capita, and possibly a less hostile disease environment, has a highly significant positive effect on life expectancy,[36] and (b) the percentage of arable land in each country, an exogenous indicator for population density, that is uncorrelated with the level of income per capita, and thus is an indicator for the extrinsic mortality risk, has a negative effect on contemporary life expectancy.

---

[35] Appendix 3 provides a comprehensive description of the data and its sources.

[36] Interestingly, as is apparent from the results presented in Table 2, the effect of the distance from the equator on life expectancy operates primarily through its effect on contemporary income per capita. Its direct effect becomes insignificant once income per capita is introduced as a control variable. Moreover, if the sample is restricted to countries that mostly consist of the descendents of the country's native population, the effect of distance from the equator vanishes, suggesting that the forces of natural selection did not operated based on distance from the equator.

Finally, Regression 3 shows that inclusion of continental dummies that capture geographical and socio-economic characteristics that are specific to each continent does not affect the significance of the results. Nevertheless, the coefficient of the effect of the timing of the Neolithic Revolution drops to 2.05 years of life expectancy for every 1000 years of earlier transition, capturing only the effect on the modest variations in life expectancy within continents in comparison to these variations across continents.

Table 1, suggests therefore, that although geographical factors are indeed important in explaining some of the observed correlation between these two variables, there exists a highly significant positive effect of the time passed since the Neolithic Revolution on contemporary life expectancy. Abstracting from variations in socio-economic characteristics, every 1000 years of earlier Neolithic transition results in 2.05 additional years of life expectancy.

Table 1. Determinants of Life Expectancy:
Accounting for Variations in Geographical Characteristics

Dependent Variable: Life Expectancy in 2000			
Explanatory Variables:	(1)	(2)	(3)
Years since Neolithic (weighted)	4.229 (0.389)***	3.302 (0.395)***	2.047 (0.484)***
Absolute Latitude		0.284 (0.044)***	0.183 (0.070)***
% arable land		-0.067 (0.04)	-0.082 (0.041)**
Continental Dummies:			
Africa			-13.482 (3.885)***
Asia			-5.202 (2.036)**
Oceania			1.379 (4.925)
North America			2.372 (3.047)
South America			1.165 (2.957)
Observations	139	139	139
R-squared	0.498	0.611	0.76

Robust standard errors in parentheses
* significant at 10%; ** significant at 5%; *** significant at 1%

Table 2 presents the analysis of the effect of the time passed since the Neolithic Revolution on life expectancy in the year 2000, accounting for variations in geographical characteristics across countries as well as for the possibility that an earlier onset of the Neolithic Revolution generated a socio-economic process that may had an impact on contemporary living standards and thereby on contemporary life expectancy, irrespective of potential changes in the composition of genetic traits. The results show that if one accounts for the effect of the contemporary socio-economic environment, as well as geographical characteristics on higher life expectancy, the effect of the timing of the Neolithic Revolution remains highly significant and rather stable in explaining contemporary variations in life expectancy.

Regression 1 of Table 2 replicates Regression 3 of Table 1 for the sample of 106 countries for which the data of socio-economic characteristics is available. It shows that for this sample of 106 countries, the effect of the time passed since the Neolithic Revolution is highly significant and, under this specification, every 1000 years of earlier Neolithic transition contributes to life expectancy 1.49 years. Regression 2 controls for the social environment index of Hall and Jones (1998), that is highly correlated (0.81) with the level of income per capita in the year 2000, but is plausibly exogenous to life expectancy in the year 2000. The effect of the time passed since the Neolithic Revolution remains highly significant and, under this specification, every 1000 years of earlier Neolithic transition contributes to life expectancy 1.90 years. Regressions 3-7, add additional controls for socio-economic development (i.e., income per-capita, education, and health expenditure per capita) that are likely to be affected by the level of life expectancy in the year 2000. It is important to note that their inclusion has virtually no impact on the magnitude of the effect of the time passed since the Neolithic Revolution on contemporary life expectancy. Regression 3 examines the effect of the level of income per-capita in the year 2000. As one would expect, the log of the level of income per capita has a highly significant correlation with life expectancy in the year 2000. Nevertheless, the effect of the time passed since the Neolithic Revolution on life expectancy remains highly significant and rather stable and, under this specification, every 1000 years of earlier Neolithic transition contributes to life expectancy by 1.72 years. Regression 4 replicates Regression 3 for a smaller sample of 86 countries on which education and health expenditure data is available. In this sample every 1000 years of earlier Neolithic transition contributes to life expectancy by 1.63 years. Regression 5 shows that the addition of a control for the level of education in the year 2000, does not alter the results and the effect of the time passed since the Neolithic Revolution remains highly significant and very stable and, under this specification, every 1000 years of earlier Neolithic transition contributes to life expectancy by 1.66 years. The level of education in the year 2000 is insignificant in explaining life expectancy in the year 2000, since it is highly correlated with the level of income per capita in the year 2000. Regression 6 adds a control for the log of the level of health expenditure per capita. Once again, this control is insignificant and it does not alter the results and the effect of the time passed since the Neolithic Revolution remains highly significant and remarkably stable. Under this specification, every 1000 years of earlier Neolithic transition contributes to life expectancy by 1.82 years.

Moreover, to further alleviate the concerns about the inclusion of potentially endogenous controls variables, we demonstrate that if one includes lagged values of these variables in the years 1960, the coefficient on the time passed since the Neolithic Revolution remains highly significant and virtually unchanged in magnitude. In particular, as reported in Regression 7, controlling for geographical and continental characteristics of each country, as well as income and education in the years 1960, under this specification, every 1000 years of earlier Neolithic transition results in 1.73 additional years of life expectancy.[37]

Finally, Regression 8, demonstrates that the migratory patterns in the world in the past 500 years and the selection that it may represents is not the source of the results. In particular, if for instance, one restricts the sample of countries to the 42 countries whose at least 90% of their population are descendants of natives in the country in the year 1500, then every 1000 years of earlier Neolithic transition results in 1.48 additional years of life expectancy.[38]

Thus Table 2 suggests that, accounting for geographical and socio-economic factors that are associated with the timing of the Neolithic Revolution as well as with contemporary life expectancy, there exists an additional highly significant positive effect of the time passed since the Neolithic Revolution on contemporary life expectancy. Every 1000 years of earlier Neolithic transition results in 1.63-1.90 additional years of life expectancy, beyond the potential contribution of an earlier Neolithic transition, and the geographical factors that permitted it, to contemporary life expectancy.

---

[37] The sample in Regression 7 is smaller, consisting of 68 countries for which data on education in the year 1960 and the rest of the variables is available. It should be noted that for the same sample of 68 countries, the coefficient remain nearly the same (i.e., 1.78) if one controls instead for education in the year 2000. Moreover, controlling instead for income per capita and the level of education in the year 1980 does not alter the results. The coefficient on the time passed since the Neolithic Revolution remains highly significant and slightly higher at a level of 1.77 years of life expectancy for every 1000 years of earlier transition.

[38] Similarly, if the sample is restricted to the 50 (32) countries whose at least 75% (95%) of their population are descendants of native in the country in the year 1500, every 1000 years of earlier Neolithic transition results in 1.61 (1.31) additional years of life expectancy.

Table 2. Determinants of Life Expectancy:
Accounting for Variations in Geographical and Socioeconomic Characteristics

Dependent Variable:	Life Expectancy in 2000							
Explanatory Variables:	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)
Years since Neolithic	1.491	1.9	1.717	1.634	1.662	1.817	1.73	1.481
(weighted)	(0.574)**	(0.554)***	(0.451)***	(0.436)***	(0.436)***	(0.441)***	(0.522)***	(0.468)***
Absolute Latitude	0.23	0.175	0.02	-0.079	-0.086	-0.052	-0.041	-0.065
	(0.080)***	(0.073)**	(0.061)	(0.052)	(0.054)	(0.061)	(0.074)	(0.110)
% arable land	-0.098	-0.034	0.021	-0.009	-0.008	0.002	-0.04	-0.056
	(0.048)**	(0.046)	(0.041)	(0.046)	(0.047)	(0.044)	(0.069)	(0.047)
Social infrastructure		15.666	3.122	1.933	1.752	3.511	8.969	-4.35
		(3.864)***	(4.190)	(4.266)	(4.261)	(3.921)	(4.358)**	(11.828)
Ln GDP/pc 2000			3.852	4.096	3.785	6.827		6.74
			(0.654)***	(0.809)***	(0.980)***	(2.471)***		(3.377)**
Education 2000					0.252	0.323		0.45
					(0.366)	(0.363)		(0.489)
Ln Health Exp/pc 2000						-3.156		-1.642
						(1.992)		(3.037)
Ln GDP/pc 1960							3.633	
							(1.183)***	
Education 1960							-0.019	
							(0.566)	
Continental Dummies:	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes
Observations	106	106	106	86	86	86	68	42
R-squared	0.799	0.829	0.87	0.883	0.884	0.884	0.87	0.926

Robust standard errors in parentheses
* significant at 10%; ** significant at 5%; *** significant at 1%

The results in Tables 1 and 2 demonstrate that the timing of the Neolithic Revolution has a significant additional effect on life expectancy beyond the ones attributed to geographical and socio-economic factors. In particular, Figure 3 demonstrates that the weighted average of the time passed since the ancestors of the population of each country today experienced the Neolithic Revolution has highly significant effect (of 1.66 years for every 1000 years of earlier transition) on life expectancy in the year 2000.

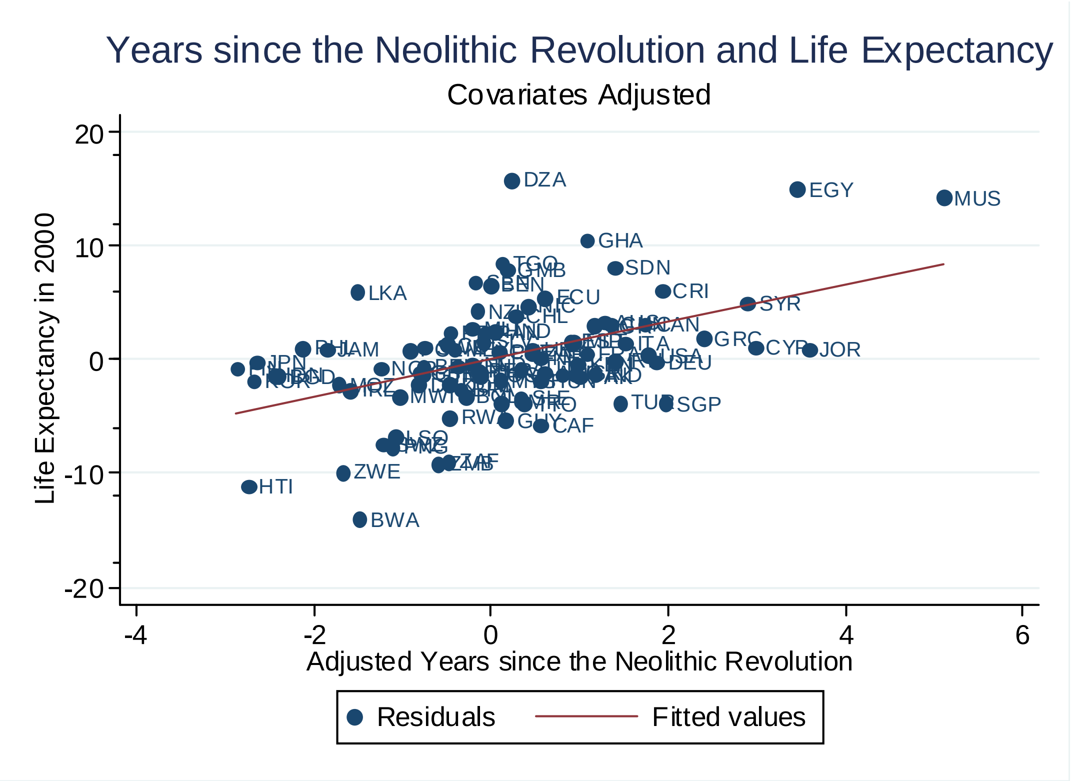

Figure 3. The Effect of the Timing of the Neolithic Revolution and Life Expectancy: Controlling for Geographical and Socioeconomic Characteristics

The remaining empirical challenge is to lend credence to the hypothesis that one of the underlying mechanisms that contributed to contemporary life expectancy is the change in the composition of genetic traits triggered by the Neolithic Revolution. Tables 3 and 4 provide additional tests that are designed to increase the confidence that changes in the genetic composition of the human population could plausibly explain the part of the effect of the timing of the Neolithic Revolution on contemporary life expectancy that could not be attributed to geographical and socio-economic factors.

Table 3 is designed to demonstrate that, consistently with the proposed theory, the Neolithic Revolution triggered a selection of individuals with a more responsive immune system. Table 3 presents the results of the examination of the effect of the time passed since the Neolithic Revolution on the fraction of years lost to infectious diseases. If other factors, that were unaccounted for, contributed to effect of the timing of the Neolithic Revolution on contemporary life expectancy then one should expect that they would have a differential effect on the sources of mortality i.e. mortality from: infectious diseases, non-infectious diseases, and all other sources (e.g., accidents, suicide, violence). The results presented in Table 3 strengthens the genetic interpretation for the effect of the timing of the Neolithic Revolution on contemporary life expectancy that could not be attributed to geographical and socio-economic factors. It shows that an earlier Neolithic transition reduces significantly the likelihood of mortality from infectious diseases in comparison to mortality from other sources.

Regression 1, in Table 3, shows that in the absence of any controls, the time passed since the Neolithic Revolution has a highly significant negative effect on the percentage of year of life lost in the year 2002 due to infectious diseases.[39] Regression 2 incorporates exogenous geographical controls for absolute latitude and the percentage of arable land. These geographical variables, as elaborated above, are likely to have an effect on the timing of the Neolithic Revolution and could be expected to directly affect mortality from infectious diseases today via climate, population density, and the level of income. The inclusion of these geographical controls does not effect the qualitative results. The effect of the time passed since the Neolithic Revolution remains highly significant and every 1000 years of earlier Neolithic transition reduces the fraction of years of life lost in 2002 due to infectious diseases by 6.67 percentage points. Furthermore, it is reassuring to note that the effects of the geographical factors on contemporary life expectancy is as one would have predicted. In particular, (a) absolute latitude (i.e., distance from the equator), that captures higher income per-capita, and possibly a less hostile disease environment, has a highly significant negative effect on mortality from infectious diseases,[40] and (b) the percentage of arable land in each country, an exogenous indicator for population density, that is uncorrelated with the level of income per capita, and thus is an indicator for the extrinsic mortality risk, has a positive, although insignificant effect on mortality from infectious diseases. Finally, Regression 3 shows that inclusion of continental dummies that capture geographical and socio-economic characteristics that are specific to each continent does not affect the significance of the results and the coefficient on the effect of the timing of the Neolithic Revolution drops to -4.48 years for

---

[39] The variable Years of life lost (YLLs) takes into account the age at which deaths occur by giving greater weight to deaths occurring at younger ages and lower weight to deaths occurring at older ages. The YLLs (percentage of total) indicator measures the YLLs due to a particular cause of death as a proportion of the total YLLs lost due to premature mortality in the population. (See Data Appendix for definition, data sources and methods of estimations).

[40] Interestingly, as is apparent from the results presented in Table 2, the effect of the distance from the equator on life expectancy operates primarily through its effect on contemporary income per capita. Its direct effect becomes insignificant once income per capita is introduced as a control variable. Moreover, if the sample is restricted to countries that mostly consist of the decedents of the country's native population, the effect of distance from the equator vanishes, suggesting that the forces of natural selection has not operated based on distance from the equator.

every 1000 years of earlier transition.

Regression 4 of Table 3 replicates Regression 3 of Table 3 for the sample of 86 countries for which the data of socio-economic characteristics is available. It shows that for this sample of 86 countries, the effect of the time passed since the Neolithic Revolution is highly significant and every 1000 years of earlier Neolithic transition reduces the fraction of years of life lost in 2002 due to infectious diseases by 3.42 percentage points. Regression 5 controls for the social environment index of Hall and Jones (1998)), that is highly correlated (0.81) with the level of income per capita in the year 2000, but is plausibly exogenous to life expectancy in the year 2000. The effect of the time passed since the Neolithic Revolution remains highly significant and every 1000 years of earlier Neolithic transition reduces the fraction of years of life lost in 2002 due to infectious diseases by 4.23 percentage points. Regressions 6, adds additional controls for socio-economic development (i.e., income per-capita, education, and health expenditure per capita) that are likely to be affected by the level of life expectancy in the year 2000. It is important to note that their inclusion has a minor impact on the magnitude of the effect of the time passed since the Neolithic on contemporary life expectancy. As one would expect, the level of income per capita and the level of education have highly significant negative effect on mortality from infectious diseases.[41] Nevertheless, the effect of the time passed since the Neolithic Revolution on life expectancy remains highly significant and rather stable and every 1000 years of earlier Neolithic transition reduces the fraction of years of life lost in 2002 due to infectious diseases by 3.91 percentage points.

Thus Table 3 suggests that the channel through which the timing of the Neolithic Revolution affect contemporary life expectancy is through reduction in mortality from infectious diseases, lending credence to the hypothesis that a selection of genetic pre-disposition towards a more responsive immune system that was triggered by the Neolithic Revolution is a major factor

---

[41] Health expenditure per capita, which is highly correlated with income per capita, has an insignificant effect on mortality from infectious diseases.

in existing variation in contemporary life expectancy across countries.

Table 3. Determinants of the Percentage of Years Lost due to Infectious Disease:

	Dependent Variable: % of Years of Life Lost to Infectious Diseases in 2002					
Explanatory Variables:	(1)	(2)	(3)	(4)	(5)	(6)
Years since Neolithic	-10.248	-6.664	-4.476	-3.419	-4.233	-3.903
(weighted)	(0.983)***	(0.933)***	(1.119)***	(1.430)**	(1.359)***	(1.091)***
Absolute Latitude		-1.026	-0.614	-0.426	-0.324	0.156
		(0.095)***	(0.158)***	(0.171)**	(0.148)**	(0.150)
% arable land		0.064	0.156	0.313	0.19	0.071
		(0.093)	(0.085)*	(0.119)**	(0.108)*	(0.086)
Social infrastructure					-29.623	7.322
					(9.490)***	(7.626)
Ln GDP per capita 2000						-7.099
						-5.107
Education 2000						-2.387
						(0.832)***
Ln Health Exp/pc 2000						-0.243
						(4.472)
Continental Dummies	No	No	Yes	Yes	Yes	Yes
Observations	139	139	139	86	86	86
R-squared	0.467	0.715	0.822	0.834	0.855	0.908

Robust standard errors in parentheses

* significant at 10%; ** significant at 5%; *** significant at 1%

The final test is designed to further disentangle the genetic mechanism from the geographical and socio-economic channels in the effect of the Neolithic Revolution on contemporary life expectancy. Consider for the sake of illustration a country whose entire current population are descendants of immigrants. The time passed since the Neolithic Revolution in this country captures the geographical attributes that permitted the onset of the Neolithic Revolution and their potential effects on the socio-economic and health environment, and thus on contemporary life expectancy. In contrast, the *weighted average of* time passed since the ancestors of the current population experienced the Neolithic Revolution, capture only the traits that are embodied in the current population and were transmitted intergenerationally either genetically or culturally. In the existing data set, the average fraction of the native population is about 0.72, and the standard error is about 0.34. Thus, the *weighted average of* the time passed since the ancestors of the population of each country today experienced the Neolithic Revolution, places more weight on the "portable" component of the Neolithic experience. Namely, the component that the population today inherited from their non-native ancestors. In contrast, the time passed since the Neolithic Revolution in each country, places relatively more weight on the effect of the Neolithic transition on individuals via the geographical mechanism.

We exploit the difference between the time passed since the Neolithic Revolution in each country and the *weighted average of* time passed since the ancestors of the population of each country today experienced the Neolithic Revolution to disentangle the genetic mechanism from the geographical and socio-economic channels in the effect of the Neolithic Revolution on contemporary life expectancy. [42]

Table 4 demonstrates that the time passed since the Neolithic revolution has indeed a stronger and more significant effect on contemporary life expectancy via the portable (genetic) component. Regression 1 shows that the weighted time passed since the Neolithic Revolution has a highly significant positive effect on life expectancy in the year 2000, capturing alone nearly 50% of the variations in life expectancy. Every 1000 year of earlier transition is associated with 4.23 additional years in life expectancy. In contrast, Regression 2 demonstrates that the time passed since the country of residence experienced the Neolithic Revolution, (i.e., an index that places more weight on the characteristics of countries as opposed to those of individuals) is less powerful in explaining the variations in life expectancy in the year 2000, capturing only 28% of the variation and associated with smaller coefficient of 2.78 years in life expectancy with every 1000 year of earlier transition. Moreover, as demonstrated in Regression 3, if both the weighted time passed since the Neolithic Revolution and the time passed since the country of residence experienced the Neolithic Revolution are included in the regression, only the time passed since the ancestors of the population of each country today experienced the Neolithic Revolution has a positive (and highly significant) effect on life expectancy in the year 2000. Finally, Regression

---

[42] It should be noted that the qualitative results are unaffected by the inclusion of a control for the percentage of the non-native population in each country.

4 demonstrates that once all the geographical and socio-economic controls, used in Table 2, are included, the effect of the portable (genetic) component as captured by the weighted years since the Neolithic Revolution remains positive, highly significant, and stable relative to its magnitude in table 2, whereas the effect of, the more geographically-based, years since transition nearly vanishes.

Table 4. Determinants of Life Expectancy:
Country-Specific vs. Individual-Specific Characteristics

Dependent Variable: Life Expectancy in 2000				
Explanatory Variables:	(1)	(2)	(3)	(4)
Years since Neolithic (weighted)	4.229 (0.389)***		6.873 (0.542)***	1.885 (0.699)***
Years since Neolithic (unweighted)		2.777 (0.392)***	-2.619 (0.421)***	-0.072 (0.635)
Absolute Latitude				-0.052 (0.061)
% arable land				0.002 (0.045)
Social infrastructure				3.52 (3.944)
Ln GDP per capita 2000				6.82 (2.498)***
Education 2000				0.314 (0.358)
Ln Health Exp/pc 2000				-3.155 (2.008)
Continental Dummies	No	No	No	Yes
Observations	139	139	139	86
R-squared	0.498	0.276	0.549	0.888

Robust standard errors in parentheses
* significant at 10%; ** significant at 5%; *** significant at 1%

It should be noted that there is a strong positive correlation between the unadjusted years since transitions and the percentage of the population who are descendants of natives in the same country in the year 1500. Namely, countries that experienced the Neolithic revolution later and thus had lower population density, were more attractive to migrants. Thus, the positive correlation between the timing of the Neolithic Revolution and contemporary life expectancy does not reflect a selection of individuals with higher life expectancy into regions that are geographically more prosperous, as reflected by earlier Neolithic Transition.

Thus, the empirical analysis demonstrates that a significant portion of contemporary variations in life expectancy across countries can be traced to the weighted average of the time passed since the ancestors of the population of each country today experienced the Neolithic Revolution. In particular, controlling for geographical and continental characteristics of each country, as well as for the contemporary socio-economic environment, every 1000 years of earlier Neolithic transition results in 1.65-1.9 additional years of life expectancy. Thus, for instance, the European population that experienced the Neolithic Revolution on average 3160 years earlier than the African population would be expected to live more than 5 years longer, even if the gap in the socioeconomic conditions between these continents will be eliminated. Alternatively, Americans from European decent would be expected to live five years longer than Americans from African decent with similar socioeconomic background.

5 Concluding Remarks

This research advances an evolutionary theory and provides empirical evidence that shed new light on the origins of contemporary differences in life expectancy across countries. The theory suggests that social, economic and environmental changes that were associated with the Neolithic Revolution affected the nature of the environmental hazards confronted by the human population, triggering an evolutionary process that had a significant impact on human longevity. The theory predicts that in a given socioeconomic environment descendants of people from regions that experienced the Neolithic Revolution earlier would have a higher life expectancy in comparison to descendants of people from regions that experienced the Neolithic Revolution later.

We exploit variations in the average time passed since the ancestors of the population of each country today experienced the Neolithic Revolution, as well as contemporary differences in life expectancy across countries, to identify the impact of the time passed since the Neolithic Revolution on life expectancy. Accounting for the contribution of geographical attributes and socio-economic factors to the observed cross country correlation between the timing of the Neolithic Revolution and contemporary life expectancy, we demonstrate that the timing of the

Neolithic Revolution has a significant additional effect on life expectancy that could be plausibly attributed to changes in the genetic composition of the human population.

The empirical analysis shows that a significant portion of contemporary variations in life expectancy across countries can be traced to the weighted average of the time passed since the ancestors of the population of each country today experienced the Neolithic Revolution. In particular, controlling for geographical and continental characteristics of each country, as well as for the contemporary socio-economic environment, every 1000 years of earlier Neolithic transition results in 1.65-1.9 additional years of life expectancy. Thus, for instance, the European population that experienced the Neolithic Revolution on average 3160 years earlier than the African population would be expected to live more than 5 years longer, even if the gap in the socioeconomic conditions between these continents will be eliminated. Alternatively, Americans from European decent would be expected to live five years longer than Americans from African decent with similar socioeconomic background.

Appendix 1

Proof of Proposition 1:

As follows from (8), the negativity of $P_x(\mu^*, x)$ and $P_{\mu\mu}(\mu, x)$, and Assumptions A1 and A2,

$$\begin{aligned} \mu^*(x) &= -\frac{F_x(\mu^*, x)}{F_\mu(\mu^*, x)} && (9) \\ &= -\frac{P_{\mu x}(\mu^*, x)\mu^* - P_x(\mu^*, x)}{P_{\mu\mu}(\mu^*, x)\mu^*} > 0. && (10) \end{aligned}$$

where A1 assures an interior solution.

Finally, since $\mu^{*\prime}(x_t) > 0$ and $P_\mu(\mu^i, x_t) > 0$,

$$\frac{dE(P(\mu^*(x_t), 0))}{dx} > 0. \tag{11}$$

$\square$

Proof of Proposition 2:

$$\frac{dP(\mu^*(x_t), x_t)}{dx} = P_\mu(\mu^i, x_t)\mu^{*\prime}(x_t) + P_x(\mu^i, x_t) > 0. \tag{12}$$

Using (9)

$$\frac{dp(\mu^i(x_t), x_t)}{dx} = -P_{\mu^i}(\mu^i, x_t)\frac{P_{\mu x}(\mu^i, x_t)\mu^i - P_x(\mu^i, x_t)}{P_{\mu\mu}(\mu^i, x_t)\mu^i} + P_x(\mu^i, x_t). \tag{13}$$

Thus,

$$\frac{dP(\mu^*(x_t), x_t)}{dx} = \frac{P_\mu(\mu, x)P_{\mu x}(\mu^*, x)\mu^*}{-P_{\mu\mu}(\mu^*, x)\mu^*} + P_x(\mu, x)\left(1 + \frac{P_\mu(\mu, x)}{P_{\mu\mu}(\mu^*, x)\mu^*}\right). \tag{14}$$

As follows the negativity of $P_x(\mu^*, x)$, the positivity of $P_\mu(\mu, x)$, and Assumptions A1-A3, noting that under A3, $P_\mu(\mu, x)/P_{\mu\mu}(\mu^*, x)\mu^* < -1$, it follows that

$$\tfrac{dE(P(\mu^*(x), x))}{dx} > 0 \quad if \quad P_\mu(\mu, x)/\mu > \left|P_{\mu\mu}(\mu, x)\right|. \tag{15}$$

$\square$

Appendix 2

Table A1. Life Expectancy: From the Epipalaeolithic Period to the Iron Age

Period	**Place**	**Dates (B.C.E)**		**Life Expectancy**	
			at age 0	**at age 15**	**at age 20**
Epipalaeolithic Mesolithic[1]		17000-7000			
	Taforalt Cave (Morocco)		21.4	26.9	23.9
	Afalou-Bou-Rommel (Algeria)				21.9
	Vassilievka (USSR)		39.88		22.8
	Hayonim Cave (Israel)		23.57	14.7	11.94
	Sahaba (Nile Valley)		34.45	25.6	21.6
	Maghreb Type Model		21.145	27.783	24.521
Neolithic[1]					
	Catal Huyuk	7000-6000		16.9	
	Vovnigi (Russia)	4000			21
	Khirokitia (Cyprus)	4000-3000	22.1	19.4	14.7
	Khirokitia (Cyprus)	4000-3000	17		16
	Volni (Ukraine) [2]	3500-2500	24.92	19.81	16.25
Copper Age[2]					
	Tiszapolgar-Basatanya (Hungary)	3500-2000	36.37	28.44	26.46
	Alsonemedi (Hungary)	2100-1900	28.86	28.44	25.66
Bronze Age[2]					
	Mezocsat	1400-1200	28.97	24.72	22.81
Iron Age[2]					
	Mezocsat	800-700	44.03	34.5	31.67

[1] Fekri (1981, Chapter 7 pp. 95-128)

[2] Acsadiand and Nemeskeri (1970, pp. 273-287)

Appendix 3: Data

Life expectancy at birth in the year 2000. Source: World Development Indicators.

Income Per-Capita in the years 1960, 1980, 2000. Source: World Development Indicators.

Education: Average schooling years in the total population over age 25. Sources: Barro and Lee (1993).

Health Expenditure Per Capita. Source: World Development Indicators.

Years Passed since the Neolithic Revolution. Source: Putterman (2006).

Weighted Years Passed since the Neolithic Revolution. The weighted average of the timing in which the ancestors of the population of each country today experienced the Neolithic Revolution. Using the recently compiled data set on the timing of the Neolithic Revolution across different regions of the world (Putterman, 2006), as well as the data on post-1500 migratory patterns across the globe (Putterman, 2007), we calculate the weighted average of the timing in which the population of each country experienced the Neolithic Revolution.

Percentage of Arable Land. Source: World Development Indicators.

Absolute Latitude. Source: CIA World Factbook. Absolute Latitude of the capital of each country.

Years of life lost to communicable diseases (%) . Source: World Health Organization. Years of life lost (YLLs) take into account the age at which deaths occur by giving greater weight to deaths occurring at younger ages and lower weight to deaths occurring at older ages. The YLLs (percentage of total) indicator measures the YLLs due to a particular cause of death as a proportion of the total YLLs lost due to premature mortality in the population. (See Data Appendix for: definition, data sources and methods of estimations).

Years of Life Lost (YLLs) due to infectious are calculated from the number of deaths multiplied by a standard life expectancy at the age at which death occurs. The standard life expectancy used for YLLs at each age is the same for deaths in all regions of the world and is the same as that used for the calculation of disability-adjusted life years (DALYs). Additionally, 3% time discounting and non-uniform age weights that give less weight to years lived at young and older ages were used, as for the DALY. With non-uniform age weights and 3% discounting, a death in infancy corresponds to 33 YLLs, and deaths at age 5 to 20 years to around 36 YLLs.

Death registration data for 112 WHO Member States, sample registration systems (India, China), available data on child and adult mortality from censuses and surveys, together with population-based epidemiological studies, disease registers and notifications systems for the estimation of mortality due to 21 specific causes of death.

Life tables specifying all-cause mortality rates by age and sex for 192 WHO Member States were developed from available death registration data for 2002, sample registration systems (India, China) and data on child and adult mortality from censuses and surveys. Cause-of-death distributions were estimated from death registration data for 107 countries, together with data from population-based epidemiological studies, disease registers and notifications systems for selected specific causes of death. Causes of death for populations without usable death-registration data were estimated using cause-of-death models together with data from population-based epidemiological studies, disease registers and notifications systems for 21 specific causes of death. Using the recently compiled data set on the timing of the Neolithic Revolution across different regions of the world (Putterman, 2006), as well as the data on post-1500 migratory patterns across the globe (Putterman, 2007), we calculate the weighted average of the timing in which the population of each country experienced the Neolithic Revolution.

The index of Social Infrastructure, Source: Hall and Jones (1998). It is an equally-weighted average of two other indexes: Government Antidiversion Policy Index and Years Open Index. The Government Antidiversion Policy Index, follows Knack and Keefer (1995) as the equally-weighted average of the following five variables from the International Country Risk Guide compiled by Political Risk Services: (1) law and order, (2) bureaucratic quality, (3) corruption, (4) risk of expropriation, and (5) government repudiation of contracts. Each of these variables is assigned its 10-yr average value across the period spanning 1985-1996. The index is normalized to take values in the [0,1]-interval. The Years Open Index, follows Sachs and Warner (1995) as measuring the fraction of years during the period 1950-1994 that the country is "open" where openness is satisfied if all the following conditions hold: (1) non-tariff barriers cover less than 40% of trade, (2) average tariff rates are less than 40%, (3) black market premium was less than 20% in the 1970s and 1980s, (4) not classified as a socialist by Kornai (1992), and (5) no government monopoly on major exports. The index takes on values in the [0,1]-interval.

References

[1] Acsa'di, G.Y., and J. Nemeskeri, (1970), *History of Human Life Span and Mortality*, (Akademiai Kiado, Budapest).

[2] Barro R. and J. Lee, (1993), "International Comparisons of Educational Attainment," NBER Working Paper.

[3] Bairoch, P. (1988), *Cities and Economic Development* (The University of Chicago Press, Chicago).

[4] Becker, G. (1976), "Altruism, Egoism and Genetic Fitness: Economics and Sociobiology", *Journal of Economic Literature,* 14, 817-826

[5] Benaim, M. and J. Weibull (2003) "Deterministic Approximation of Stochastic Evolution in Games", *Econometrica* 71, 873-903.

[6] Bisin, A., and T. Verdier (2000), "Beyond the Melting Pot: Cultural Transmission, Marriage, and the Evolution of Ethnic and Religious Traits", *Quarterly Journal of Economics* 115: 955-988.

[7] Borghans, J.A.M., L. Borghans and B. ter-Weel, (2004), "Economic Performance,Human Cooperation,and the Major Histocompatibility Complex," Maastricht.

[8] Boserup, E., (1965). *The Conditions of Agricultural Progress*, (Aldine Publishing Company, Chicago).

[9] Botticini M. and A. Siow (2005) "The Value of Sons in Pre-modern Economies: A View from the Marriage Market", Boston Universty.

[10] Boucekkine, R, D. de la Croix and O. Licandro.(2003), "Early Mortality Declines at the Dawn of Modern Growth," *Scandinavian Journal of Economics*, 105: 401-418.

[11] Bowles, S. (1998), "Endogenous Preferences: The Cultural Consequences of Markets and other Economic Institutions," *Journal of Economic Literature* 36: 75-111.

[12] Boyd, R., and P.J. Richardson (1985), *Culture and the Evolutionary Process* (University of Chicago Press, Chicago).

[13] Boyer, G. (1989), "Malthus was Right After All: Poor Relief and Birth Rates in South-Eastern England", *Journal of Political Economy* 97: 93-114.

[14] Cavalli-Sforza, L.L., and M.W. Feldman (1981), *Cultural Transmission and Evolution: A Quantitative Approach* (Princeton University Press, Princeton).

[15] Cervellati, M. and U. Sunde (2005), "Human Capital Formation, Life Expectancy, and the Process of Development ," *American Economic Review*, 95, 1653-1672.

[16] Clark, G. and G. Hamilton. (2006), "Survival of the Richest: The Malthusian Mechanism in Pre-Industrial England" *Journal of Economic History,* 66: 707-736

[17] Cody, M. L. (1966), "A General Theory of Clutch Size," *Evolution*, 20 174-184.

[18] Cohen M. N.,(1989), *Health and the Rise of Civilization* (Yale Uni. Press: New Haven).

[19] Dawkins, R. (1989), *The Selfish Gene* (Oxford University Press, Oxford).

[20] De Vries, J. (1984). *European Urbanization, 1500-1800* (Harvard University Press, Cambridge).

[21] Diamond, J. (1997),.*Guns, Germs, and Steel: The Fates of Human Societies.*(Norton, New York).

[22] Durham, W. (1982), "Interaction of Genetic and Cultural Evolution: Models and Examples", *Human Ecology* 10: 289-323.

[23] Endler, J.A. (1986), *Natural Selection in the Wild* (Princeton University Press, Princeton).

[24] Erlich, I. and F. T. Lui (1991), "Intergenerational trade, Longevity, and Economic Growth," *Journal of Political Economy 99: 1029-1059.*

[25] Fekri, A. H., (1981), *Demographic Archaeology*, (Academic Press: New York).

[26] Fogel, R. W.(1994), "Economic Growth, Population Theory, and Physiology: The Bearing of Long-Term Processes on the Making of Economic Policy." *American Economic Review* 84: 369-95.

[27] Galor, O. and O. Moav (2002), "Natural Selection and the Origin of Economic Growth", *Quarterly Journal of Economics* 117: 1133-1192.

[28] Galor, O. and D.N. Weil (1999), "From Malthusian Stagnation to Modern Growth", *American Economic Review*, 89: 150-154.

[29] Grant, B.R. and P.R. Grant (1989), *Evolutionary Dynamics of a Natural Population* (University of Chicago Press, Chicago).

[30] Hansson, I., and C. Stuart (1990), "Malthusian Selection of Preferences", *American Economic Review* 80: 529-544.

[31] Hazan, M. and H. Zoabi (2004). "Longevity, Fertility and Economic Growth," Hebrew University.

[32] Iyigun, M. F. (2005), "Geography, Demography, and Early Development," *Journal of Population Economics* 18, 301-321.

[33] Jones, E.L. (1981), *The European Miracle: Environments, Economies and Geopolitics in the History of Europe and Asia* (Cambridge University Press, Cambridge).

[34] Kalemli-Ozcan, S., H.E. Ryder and D. N. Weil (2000), "Mortality Decline, Human Capital Investment, and Economic Growth" *Journal of Development Economics*, 62: 1-23

[35] Kelly M. (2004) Living Standards and Population Growth: Malthus was Right. University College Dublin.

[36] Kettlewell, H.B.D. (1973), *The Evolution of Melanism* (Clarendon Press, Oxford).

[37] Kirkwood T.B.L. (1998), Evolution Theory and the Mechanisms of Aging. In: Textbook of Geriatric Medicine, 5th ed. (Brocklehurst JC, Tallis RC, eds). London: Churchill Livingstone, 45-49.

[38] Kirkwood T.B.L (1977) "Evolution of Aging", *Nature*, 270, 301-304.

[39] Kirkwood T.B.L and F.R.S. Holliday (1979) "The evolution of ageing and longevity", *Proceedings of the Royal Society of London* B 205: 531-546.

[40] Kohler, H., J.L. Rodgers and K. Christensen (1999), "Is Fertility Behavior in our Genes? Findings from a Danish Twin Study", *Population and Development Review* 25: 253-263.

[41] Lack, D., (1954), *The Natural Regulation of Animal Numbers* (Oxford: Clarendon Press).

[42] Lagerlof, N., (2003), "From Malthus to Modern Growth: The Three Regimes Revisited", *International Economic Review* 44: 755-777.

[43] Lagerlof, N.P. (2007), "Long-Run Trends in Human Body Size," *Macroeconomics Dynamics*, 11, 367-387

[44] Laxton, P. and N. Williams (1989) "Urbanization and Infant Mortality in England", in M.C. Nelson and J. Rogers, eds. *Urbanization and the Epidemiological Transition* Uppsala University.

[45] Lee R. D. (2003) "Rethinking the evolutionary theory of aging: Transfers, not births,shape senescence in social species" *PNAS,* 100, 9637-42.

[46] Livi-Bacci, M. (1997), *A Concise History of World Population* (Blackwel, Oxford).

[47] Livingston F, (1958), "Anthropological Implications of Sickle Cell Distribution in West Africa", *American Anthropologist* 60: 533-562.

[48] Malthus, T.R. (1798), *An Essay on the Principle of Population* (printed for J. Johnson, in St. Paul's Church-Yard, London).

[49] McNeil, W.H., 1998, Plagues and Peoples, Anchor press, Doublebay.

[50] Medawar, P.B. (1952) *An Unsolved Problem of Biology* H.K. Lewis & Co. London

[51] Mekel-Bobrov, N., S. L. Gilbert, P. D. Evans, E. J. Vallender, J. R. Anderson, R. R. Hudson, S. A. Tishkoff, and B.T. Lahn (2005), "Ongoing Adaptive Evolution of ASPM, a Brain Size Determinant in Homo sapiens." *Science* 309, 1720-1722.

[52] Mokyr, J.(1998), "Induced Technical Innovation and Medical History: An Evolutionary Approach." *Journal of Evolutionary Economics,* 8: 119-137.

[53] Ofek, H. (2001), *Second Nature: Economic origin of Human evolution.* Cambridge: Cambridge University Press.

[54] Putterman, L. (2006) "Agricultural Transition Year Country Data Set", Brown University.

[55] Putterman, L. (2007), "Agriculture, Diffusion, and Development: Ripple Effects of the Neolithic Revolution," *Economica* (forthcoming).

[56] Reznick, David N., Michael J. Bryant, Derek Roff, Cameron K. Ghalambor and Dionna E. Ghalambor (2004), "Effect of Extrinsic Mortality on the Evolution of Senescence in Guppies," *Nature*, 431, 1095-1099.

[57] Robson, A.J. (2002) "Evolution and Human Nature," *Journal of Economic Perspectives* 16 , 89-106.

[58] Robson A. J. and H. S. Kaplan (2003), “The Evolution of Human Longevity and Intelligence in Hunter-Gatherer Economies,” *American Economic Review* 93: 150-169.

[59] Rodgers, J.L., and D. Doughty (2000), “Genetic and Environmental Influences on Fertility Expectations and Outcomes Using NLSY Kinship Data”, in: J.L. Rodgers, D.C. Rowe and W.B. Miller, eds., *Genetic Influences on Human Fertility and Sexuality* (Kluwer, Boston).

[60] Rodgers, J.L., K. Hughes, H. Kohler, K. Christensen, D. Doughty, D.C. Rowe and W.B. Miller (2001a), “Genetic influence helps explain variation in human fertility: Evidence from recent behavioral and molecular genetic studies”, *Current Directions in Psychological Science* 10: 184-188.

[61] Rodgers, J.L., H. Kohler, K. Ohm Kyvik, and K. Christensen (2001b), “Behavior Genetic Modeling of Human Fertility: Findings from a Contemporary Danish Twin Study”, *Demography* 38: 29-42.

[62] Saint-Paul, G. (2003), *“*On Market and Human Evolution*”* CEPR Discussion Paper No. 3654.

[63] Soares, R. R. (2005), “Mortality Reductions, Educational Attainment,and Fertility Choice,” *American Economic Review*, 95, 580-601

[64] Stearns, Stephen C. (1992), *The Evolution of Life Histories*, Oxford: Oxford University Press.

[65] Steckel R. (2004): “The Best of Times, The Worse of Times: Health and Nutrition in Pre-Columbian America” NBER.

[66] Strulik, H. (2007) ”Geography, Health, and Demo-Economic Development”, Journal of Development Economics, 2007, forthcoming.

[67] Voight, B.F., S. Kudaravalli, (2006), X. Wen, and J.K. Pritchard. “A Map of Recent Positive Selection in the Human Genome.” *Plos Biology.*

[68] Weil, D. (2005) "Accounting for the Effect of Health on Economic Growth" NBER, Working Paper 11455.

[69] Weisdorf, J. L. (2004) “From Stagnation to Growth: Revisiting Three Historical Regimes.” *Journal of Population Economics*, 17, 445-472,

[70] Wesidorf, J. L. (2006) “From Foraging to Farming: Explaining the Neolithic Revolution,” J*ournal of Economic Surveys,* 19, 561-586.

[71] Weismann, A. (1882) *Uber die Dauer des Lebens,* Gustav Fischer, Jena, Germany.

[72] Weisenfeld, S.L. (1967), “Sickle Cell Trait in Human Biological and Cultural Evolution”, *Science* 157: 1135-1140.

[73] Westendorp, R.G.J., Kirkwood, T.B.L. (1998), “Human Longevity at the Cost of Reproductive Success,” *Nature*, 396: 743–746.

[74] Williams, G. (1957) “Pleiotropy, Natural Selection and the Evolution of Senescence” *Evolution* 11, 398-411

[75] Williams P. D. and T. Day (2003) “Antagonistic Pleiotropy, Mortality Source Interactions, And The Evolutionary Theory Of Senescence” *Evolution,* 57, 1478-1488.

[76] Wilson, E.O. (1975), *Sociobiology: The New Synthesis*, Cambridge, Mass.: Harvard University Press

[77] Wrigley, E.A., and R.S. Schofield (1981), *The Population History of England 1541-1871: A Reconstruction* (Harvard University Press, Cambridge).