

Population and Technology: Human Genetic History and the African Advantage

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Abstract

This paper argues that human populations in sub-Saharan Africa were larger than populations in Eurasia and the Americas through out most of human history but that the population advantage in Africa failed to materialize in technological sophistication such as an early onset of agriculture or in post-agricultural developments such as urbanization. We study the patterns of genetic diversity within human populations (as diversity proxies past population size) and compare the date of origin of agriculture. African agriculture originated later than in any other region. Post-agricultural population growth in Africa was also faster than in the Americas (a comparable region) but urbanization was more common in the Americas, i.e., there were no large cities south of the Sahara at the time of the European expansion. Instead of a positive effect of population on induced innovation, we propose an explanation for the changes in technological leadership in the very long run based on a leapfrogging view and lock-in effects.

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1 Introduction

This paper studies the relationship between population and technology in the very long run and argues that human populations in sub-Saharan Africa were larger than populations in Eurasia and the Americas through out most of human history but that the population advantage in Africa failed to materialize in technological sophistication such as an early onset of agriculture or in post-agricultural developments such as urbanization. To argue for an African advantage in population, we draw inferences from anthropology, archeology, biology, demography, and from the patterns of genetic diversity within human populations (as diversity proxies past population size). We show that Africa was the last of several widely dispersed and independent origins of agriculture and that compared to the Americas, sub-Saharan Africa also failed to produce large cities in post-agricultural times. Today, sub-Saharan Africa remains economically stagnant despite a pre- and post-agricultural population advantage over comparable regions.

Understanding the relationship between population and technology is important because opinions have been traditionally divided into two opposite sides: Malthusians (or pessimists) and Boserupians (or optimists). Malthus [59] considered the pressure of population against available resources as the fundamental cause of human misery. According to Malthus [59], changes in the technology for food production were essential for population growth since they temporarily relieved the pressure of population on the food supply. In the absence of technological change, Malthus [59] argued, checks on population would prevent the human population from growing at rates faster than available resources. Rather than technological change determining population growth through food supply pressure, Boserup [7] considered population pressure as the driving force behind technological change. Based on Southeast Asian observation and Western European cases, she showed that agricultural technologies improved in response to population pressure. Hence, population growth and higher population densities constituted exceptional blessings.

Synthesis of both views are now available, notably Kremer [52], in which population growth is

limited by economic growth and economic growth is limited by population growth.¹ A key testable prediction of Kremer' [52] synthesis is that population should experience increasingly increasing growth rates or hyperbolic growth. This prediction comes about since changes in population growth improve technology and production (the Boserup side), and gains in production or technology lead to faster population growth (the Malthusian side).

At first sight, a prediction of increasingly increasing growth rates is not hard to reconcile with historical evidence. It took almost all of human's history up to 1800 to reach 1 billion people. The second billion took 125 years, the third 35 years, the fourth 15 years, the fifth 10 years and the sixth less than 10 years. This pattern of population change is inconsistent with exponential growth which predicts constant not decreasing doubling times. But the possibility of increasingly increasing growth rates is more difficult to establish in pre-modern samples mostly because of severe data limitations. If we extend the analysis back in time, past estimates of the human population would suggest increasingly increasing growth rates by construction. To derive population estimates in the past, Deevey [21] (a common source for past estimates) assumed that the area populated by humans has constantly increased since 1 million years ago (MYA) and that the density of the population in a given area has also increased.² These assumptions generate a form of increasing returns responsible for increasingly increasing growth.

Of course there is no reliable information on the past of the human population but the assumption of range expansions accompanied by higher densities deserves some comments. Archeological data on human settlements provide estimates of population size in the past but physical evidence for very early periods is less well preserved and less attention has been paid to population declines since available methods in archeology are better suited to find explosions rather than crashes

¹Previous synthesis of Malthus and Boserup include Lee ([55], [56]) and Pryor and Maurer [71]. An additional synthesis is available in Wood [97]. Jones [45], Johnson [44], Galor and Weil [33], Korotayev [51], and Cohen [18] are some examples that build on the important contribution of Kremer [52].

²Deevey himself remarked: "my own treatment of this, published some years ago in *Scientific American*, was not very professional," Deevey ([22], 248). For example, the following growth rates provide a remarkably good fit to the data: 0.0004 percent per-year until 10,000 years ago, 0.05 percent from 10,000 to 300 years ago, and 0.7 percent per year during the last 300 years. Although the growth rates increase, population growth becomes the combination of exponential models and not hyperbolic. This possibility was also studied by Kremer [52].

(see Schacht [84] and Petersen [70]). Since extinction and re-colonization are pervasive in hunter-gatherers societies, it is difficult to interpret range expansions as sustained increases in occupied area (as Deevey [21] did). Population densities for actual hunter-gatherers also exhibit large variation and extrapolations as far as 1MYA are difficult (however, see Hassan [37]). Information from current hunter-gatherers suggests that range expansions into temperate areas were associated with a decline in population density and not an increase in densities since there is more food available in tropical forests and grasslands, i.e., Hassan ([37], Table 12.5). Only recently, since the Neolithic agricultural revolution when permanent settlements in cities first appeared, the concentration of populations has increased considerably.

Elucidating the dynamics of the human population is essential to validate hyperbolic growth or the possibility of scale effects in technological change but a direct estimate of the time series of the human population requires too much speculation. Rather than relying on time series tests, this paper studies cross-sectional patterns of population and their relationship to technology in the past. We examine new information on past demography through the applications of genetic analysis to living humans, we offer tests that complement Kremer's [52] important study, and we give a new interpretation to the relationship between population and technology in the very long run.

The paper offers two cross-sectional tests. First, we study populations before the Neolithic agricultural revolution, and second, we study comparable post-agricultural populations. For comparability, we focus on the post-agricultural development of sub-Saharan Africa and the Americas. Although in the same spirit, our post-agricultural tests differ from Kremer's [52] cross-sectional comparison between the Old World and the Americas because we argue, based on Diamond [23], that the standard comparison between the Old World and the Americas captures aspects other than a difference in population size. That is, Eurasia's clear post-agricultural advantage over the Americas and Australia could in part be attributed to better geography or endowments and not

necessarily to a larger population size.

It is possible to see the isolation of the Americas as a dichotomous “treatment” in the modern statistical sense. To evaluate the effect of isolation as a natural experiment, in addition to a treatment group, one needs to define a suitable control group with similar pre-treatment characteristics. (In our case they can be seen simply as similar geography.) Instead of using all regions in the Old World, our post-agricultural test treats sub-Saharan Africa as a control. Africa and the Americas have similar geography in terms of their North-South orientation, landmass, and both cross the Equator. Also, both lacked suitable animals for domestication and very few plants were available for agriculture (in contrast to Eurasia as Diamond [23] notes). Agriculture originated independently in both areas at about the same time and to some extent Africa was also isolated from Eurasia because the Sahara offered a barrier to human passage especially since after 4000 B.C., or some 6 thousand years ago (KYA), when the desert area became more inhospitable, see Fagan ([27], 152).³

Our post-agricultural comparison between Africa and the Americas, done up until 1500, contradicts a population-induced innovation view since post-agricultural populations in Africa were larger and grew at faster rates than in the Americas but their technologies were not beyond the technologies and organization of the pre-Columbian empires. For example, while there were no large cities south of the Sahara at the time of the European expansion, Teotihuacán (currently Mexico city) was among the ten largest cities of the world in 400, Chandler ([13], 464). The number of medium-size cities was also larger in the Americas and despite Eurasian influence, agricultural technologies were not more advanced in Africa as we will later show.

Our pre-agricultural test also fails to find support for a population-induced innovation view.

To estimate pre-agricultural population size, we rely on patterns of genetic diversity within human

³The issues raised by this comparison are discussed later on, but most of the population changes were due to migrations within populations in sub-Saharan Africa (i.e., the Bantu migrations) and not by influence of Arab or Chinese traders (who initiated the contact with African populations), Hopkins [30]. Throughout the paper we treat North Africa as part of Eurasia because biogeographically it is closer to Eurasia than to sub-Saharan Africa (Diamond [23], 161). Our analysis of the Eurasian influence in Africa is also discussed later on. The influence seems minimal in part because Eurasian technologies were not appropriate for Africa.

populations as genetic diversity proxies past population size. The underlying principle that makes such an estimate valid is pretty straightforward. It is a biological fact that species develop over long periods of time and that as they develop, they accumulate genetic variations. When a large reduction in the population takes place, an event defined as a *bottleneck*, a loss of genetic diversity is inevitable among the survivors. The smaller the surviving population that comes through a bottleneck, the smaller the diversity among the survivors. On the contrary, when a population *explosion* takes place, the amount of genetic diversity increases since genetic changes appear in proportion to population size (see Rogers [81], Relethford [76], and Jobling et al. [42]).⁴

Since genetic changes such as mutations are random events more commonly observed in larger populations, a link between population size and genetic diversity can be seen as reminiscent of Kuznets [54] and Simon [87] views in which technological innovations take place randomly within a population. In such a view, a higher population increases the likelihood of new ideas and better technologies by a “law of large numbers” (see also the related discussion in Kremer [52]). In biological terms, a large population increases the likelihood of mutations and for that reason diversity provides a reliable signal to make inferences of human demography in the past.⁵

Some relevant facts have already been established in the genetic analysis of the human population. First, humans carry low genetic diversity compared to other hominoids, and second, genetic diversity in human populations is allocated mostly within rather than between populations with Africans as the most genetically diverse group (Jorde et al. [48] and Relethford [78]).⁶ Thus, the

⁴It is very important to avoid misunderstandings in the study of genetic homogeneity between populations. Genetic homogeneity is neither good nor bad and it provides no indication of genetic inferiority. On one hand, homogeneity means that the population lacks deleterious genes. On the other hand, homogeneity increases susceptibility to disease. For example, while Africans (whose genetic diversity is large) have some resistance to malaria by the sickle cell trait, the Americas before Columbus (one of the more homogeneous regions genetically speaking) were apparently free of a number of genetically transmitted diseases, see Mann ([60], 103-105).

⁵Analyses of technological change are also often related to mutations or to sudden changes in technology, see for example Mokyr [65]. An alternative role for mutations was considered by Galor and Moav [32]. In Galor and Moav [32], mutations arise to tilt the balance between the quantity and quality of children in models of fertility by changes in preferences. Spolaore and Wacziarg [90] also employ genetic distance to study barriers for development. The relationship between the two papers will be discussed in detail later on and remarks will be offered when the interpretation of the data conflicts between the two papers.

⁶Comparisons between humans and other hominoids like gorillas, chimpanzees, bonobos, orangutans, and even archaic humans like Neanderthals reveal low genetic diversity in humans (Gagneux et al. [31], Kaessman et al. [49] and Yu et al. [98] present technical treatments). Since great apes have smaller population sizes and restricted geographical ranges, the low diversity in humans must be the result of a relatively recent reduction in size due to

main new conclusion drawn from the genetic analysis of the human population is that prior to the Neolithic agricultural revolution 12KYA, sub-Saharan Africa had the largest and/or the oldest human population in the world. Archeological research also indicates that Africa was in the forefront of world progress early on (Mellars [62]). Yet, the population and technological advantages prior to agriculture were reversed and non-African populations leapfrogged thanks to agriculture. In sub-Saharan Africa, the initial advantage in population size and tool making technologies also failed to conduce to an early onset of agriculture.

We conclude that human demography in the past fails to offer strong support for a population-induced innovation view and instead favors the old interpretation of a population-technology relationship in which technological progress comes in waves producing demographic transitions or population explosions. The favorite technological revolutions are stone-tool manufacture, agriculture, and industrialization (see Deevey [21], Coale [17], and Livi-Bacci [57]).

For the purpose of understanding the relationship between population and technology, it is important to note that each technological revolution thrived in a different geographic area but not necessarily in the most advanced or populous regions at the time. Advanced tool making technologies allowed modern humans from a small region of Africa spread over archaic humans in African and non-African regions (Mellars [62]). Farmers from Asia displaced hunter-gatherers through out most of the Old World, Europe included (Richards [79]); while industrialization took off in regions where agriculture was never independently invented: Europe, North America and Australia.

Generalizations are useful but obviously very difficult when data limitations are as pervasive as in studies of very long time spans. In the paper we argue that Africa's relative post-agricultural backwardness with respect to the Americas is not due to differences in factors of production such as land or land quality but to technological differences or differences in the organization of production.

a population bottleneck followed by a population explosion that has been unable to restore diversity. With the current available methods, however, is not possible to determine if modern humans evolved from a small population due to small population levels for very long periods of time or from larger populations subject to regular population reductions (see Harpending et al. [36] and Rogers and Harpending [80], and Yu et al. [98]).

We specifically argue that the technological revolutions described above originated in ‘backward’ regions and that technological leapfrogging is an important aspect of progress in the very long run. Africa’s initial advantage seems to have generated a technological lock-in that delayed the adoption/invention of agriculture and urbanization. Before agriculture, it seems Eurasia was less technologically advanced than Africa. Due to agriculture, Eurasia gained a population and technological advantage over the Americas, Australia, and Africa. Within Eurasia, industrialization first occurred in Europe rather than in Asia. Out of all regions of Eurasia, Europe was the most backward up until modern times because agriculture did not originate independently in Europe. This absence of an independent origin of agriculture in Europe is suggestive of the advantages of backwardness for industrialization within Eurasia. Note also that industrialization first moved from Europe to regions where agriculture did not flourish or arose independently.

By the use of genetic information, the paper can be related to Spolaore and Wacziarg [90] who first documented and discussed the relationship between genetic distance and differences in income per capita across countries. Despite the fact that the measures of genetic distance in Spolaore and Wacziarg [90] are not based on DNA analyses, the finding of large genetic diversity in African populations is also supported by Cavalli-Sforza et al. [12]; the main source in Spolaore and Wacziarg [90]. Our use of genetic indicators to measure past demography, however, differs from the application of genetic distance in Spolaore and Wacziarg [90] since they considered genetic diversity as a measure of elapsed time between populations and not as an indication of size differentials between past populations. Moreover, Spolaore and Wacziarg [90] assumed that genetic distance measures genetically transmitted features and culturally transmitted human characteristics while we abstain from assigning any role to genetic material per se. Since current methods cannot separate time and size influences in genetic diversity, a clear differentiation between both sources of variation is not yet available. (Shortcomings originated on the failure to recognize differences in population size as a factor that affects genetic differences are discussed in detail in Relethford

[76] and Relethford and Harpending [74].)

An more subtle difference with Spolaore and Wacziarg [90] lies in the interpretation of the genetic evidence. While Spolaore and Wacziarg [90] considered a diffusion view in which genetic homogeneity facilitates technological diffusion, we stress the role of backwardness and technological leapfrogging in technology creation rather than in diffusion. The differences in the interpretation complement each other. Consider for example the origin and diffusion of industrialization. The Industrial Revolution originated in Europe despite an Asian advantage in population and technology (granted by an early onset of agriculture in China and the Near East). Genetically, Europe must have been more homogenous than Asia since Europe had a relatively low population level compared to Asia. Also, European industrialization moved initially to North America and Australia. Both regions were, at the time of the European expansion, very homogeneous because their populations were small compared to South and Central America, Asia, and Africa. (Populations were small as a consequence of a lack of an independent origin of agriculture.) Since populations in North America and Australia were small, an analysis of diffusion would suggest that homogeneity is the cause of the rapid spread of industrialization into both regions. Our findings suggest that homogeneity also contributed to the origin of industrialization although not as the result of cultural transmitted attributes but because homogeneity is a reflection of small population sizes and technological backwardness.⁷

The rest of the paper proceeds as follows. In Section 2 we study the time series properties of the human population. We do so because hyperbolic population growth turned out to be very accurate in predicting world population during the modern demographic transition although the ideas have been objected theoretically at least since the 1960s (see Serrin [85], Umpheby [94], Solow [91], and Coale [16]). We consider some simple tests to evaluate the possibility of hyperbolic growth (formal

⁷Spolaore and Wacziarg [90] considered a wide variety of geographic and cultural factors that could account for the effect of genetic distance on economic variables. Despite the controls, genetic distance remains important in explaining income differences today. They also studied the diffusion of industrialization within Europe and showed that genetic homogeneity also mattered within Europe. Genetic differences also had predictive power for understanding income differences in 1500.

aspects are left to the Appendix). We show that the hyperbolic growth that arises with current population estimates is highly sensitive to changes in the sample, especially to the exclusion of modern data points. This suggests that the evidence in support of increasingly increasing growth rates is due to recent changes in the growth rate of population and not to a secular trend.

The genetic findings we report use tools discussed (in very basic terms) in Section 3. (Cavalli-Sforza and Bodmer [11], Cavalli-Sforza et al. [12], and Rogers [81] present a technical treatment of the issues discussed below.) In Section 3 we also provide an overview of the findings and the interpretation of current results. The findings point to an African advantage in population. Alternative views are also considered in Section 3. Section 4 shows that the population advantage in Africa did not conduce to an early Neolithic agricultural revolution first experienced in the Near East and China. Section 5 compares the economic and technological conditions available in the Americas and sub-Saharan Africa and concludes that despite being populated much later, post-agricultural America achieved higher levels of urbanization than sub-Saharan Africa. In fact, no archaic humans existed in the Americas before the arrival of modern humans some 15KYA (the New World was the last continent to become populated by modern humans some 30 thousand years after Australia). We conclude that Africa's advantage in population size did not granted leadership in agriculture over Eurasia or even in the formation in cities over the Americas before 1500. Section 6 considers some possible explanations and Section 7 offers additional remarks on the technological leapfrogging described in the paper. Section 8 concludes.

2 Time series tests

As Kremer [52] notes, the idea that population growth has increased in proportion to population levels (also known as hyperbolic growth) was first studied in 1960 by Foerster et al. [28] in a paper titled "Doomsday: Friday 13, November A.D. 2026" in which they gave November 13, 2026 as the date of the Doomsday; the day in which the human population will be so large that it

will become unstable. Under hyperbolic growth, populations are unstable because the cumulative effect of nonlinearities on population levels implies that population escapes to infinity in a finite amount of time (the Appendix contains formal arguments).⁸

To study the origin of increasingly increasing growth rates consider Kremer's [52] model of population. Let $N(t)$ denote population at date t and assume that the initial population $N(t_0) > 0$ is given. Technology is represented by $A(t)$ and evolves in proportion to population (the Boserup side) from a given level $A(t_0)$. That is, $d \ln A(t)/dt = nN^\gamma(t)$ with $n > 0$ and $\gamma > 0$.⁹ In the Malthusian side, any change in technology translates into higher population levels and not into higher income per capita: $d \ln N(t)/dt = d \ln A(t)/dt$. The dynamics of population are then given by

$$\frac{dN(t)}{dt} = nN(t)^\alpha, \quad (1)$$

with $n > 0$ and $\alpha = 1 + \gamma > 1$. As in Solow's growth model, the previous is a Bernoulli differential equation whose solution is given by $N(t)^{1-\alpha} = n(1-\alpha)t + N(t_0)^{1-\alpha}$, or in a logarithmic scale by

$$\ln [N(t)] = \frac{\ln [n(1-\alpha)t + N(t_0)^{1-\alpha}]}{1-\alpha}. \quad (2)$$

Equations (1) and (2) suggest two time series tests for increasingly increasing growth. First, one can consider the relationship between population levels and population growth directly as in equation (1). Such a figure fails to provide evidence for a strong relationship between population levels and population growth rates if the modern demographic transition is excluded from the sample, see Figure 1. Only when the data is extended to cover the last 500 years one can find a

⁸Foerster et al. [28] cited examples of hyperbolic growth from accepted models in physics. Smith ([89], 193) and Johansen and Sornette ([43], 467) include additional references of hyperbolic growth and estimates for the human population using data from 1MYA. See also Varfolomeyev and Gurevich [95] for estimates of hyperbolic growth and (blow-up) singularities.

⁹Kremer [52] considered a much richer set of possibilities for technological change that includes dependency of income and of past technologies $A(t)$. Variations in population densities have been considered by Klasen and Nestmann [50]. In the generalizations, population growth is still a function of population as in our equation (1). Kremer [52] also discussed the reversal of the income-population growth relationship at the later stages of the demographic transition. An inverted U-shaped relationship has been studied in unified models of growth initially considered by Galor and Weil [33].

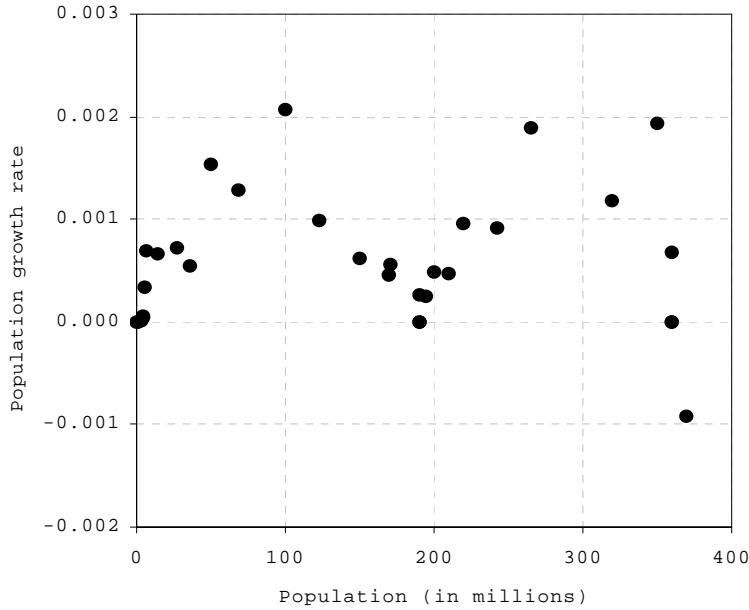


Figure 1: — Population growth versus population in pre-modern samples, 1MYA to 1400. Data from Kremer ([52], Table 1) and additions described in footnote 2. We excluded the years after 1400 from the figure because otherwise the growth before 1400 would not be visible by the large growth rates in the last 500 years.

positive relationship between the growth rate of population and its level, see Kremer ([52], Figure 1).

Alternatively, since $\ln[N(t)]$ is roughly a linear function of log-time in equation (2), hyperbolic growth can be detected through a double logarithmic plot between population and time. Under hyperbolic growth, log-population and log-time should lie on a straight line with slope $(1 - \alpha)^{-1}$. When α tends to one, population growth becomes exponential instead of hyperbolic so a direct test for hyperbolic growth is to test whether or not α is statistically larger than one in estimates of equation (2). Those tests are reported in the Appendix.

Figure 2 depicts the human population in a double logarithmic scale.¹⁰ The double-log plot

¹⁰Time series estimates of the human population are certainly an exercise in speculation and it would seem unfruitful to describe the shortcomings of such exercises. However, we should point out a very important inconsistency. While genetic and archeological evidence favor a view of population growth with notable fluctuations, the years that followed the Black Death are the only episode in human history in which the world population experienced a decline according to McEvedy and Jones ([61], Figure 6.2) or Kremer ([52], Table 1).

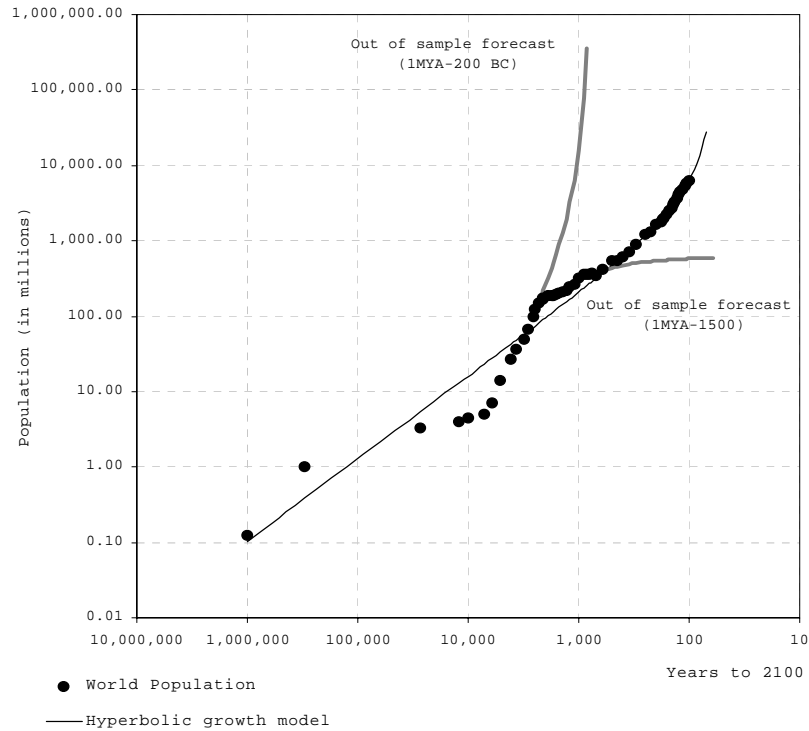


Figure 2: — Human population in the long run. Population from 1 MYA to 1990 from Kremer ([52], Table 1) and additions described in footnote 2. The time axis is taken as years to 2100 to make time always positive. Both scales are logarithmic. The hyperbolic growth model and the out of sample forecasts use nonlinear estimates of equation (2) available in the Appendix.

shows that population growth has been strongly non-linear, positive, and faster than exponential. The figure also shows large deviations from predicted values. Population growth between 10KYA and 200 B.C. is even faster than what the overall hyperbolic growth trend would predict.¹¹ Figure 2 also includes two out-of-sample forecasts. The first uses information up to 200 B.C. and the second ends just before the modern demographic transition in 1500. Hyperbolic growth cannot be rejected in the first sample (see also Figure 1). In fact, the trend in the years between 200 B.C. and 1500 was to slow down population growth; had the trends of the Neolithic agricultural revolution continued after 200 B.C., the current size of the human population would have been reached in

¹¹ Alternative ecological estimates of the prehistoric human population, for example Hassan ([37], Chapter 12), give almost identical results because they suggest an increasingly increasing growth rate by construction. As in Deevey [21], estimates tend to feature an increase in densities and in higher occupied area. Evidence in favor of higher densities and a range expansion is limited but some support exists for the middle Paleolithic in Africa, see Hawks et al. ([38], 12).

the year 1000 (see Figure 2). In the sample that ends in the year 1500, the evidence suggests no hyperbolic growth at all. Using information up until 1500 would suggest that the population in the year 2000 would still be below the 1 billion mark.

Further inspection of the time series properties of the human population might shed light on the adequate long-run representation of population growth as hyperbolic growth or as a sequence of discrete changes. However, any interpretation with extreme uncertainty over most of the data points would clearly be inconclusive. Rather than dwelling into the specific stochastic properties of the time series of the human population, we next review recent evidence that serves to study cross sectional patterns of population in the past through information contained in living humans.

3 Diversity, population size, and genetic history

Progress in the technology for sequencing the DNA molecule has generated a renewed interest in the origin and dynamics of the human population. Genetic evidence has shed light on historical questions such as the divergence of humans from other hominoids, the patterns of migration into Europe associated with the Neolithic agricultural revolution, the origin of Polynesian populations and the settlement of the Americas (see Jobling et al. [42] and Relethford [78] for technical analyses. Cavalli-Sforza and Bodmer [11] and Cavalli-Sforza et al. [12] are classical references on human genetics). The findings regarding the origin of modern humans and the dynamics of the human population, while still debated, have made extensive use of genetic analysis of DNA sequences.¹²

Because the transmission of genetic material follows well established rules, it is possible to reconstruct past events through the analysis of current differences between DNA sequences as a

¹²DNA is a molecule genetically transmitted and composed of combinations of four chemical units or bases: A (adenine), T (thymine), G (guanine), and C (cytosine). A DNA sequence is a succession of letters that represent the structure of the DNA molecule or strand; an example is: CCTTAACAGT which corresponds to the sites 16295 to 16305 of the human reference sequence (Relethford [78], 85). Every individual can be identified with a DNA sequence so differences in sites serve to calculate differences between individuals or species. DNA sequences are very long so analyses break sequences into small pieces or locus such as mitochondrial DNA (mtDNA) and nuclear DNA.

small genetic distance between two sequences may suggest a recent common ancestor. In certain cases it is even possible to estimate the rate at which DNA changes by mutations so a backward projection gives the most recent generation in which two sequences shared a common ancestor. For instance, if the rate of change is one base per million years, a difference in one base between two sequences suggests that the two sequences differ by one million years of evolution or that they shared a common ancestor one million years ago (applications of such molecular dating are discussed in detail in Cavalli-Sforza et al. [12], Jobling et al. [42], and Relethford [78]).

As molecular dating can provide the date of the most common ancestor for a given number of DNA sequences, the patterns of genetic diversity in humans have been used to fuel the debate on modern human origins.¹³ For example, Cann et al. [10] first used the association between genetic diversity and age to argue that the high African diversity is an expected consequence of a recent African origin of the human population. As the observed genetic diversity is higher within Africa, those populations should be older than non-Africans. Additional support for the importance of Africa in human evolution comes from the observation that in nearly all human genetic systems there is a primary division between African and non-African populations. That is, interpopulation genetic distances cluster in two major groups of African and non-African populations, see Jobling et al. [42] and Cavalli-Sforza et al. [12]. If correct, an exclusive African origin of the human population suggests that populations living outside of Africa before 150KYA were not ancestral to living humans and that ecological estimates of the population, such as Deevey [21] and Hassan [37], need to be modified accordingly.

It is important to note that an association between genetic diversity and time of origin assumes that population age is the only determinant of genetic variations. Differences in effective population size are also important for understanding diversity. Genetic diversity is an adequate indicator of

¹³Crudely described, the debate on human evolution is centered on whether evolution takes place as adaptations within a specie or by speciation. The most extreme version of the “African replacement” hypothesis assumes that speciation generated modern humans as a separate specie in East Africa, as early as 150KYA, from where they expanded and fully replaced the other human forms that existed at the time. The “multiregional evolution” view assumes similar evolution within each region of the world. Jobling et al. [42] and Relethford [78] provide summaries and references on the different views.

molecular time if and only if differences in population levels are accounted for (see Relethford [76]).

3.1 Heterogeneity (heterozygosity) and past population size

Genetic diversity or heterozygosity is often studied through classical models of population genetics and demographic change (see Cavalli-Sforza and Bodmer [11], Rogers [81], and Relethford [77] for authoritative technical treatments). The models assume random mating within a population and a constant population level. To understand how genetic diversity serves to estimate population and to describe population dynamics in the past consider a sub-population of N^e individuals and assume that all individuals mate randomly within such population and have unisex genetic transmission.¹⁴

A gene is a sequence of DNA nucleotides. Suppose that a gene can exist in two different states or alleles A and a (the difference between the two might be only one nucleotide position or many). Individuals who carry two genes of the same type (either AA or aa) are said to be homozygotes. Individuals who carry a pair of different genes (Aa) are called heterozygotes. Homozygosity is measured as the probability that two genes drawn at random from a parent generation are copies of the same allele.

Let J_t represent the homozygosity of the population in generation t . We are interested in the dynamics of homozygosity in a population of effective size N^e . Note that two randomly drawn genes from the offspring generation $t + 1$ will share the same allele if they are copies of the same gene in generation t , an event with probability $1/N^e$, or if they are copies of different but already identical

¹⁴For example, the Y-chromosome is transmitted only by fathers while mtDNA is only transmitted by mothers. Nuclear DNA is inherited from both parents. If both parents contribute to the genetic characteristics of offsprings, we just need to change N^e by $2N^e$ and if sex ratios differ, the effective population is $4N_f^e N_m^e / (N_m^e + N_f^e)$. With population growth, we require an additional normalization using the harmonic mean of population. See Cavalli-Sforza and Bodmer ([11], 504-505) for a technical treatment of structured populations in human genetics.

genes in t , an event with probability $(1 - 1/N^e)J_t$. This generates the following recurrence:¹⁵

$$J_{t+1} = \frac{1}{N^e} + \left(1 - \frac{1}{N^e}\right) J_t,$$

in which genetic diversity or heterozygosity can be defined as $H_t = 1 - J_t$.

In the absence of genetic changes due to gene flow or migration, all genetic diversity is lost in the steady-state for finite populations because inbreeding takes place (i.e., $J^* = 1$ as breeding between closed relatives is a force toward homogeneity). In a closed economy, diversity would only be restored by mutations, μ . Assuming that all types of mutations are equivalent and produce genes that never existed before (the infinite-sites model), two genes will be equal if there is no mutation in the path that connects them. Thus,

$$J_{t+1} = (1 - \mu)^2 \left[\frac{1}{N^e} + \left(1 - \frac{1}{N^e}\right) J_t \right], \quad (3)$$

with $(1 - \mu)^2$ representing the probability that neither of the two genes has mutated in the past generation. Ignoring small terms, in the steady state, the probability that two individuals share the same gene can be approximated by: $J^* \simeq \frac{1}{1 + 2\mu N^e}$, and the amount of genetic diversity is given by:

$$H^* = 1 - J^* = \frac{2\mu N^e}{1 + 2\mu N^e}, \quad (4)$$

that can be approximated by $H^* \simeq 2\mu N^e$, an increasing function of effective population size and the mutation rate.

Two important implications from genetic diversity for the understanding of the human population are the following. First, larger populations are expected to have higher genetic diversity. If populations are very large (as microbial organisms) or if mutation rates are high, heterozygosity

¹⁵The transmission of genetic material follows the same rules as the transmission of surnames in most societies. Two individuals share the same surname if they have the same father or if they have different fathers, but those fathers already have the same surname. An alternative derivation of homozygosity is described in Cavalli-Sforza and Bodmer ([11], 503-504).

will approach one. And second, it follows from the dynamics of J_t that a reduction in the effective population size by a bottleneck reduces the amount of genetic diversity in the population. Diversity will slowly increase until it reaches H^* again because J_t , being a stable difference equation, will return to a steady-state after transitory declines.

3.2 Measured diversity

A measure of gene diversity or heterozygosity that corresponds to the theoretical notion derived in (4) counts the differences in sites between any two DNA sequences by $H = 1 - \sum_i (n_i/n)^2$, in which (n_i/n) represents the frequency of copies of type i and $n = \sum_n n_i$ is the number of sites. For example, if a sequence has ten sites and one differs between the two sequences, $H = 1 - (0.9)^2 = 0.19$. When more than two sequences are being compared, genetic diversity employs mean pairwise differences. In that case, if there are m sequences, there will be $m(m-1)/2$ potential comparisons. The mean pairwise difference is represented by: $\pi = m(m-1) \sum_{i<j} d_{ij} \left(\frac{n_i}{n}\right) \left(\frac{n_j}{n}\right)$, with d_{ij} as the proportion of sites that differ between the i -th and j -th sequences, see Rogers [81] and Relethford [77]. Additional measures of diversity tend to correlate well with previous measures.

Table 1. Genetic diversity (mean pairwise differences) between populations in Africa, Europe, and Asia.

Region	Mitochondrial DNA		Nuclear DNA	
	(a)	(b)	(c)	(d)
Africa	0.022	0.030	0.076	0.085
Europe	0.009	0.010	0.045	0.077
Asia	0.015	0.011	0.047	0.075

Source: Tishkoff and Verrelli ([93], Table 2). (a)-(d) denote different coding regions of DNA, (a) refers to marker system HVS-I, (b) to HVS-II, (c) to (1q24), and (d) to marker system (22q11). The number of chromosomes in mtDNA for Africa, Europe and Asia is: 72, 120, and 63 respectively. For nuclear DNA the number of chromosomes is 20 in all instances except for Europe in column (c) that has 21 chromosomes.

Estimates of genetic diversity in the human population are robust in showing that sub-Saharan African populations exhibit higher levels of genetic variation compared to any non-African popu-

lation. For example, Table 1 presents a selection taken from Tishkoff and Verrelli [93] for two of the most common genetic locus: mtDNA and nuclear DNA (see also Relethford [77], Figure 5.2). In many other DNA locus, as the ones reviewed by Tishkoff and Verrelli [93], Jorde et al. [47], and Jorde et al. [48], the diversity in Africa is also larger than in any other geographic region.

Estimates of effective population size from Table 1, using equation (4), would be biased for comparisons between regions as they fail to account for variations due to gene flow associated with migrations between Africa and non-Africa regions. However, when migrations are allowed, the estimates of relative size indicate that the population in sub-Saharan Africa should have been 4 or more times larger than any of the populations in Europe, Australasia, and the Far East. According to Relethford and Jorde [75], in terms of effective population size, out of 100 humans, 73 should have lived in Africa, 9 in East Asia and 18 in Europe prior to the Neolithic agricultural revolution.¹⁶

The patterns of genetic diversity are shared by many other characteristics. Craniometry also suggest a larger population size in sub-Saharan Africa, see Relethford and Harpending [74]. High African diversity is also featured in body size variation because Central Africa hosts one of the tallest and the shortest populations of the world: the Tutsi and Pygmy tribes. Other measures of quantitative traits such as skin color also lend support to higher African diversity, Relethford ([77], Figure 5.4). Language and genetic maps show considerable concordance in human populations (see Cavalli-Sforza et al. [12]). Linguistically, Africa is also the most diverse continent. Sub-Saharan Africa, a relatively restricted geographical area, contains four distinct and very diverse language families whereas in North Africa, Europe, and Asia there is a single Eurasian family. In the Americas, there is also a single linguistic family, the Amerind, see Ruhlen ([82], Map 8).

¹⁶Measures of effective population size do not correspond exactly to census estimates of population levels (see Hawks et al. [38]). Nonetheless, variations predicted by effective size are not inconsistent with the idea of larger African populations. One of the most compelling reasons for small effective population size is local extinction and recolonization (Hawks et al. [38], 16). If extinction and colonization were more common in regions out of Africa, those regions are expected to have lower effective sizes. Since most of the actual population movements were largely outward from Africa, and since actual "population size were smaller toward the peripheries of the human range," Hawks et al. ([38], 16), differences in effective size still point to Africa as the most populated area through most of the Pleistocene (Relethford [78]).

There is no dispute over the fact that archaic humans (i.e., the *H. erectus*) existed in the Old World as early as 1MYA as documented in fossil records, see Jobling et al. ([42], Chapter 8). Yet, despite the presence of archaic humans outside of Africa, African diversity is higher than diversity in any non-African population and for that reason a pattern in which Africa is the most genetically diverse region is suggestive of a larger population size for a very long period of time.¹⁷

3.3 Alternative explanations for the high African diversity

We have employed the relationship between effective population size and genetic diversity to draw inferences of population size in pre-agricultural populations but there are alternative explanations for the high African diversity not based on population size. As we noted before, ‘molecular time’ instead of ‘effective size’ could also account for a large genetic diversity as older populations experience more mutations and hence more diversity (see Cann et al. [10]).¹⁸ (See also Spolaore and Wacziarg [90] who considered a ‘molecular time’ interpretation for the genetic diversity of the populations in the world.) Since the idea that archaic humans evolved independently into modern humans in Asia and Europe is less considered nowadays, the difference in time or in size still assign an important role to Africa.

For example, the earliest demographic expansion in the human population took place among the ancestors of contemporary sub-Saharan Africans (Harpending et al. [36]). In that sense, sub-Saharan Africa hosted either the largest population of modern humans in the past or, for a long period of time, the only population of modern humans.¹⁹ Then, in terms of age rather than

¹⁷Fossil evidence also corroborates the important place of Africa in human evolution because anatomically modern humans appeared by 150KYA in Africa and then spread over the Old World (see Templeton [92] for an attempt to date movements in and out of Africa through molecular markers). The way the diffusion of modern humans took place from out of Africa has not yet been resolved. For alternative models see Cann et al. [10] and Eswaran et al. [26].

¹⁸The time series patterns of population have also been subject of study from molecular data and multiple hypotheses on population growth have been tested using DNA sequences. Most of the tests have been designed to distinguish between two simple models: a model of a stable population level, as the one implicit in equation (4), and a model of a population bottleneck and subsequent expansion (Harpending et al. [36]). Some examples that study past population bottlenecks and explosions include Rogers and Harpending [80], Excoffier and Schneider [25], and Sherry et al. [86]. See also Hawks et al. [38] and Eswaran et al. [26].

¹⁹Fossil records indicate the presence of modern humans in the Middle East at about 90KYA, East Asia at 40KYA and Europe at 30KYA, see Jobling et al. ([42], Section 8.2.4). As Jobling et al. ([42], 245) argue: “it is clear that

size, the lag between the African origin, 150KYA, the expansion in Africa, and the advance to non-African regions still give Africa a head start.

The basis for the association between population and diversity assumes neutral mutations or changes not driven by natural selection. Support for population expansions has mostly been limited to mtDNA and Y-chromosome data. Since natural selection usually affects a single genetic locus, the variations in mtDNA consistent with population changes are often considered as outcomes of positive selection. For instance, nuclear DNA has weaker or no signals of population expansion (Hawks et al. [38] and Eswaran et al. [26]). In Table 1, diversity was higher for mtDNA than for nuclear DNA. Since nuclear DNA is the result of contributions of fathers and mothers, while the genetic transmission in mtDNA does not allow for recombination (as fathers have zero contribution to mtDNA), there could be selection effects responsible for the seemingly population advantage in Africa.

In general, it is difficult to differentiate selective from demographic factors but evidence for selection is not definite. A size or an age advantage in Africa is observed in selective-neutral sites and an African advantage matches fossil and archeological records from anatomically modern humans in Africa (see Reich and Goldstein [73] and Tishkoff and Verrelli [93] for additional analyses). For example, archaeological research in southern and central Africa indicates advanced tool making technologies and cultural features some 80 to 60KYA and credits them for the population dispersal out of Africa (Mellars [62]).²⁰

modern human morphology appeared considerably earlier in Africa than elsewhere.”

²⁰Climatic events, as the eruption of Mount Toba in Sumatra dated to approximately 70KYA, have been used to support the low levels of differentiation in human populations and the extinction of archaic humans (as a bottleneck that predates the Pleistocene population expansions), see Ambrose [2]. Ambrose ([2], 627) also presents estimates for the Old World breeding effective population that range from 40 to 10,000 females of reproductive age as the maximum. The estimates are small because of the genetic uniformity of the human population.

4 Agriculture came late to Africa

Anatomically and genetically modern humans evolved exclusively or mostly in sub-Saharan Africa and for a long period of time Africa enjoyed a population advantage over non-African regions. Africa is also a large continent, much larger than Europe. African achievements in population and technology, however, are secondary to Asia, Europe, and maybe even to the Americas populated only since 15KYA (or less). The first ever recorded census, taken in the fall of 2 A.D., counted 57.5 million people in imperial China. When Augustus died on August, 14 A.D., the population of the Roman empire was 54 million. At that time, sub-Saharan Africa and the Americas each had an estimated population of 12 million inhabitants (see Biraben [6] and Table 3). Disparities today are even larger than in the first millennia or before the European expansion mostly because the African advantage in population failed to conduce to technological sophistication.

Table 2. First domestication of plants and animals, population in 400 B.C., and large cities.

Region	Time of origin (KYA)	Population in 400 B.C. (in millions)	Number of large cities in the classical world (in 1000 only)
Near East (Fertile crescent)	10.00	42	31 (10)
China			
South (Yangtze river)	8.50	} 19	} 58 (6)
North (Yellow river)	7.75		
The Americas			
Central Mexico	4.75	} 7	} 8 (1)
South Central Andes	4.50		
Eastern United States	4.50	1	0
Sub-Saharan Africa	4.00	7	0

Source: Time of origin is taken from Smith ([88], 13). Population size in millions from Biraben ([6], Table 2). McEvedy and Jones [61], suggest higher population for China (42 millions in 200 B.C.), lower population in the Near East (about 20 millions in A.D.) and slightly smaller populations in the other regions. The number of large cities is cumulative and include cities with more than 100,000 inhabitants between the years 1000 B.C. and 1000. In parentheses is the number of cities in 1000 only. The Mediterranean had 58 (4) cities and Southeast Asia 31 (4), see Modelski ([63], Table 11).

Table 2 reports the time of origin of agriculture in several regions with independent origin. As

the table shows, Africa's relative stagnant position in post-agricultural times is in part due a late origin of agriculture. Agriculture started in Africa much later than in the Near East and despite an independent origin in the African Sahel and tropical West Africa, permanent farming in sub-Saharan Africa only began 4KYA.²¹ Table 2 also shows that sub-Saharan Africa played no part in the development of urban systems, an Eurasia and Mesoamerican product. In fact, before the European expansion, there were no large cities in North America or south of the Sahara (Modelski [63] and Chandler [13]).

Agriculture produced an unambiguous increase in population size and density during the Neolithic and ancient Egypt, whose agriculture was introduced from the Near East, presents direct evidence of the Malthusian effects of technological change on population growth. In 4000 B.C., archeological reconstructions suggest a population of 350,000 inhabitants in Egypt (Whitmore et al. [96]). By 2000 B.C., the population of Egypt was near 2 million. By 400 B.C., population in North Africa was already as large as the population in sub-Saharan Africa (Biraben [6] and McEvedy and Jones [61]). Similar population explosions are well documented in all agricultural transitions, even modern hunter-gatherers with fairly recent settlements, Livi-Bacci ([57], 45).²²

That agriculture failed to originate first in sub-Saharan Africa, despite a long run African advantage in population, is not surprising because the role of population size in inducing agriculture has been less consistently argued nowadays (Harlan [35]). People were not driven into agriculture by a decline in diets due to a population pressure as agriculture produced large health disadvantages (Armelagos et al. [3]). Moreover, since agriculture had many independent beginnings, assuming a single driving force in all places of origin is highly problematic (Harlan [35] and Smith [88]). The

²¹An independent origin of agriculture in the Fertile Crescent, China, Mesoamerica, and the Andes is well established but the case of Ethiopia, New Guinea, and North America is more problematic as diffusion rather than innovation could have taken place, see Smith [88]. For example, corn was domesticated in Central America but it reached North America only after 900 A.D. due to limited diffusion. Note that the possibility of an independent origin in New Guinea is particularly interesting because despite the advantage in size and constant trade with New Guinea, Australia remained a land of hunter-gatherers until European contact.

²²Archaeological material, beginning at least since 6KYA, show regional population patterns in which population growth is neither smooth nor exponential. Population change in the Egyptian Nile valley, the Tigris-Euphrates lowlands, the Basin of Mexico, and the central Mayan lowlands of Mexico and Guatemala reveal considerable diversity and several episodes of population declines (Whitmore et al. [96]). Additional case studies of population collapse, mainly blamed on environmental externalities, are studied in Diamond [24].

relatively large degree of synchronization suggests that a global factor played a more important role than population pressure (Fagan [27]).

Agriculture seems to have arisen independently in seven widely separated places on the world leading to dispersals and replacement of previously existing hunter-gatherers.²³ An expansion of farming in the Near East has been proposed for understanding the population of Europe since agriculture was never independently developed in Europe (Australia or California).²⁴ While the demographic consequences of agriculture are more or less well understood, there is no agreement in archeology, anthropology, biology, economics, demography, or geography, on the motivations that originated agriculture (Harlan [35]). Eurasia's advantage before individualization is clearly tied to agriculture but the population size in Eurasia rather than a cause seems to be a consequence of agriculture.

5 Cities also came late to Africa

The multiple consequences of agriculture for economic development and technological change have been largely discussed in Diamond [23] where natural experiments are used to study the role of environmental factors and geography in explaining the origin and diffusion of technologies such as animal and plant domestication, metallurgy, and weaponry to name a few. Permanent farming is also associated with a general but not unproblematic concept of 'civilization' since cities, writing and science (i.e., astronomy and mathematics), money and market exchange, religion, and state formation are all related to agriculture.

A similar use of natural experiments was considered by Kremer [52]. Assuming that populations

²³Examples of migrations associated with farming are described in Diamond [23]. They include China, the Bantu expansion in Africa, and the Pacific islands but not Australia. Because health conditions deteriorated with the transition into agriculture, evidence suggests that population grew in agricultural settings due to higher fertility in turn generated by reduced energy expenditure (due to a sedentary life) and by an early puberty (Livi-Bacci [57]).

²⁴The contribution of Neolithic farmers to the gene pool of modern Europeans is still debated. The contribution varies from around a quarter or less to more than half in regions closer to the Near East (Relethford [78]). The interpretation of the genetic evidence suggests that diffusion of ideas was as important as mass-migration in the diffusion of farming (see Richards [79] for a detailed review of genetic traces of population movements in Europe that suggests that movement of ideas were more important than movements of people).

were randomly allocated among the continents, and that population densities were the same in the Americas, Australia, and the Old World some 12KYA, it is possible to evaluate the impact of population size on technological change as in a natural experiment, the melting of the ice caps that divided the continents.²⁵ Since the land bridges that connected the Americas with Asia and New Guinea with Australia (also Tasmania and Flinders Island) disappeared, some populations became isolated leading to different patterns of development. As Kremer [52] notes, the results from this natural experiment clearly give an indication of the importance of the Eurasian populations in 1500 compared to the Americas and Australia. Eurasia had the largest population in the world around 1500 and the highest level of technological sophistication.

The natural experiment that followed the melting of the ice caps is not unproblematic. Even if one assumes that population densities before agriculture were close in all regions of the world, and that populations were randomly divided, factor endowments were not equally distributed in the different areas and this leads to important confounding problems. In fact, the Eurasian importance assigned to population size could be attributed to advantages in geography such as a large number of domesticable species or Eurasia's East-West orientation which, according to Diamond [23], favored the diffusion of technology (this is consistent with a single Eurasian linguistic family, Ruhlen [82], and with the diffusion of certain agricultural innovations described in Diamond [23]. See also Olsson and Hibbs [68] for long-term effects differences in biogeography).

We build upon Kremer's [52] analysis and evaluate the isolation of the Americas with respect to Africa rather than with Eurasia or the Old World. The main advantage of a comparison between Africa and the Americas is that both have axes that run mostly from North to South, Diamond ([23], 177). Since the geographic orientation will be similar, the expected difference between the development of the Americas and Africa will be given due to population differences not related to geography.

²⁵The tests are a direct application of (2), see for example equation (16) in Kremer [52]. A more general version of the model in Kremer [52] is available in Klasen and Nestmann [50] where densities do not have to be assumed equal between populations.

Not only there is a similar orientation, but a comparison between Africa and the Americas is more informative of the role of population in technological change since South and Central America have an area that is somewhat comparable to sub-Saharan Africa's (Table 3) and, natural conditions and climate variety are similar as both continents cross the Equator. Also, agriculture originated in both regions roughly at the same time (Table 2), both had similar population sizes in 400 B.C. (Table 3), and in neither of them there were many domesticable animals. (In the Americas there was the llama while there were no mammalian candidates for domestication in sub-Saharan Africa, Diamond ([23], Table 9.2).) The number of large-seeded grass species in sub-Saharan Africa (4) is closer to South and Central America (with 2 and 5 respectively) than to Eurasia (with more than 30), see Diamond ([23], Table 8.1). To add to the similarities, the deserts of northern Mexico, obviously not at the same scale as the Sahara, separated the urban centers of Central America from North America. For instance, Mexican corn reached the current US territories only at around 900 A.D., Diamond ([23], 109). Since communication between Central and South America was far more common than between Central and North America, we treat South and Central America as a single unit throughout. (In terms of biogeography, the West Indies, South, and Central America also conform a single Neotropical region.)

To elaborate a post-agricultural test we proceed in two steps. First, we document a population advantage in Africa and then we evaluate if such an advantage generated differences in technology according to the population-induced innovation view. Since we have considered the isolation of the Americas as a "treatment," the estimate of the advantage would usually be given in terms of the difference between the treatment and the control group or in terms of an American advantage (over Africa). Our case computes the difference in population measures between the control and the treatment group so a simple change in signs would generate the standard representation. This is done since in almost all of our estimates, Africa exhibits an advantage over the Americas.

To estimate a population advantage one would ideally like to know the size of the population

of original settlers to the Americas and the size of the population in Africa at two points in time: prior to the isolation of the Americas and around 1500 when the European expansion integrated the isolated areas once again. Those measures are not available and it is unlikely that they will ever be. Instead, we rely on modern estimates of past populations beginning in 400 B.C. to produce estimates of a post-agricultural advantage.

5.1 Africa’s post-agricultural advantage

Evidence on the size of the population in America before Columbus has a low degree of accuracy.²⁶ For tax purposes, Spanish authorities in 1574 reported a total of about 8 to 10 million inhabitants in Hispanic America although estimates are as high as 100 millions, Livi-Bacci ([58], Table 1).²⁷ Numbers in Africa also vary widely. Early estimates suggested an African ‘consensus’ around 100 million inhabitants with a stationary population up until 1650. As Caldwell and Schidlmayr [9] note, it is very likely that population in Africa increased as a result of the appearance of stock raising and agriculture as early as 3KYA. Connections with Eurasia also provided a continuous inflow of plants and seeds such as the “Asian yams, cocoyams [taro], bananas and plantains.” Those crops were introduced between the first and the eight centuries A.D., Hopkins ([30], 30). In 1500, Caldwell and Schidlmayr [9] suggest an estimate of the population in Africa around 50 million inhabitants near 1500.

In addition to the estimates at the time of the European expansion, one would like to know the time path of population change in Africa and the Americas. Beginning with Colin Clark’s [15],

²⁶ Although some earlier estimates are based on an “extraordinary amount of material,” they are either informed guesses based on travelers’ observations or impressions based on relative densities. According to Johann Peter Süßmilch compilation, published in the mid-eighteenth century, Africa and the Americas had the same populations circa 1650 (150 millions each), Caldwell and Schidlmayr ([9], 188). Caldwell and Schidlmayr ([9], Table 2) present additional estimates of regional populations circa 1650. In all estimates but in Riccioli’s 1661 figure (which assumed 100 million inhabitants in Australia), Africa is more populous than the Americas. The same case can be made for modern estimates of population so our analysis is more qualitative as we are not much interested on the magnitude of the African advantage but on the existence of an advantage at all.

²⁷ As Livi-Bacci [58] notes, a large population is used mostly to give credit to “germs” as an important factor in the population decline after the Conquest. Livi-Bacci [58] also argues that the new pathologies were important in the depopulation of the Americas but additional factors related to violence, civil conflicts, famine and hunger, confiscation of labor, and economic and social disruptions were also powerful factors in the decline.

there have been some attempts to provide longitudinal estimates of regional populations in post-agricultural times. The estimates from Biraben [6] and McEvedy and Jones [61] are useful for a first comparison between sub-Saharan Africa and the Americas because Biraben [6] and McEvedy and Jones [61] are independent sources, see Caldwell and Schidlmayr [9]. Moreover, alternative estimates are very correlated with either source. For example, the estimates by Colin Clark ([15], Table 3.1) are very close to Biraben [6] as the historical consensus suggests, at least for Africa and the Americas, larger populations in Africa (see Caldwell and Schidlmayr [9] for a more detailed study of the historical estimates).

Table 3. Estimated population in Africa, the Americas, and the Indian subcontinent.

Region	Area	Biraben [6]				McEvedy and Jones [61]		
		400 B.C.	A.D.	1000	1500	A.D.	1000	1500
Africa								
North	2	10	14	9	9	8	11	8
Sub-Saharan	25	7	12	30	78	8	22	38
The Americas								
North	20	1	2	2	3	0.4	0.7	1.3
South and Central	20	7	10	16	39	4	8	13
Indian subcontinent	5	30	46	40	95	34	77	100
World population		153	252	253	461	170	265	425

Notes: Population in millions. Area (mill. km²) from McEvedy and Jones [61]. North Africa includes the Maghreb, Libya and Egypt. The area in North Africa does not include the Sahara. North America includes the US, Canada, and the Caribbean.

Tables 3 and 4 reproduces the estimates of Biraben [6] and McEvedy and Jones [61]. First note that the estimates of population levels and population increase differ but both share a common feature: sub-Saharan Africa had a large population size and the fastest population growth in the world in the years between 400 B.C. (or A.D.) and 1500 (or 1000). Population increased between four- and ten-fold, much faster than the populations in the Americas, India, and Eurasia. Population grew at rapid rates in sub-Saharan Africa because of a series of long-range geographic expansions of the Bantu-speaking agricultural populations and not because of the influence of

non-African populations (see Connah [19] and Austen [4]). The internal migrations, beginning as early as 3KYA, have been documented through linguistic, archeological and even genetic basis. Signatures of the Bantu expansion exist for mtDNA and Y-chromosome data, see Tishkoff and Verrelli ([93], 309).

A first estimate of the African advantage in population could be defined by the cross-sectional difference in population levels between Africa and the Americas: $\Delta_D = \ln N_t^{Africa} - \ln N_t^{Americas}$. Since populations in sub-Saharan Africa were larger than in the Americas, Δ_D suggests an advantage in population before 1500. (A first difference with Europe would also suggest an African advantage over Europe because Europe was not very populous. However, since Europe had constant contact with Asia, the size of the European population is not a relevant indication of the role of population on technological change.)

A cross-sectional difference might not provide an adequate measure of the African advantage. A difference-in-difference or a double difference estimator would discount systematic factors that arise by possible differences in trends. That is, a low population in the Americas in 1500 might be due to fast population growth but a small initial population size. If such is the case, a comparison in population levels would mistakenly generate an advantage in favor of Africa. (This is unlikely though since the population size in 400 B.C. and total area are similar for Africa and South and Central America.)

A difference-in-difference estimator of the African advantage is: $\Delta_{DD} = n_t^{Africa} - n_t^{America}$, with $n_t = \ln N_t - \ln N_{t-1}$. Ideally, the growth rate in Δ_{DD} would refer to the difference in populations pre- and post-isolation. Since there are no reliable estimates of the size of the founding population in the Americas, we estimate Δ_{DD} using growth rates based on the first available estimate of population size in Table 3.²⁸

²⁸Only hunter-gatherers settled on the Americas so a differential in trends seems less problematic. However, it is possible that North America had a faster growth initially due to the availability of large mammals. The debate on the role of modern humans in the extinction of large mammals in the Americas is not yet resolved. Diamond [23] cites evidence in favor of the “overkill” hypothesis. Fagan ([27], 35-40) argues that human hunters had a very minor role in the extinction since most species were extinct before modern humans populated the New World.

Table 4 presents estimates of Δ_{DD} for several periods. As population growth was also faster in Africa in all instances, a difference in growth rates or a difference-in-difference estimator also suggest an advantage of sub-Saharan Africa over the Americas. Finally, the isolation of sub-Saharan Africa was never as complete as the isolation of the Americas. Africa had contact with Eurasia before the European expansion and for that reason we can study if the African advantage in population was due to the influence of Eurasian technologies on Africa. (America had negligible contact with Eurasia during the Norse voyages and in Alaskan communities so this contact is unproblematic.)

Table 4. Difference-in-difference estimates of the African advantage.

	Biraben [6]				McEvedy and Jones [61]	
	400 B.C. to 1000		A.D. to 1500		A.D. to 1500	
	1000	1500	1000	1500	1000	1500
Baseline population increase						
A. Sub-Saharan Africa	3.3	10.1	1.5	5.5	3.5	1.6
B. The Americas						
B ₁ . North	1.0	2.0	0.0	0.5	2.3	0.8
B ₂ . South and Central	1.3	4.6	0.6	2.9	2.0	1.0
Difference-in-difference estimate of Africa's advantage, Δ_{DD}						
C ₁ (=A-B ₁). North America	2.3	8.1	1.5	5.0	1.2	0.8
C ₂ (=A-B ₂). South and Central	2.0	5.5	0.9	2.6	1.5	0.6
Controls for Eurasian influence over Africa						
Population increase in						
D ₁ . Indian subcontinent	0.7	2.2	0.0	1.1	1.9	0.6
D ₂ . Eurasia	0.0	1.4	0.0	0.4	1.3	0.0
Double difference-in-difference estimate, Δ_{DDD}						
Indian subcontinent as control						
E ₁ (=C ₁ -D ₁). North America	1.6	6.0	1.5	3.9	-0.7	0.3
E ₂ (=C ₂ -D ₁). South and Central	1.3	3.4	0.9	1.5	-0.4	0.1
Eurasia as control						
F ₁ (=C ₁ -D ₂). North America	2.3	6.7	1.5	4.6	0.0	0.9
F ₂ (=C ₂ -D ₂). South and Central	2.0	4.2	0.9	2.2	0.2	0.6

Notes: Data from Table 3. Eurasian population discounts the Americas and Africa from the information in Table 3 with no adjustment for Australia (which is too small to have any significant effect). Population increase is not taken on uniform time units but simple normalizations will make rates comparable between periods.

Since part of the population growth in Africa can be related to contact with Eurasia, we can discount the role of Eurasia using a double difference estimator of the African advantage. A double difference-in-differences is given by: $\Delta_{DDD} = (n_t^{Africa} - n_t^{Eurasia}) - n_t^{America}$, with $n_t^{Eurasia}$ representing a control for the contact of Africa and Eurasia. Hence, discounting the growth rate of a control region (a region that had contact with Eurasia and shared geographic similarities with sub-Saharan Africa) would eliminate all the factors that could be attributed to Eurasian influences. For instance, if the Eurasian influence is large, once $n_t^{Eurasia}$ is included, we should observe no advantage whatsoever in favor of Africa or Δ_{DDD} near zero.

In the Δ_{DDD} estimates of the African advantage we use as a control the population increase in the Indian subcontinent and the growth in Eurasia. The reason for using India as a control is that India also has a North-South axis and had clear contact with Eurasia.²⁹ The key assumption for India to be a valid control, is that India’s population growth captures the trend in Eurasia’s influence over Africa. Our control for Eurasian influence in Africa through Indian growth would most likely overstate the influence of Eurasia because since the end of the last ice age, the Sahara offered a major barrier to population only interrupted by the Nile River, the Arab trade thought the Sahara since the seventh century A.D., and East African trade through the Indian ocean in medieval times. Still, if we employ North Africa as a control, we will obtain a much larger advantage in Africa. North African population growth was negative in most of the years considered in Table 3. The same advantage will apply if we use Eurasia’s growth or the rate of world population growth because they were smaller than India’s growth.

As Table 4 shows, even after a control for Eurasian contact is taken into account, there is a population advantage for Africa. The African advantage is higher over North America than over South and Central America, and the only instance in which there is no advantage is for the first

²⁹ Africa did not adopt the European plow. As Hopkins ([30], 37) notes, “pre-colonial West Africa, [...] like India, developed a relatively simple technology, but one that was well suited to its requirements.” Austen ([4], 13) also notes that “within the West African forest, it is also impossible to cultivate millet or sorghum related plants,” although Asian and South American crops are more appropriate. We will discuss the role of the plow, the transfer of crops, and technology adoption in the next sub-section.

millennia in the population data from McEvedy and Jones [61].³⁰ Since the growth in India and in Eurasia was small during the periods considered, the contact of Africa with Eurasia does not help explain the rapid population growth in Africa. As we have noted throughout the paper, the main reason for the rapid population growth in Africa is the migration and expansion of agricultural populations into sub-Saharan Africa. (As noted in Austen [4], Davidson [20], and Diamond [23], for example, the Bantu expansion is mainly a consequence of the spread of farming in Africa.)

Information in Tables 3 and 4 thus suggests a population advantage in Africa under a wide variety of specifications. Africa's higher population level and faster population growth indicate that if population has an important role in inducing technological innovation, Africa should have achieved much higher levels of technological and social sophistication than the Americas at the time of the European expansion. (The connection between sub-Saharan Africa and Eurasia would only reinforce the previous claim as the relevant measure of population would be much larger than what Tables 3 and 4 consider.)

Africa's population advantage can be seen as a right-hand side variable in a regression. To study the relationship between population and technology, our second step describes a relevant outcome measure, a left-hand side variable. There is no standard measure of development or technological sophistication in pre-modern societies but at first sight, it seems that the Americas had a performance that in many respects seems similar to the case of sub-Saharan Africa. Both areas shared similarities in terms of their social structure and social differentiation, the patterns of barter and monetary trade, and their non-utilitarian use of precious metals. Yet, urbanization was far more pervasive in America. While the organization of States in the Americas paralleled that of Eurasia, see Diamond ([23], Table 18.1), no similar development took place in Africa. In

³⁰The numbers in sub-Saharan Africa in 1500 seem too low in McEvedy and Jones [61]. Hopkins ([30], 121) suggests an estimate of 25 million in West Africa alone during 1700. Caldwell and Schindlmayr [9] also argue in favor of larger estimates in Africa. Note also that about 10 million slaves were transported mostly from West Africa during the European slave trade, see Fogel and Engerman ([29], Figure 2). If the assignment of slaves was based on productivity considerations, and if there are decreasing returns to scale in population, the fact that more than five million slaves were transported to South and Central America, i.e., Fogel and Engerman ([29], Figure 3), also supports an African population advantage. The demographic and economic impact of slavery however seems small, see Hopkins ([30], 23, and 120-122). Slavery was already practiced in smaller scale in Africa "long before the rise of the Atlantic trade."

fact, by 400 A.D., the Americas had at least three cities with more than 100 (or at least 50) thousand inhabitants (Modelski [63] and Chandler [13]). The cities in sub-Saharan Africa were scarcer, less densely populated, and often attributed to external influences (however see Davidson [20] and Connah [19]).

The use of city formation to evaluate development is not unproblematic but as a measure of sophistication it offers many advantages since cities are a complex form of organization (see Connah [19] for an overall discussion on African civilizations and the meaning of ‘civilizations’). Cities are more complex than movable agricultural settlements and they exhibit a significant degree of division of labor. Cities often result from advances in agricultural productivity or incentives given by external or internal trade and physical evidence on the existence of cities tends to be well preserved. Urbanization has also been fruitfully employed to study patterns of development in pre-modern economies (see Acemoglu et al. [1]).³¹

Cities in the Americas were clearly an independent innovation but there is some disagreement on the nature of African civilizations. It is often argued that outside stimuli was mainly responsible for African cities although some cities seem to be an indigenous African development (Davidson [20] and Connah [19]). Pre-colonial cities can be found in the West African savannah, the West African forest, the middle Nile, the Ethiopian highlands, Nubia, the East African coast, and Zimbabwe. Since the extent of external influence is different across time and across regions, we can contrast the role of Eurasian influences and the indigenous formation of cities by comparing the Americas with Africa at different time periods or by looking at city formation in regions where cities arose independently in Africa.

Table 5 presents an inventory of cities with sizes over 20 and 40 thousand inhabitants from Chandler [13]. (The inventory in Chandler [13], according to Connah [19], provided accurate

³¹Africa seems to have experienced an independent origin of iron work often cited as being part of the advancements spread with the Bantu expansions. However, “iron apparently made no dramatic impact upon early African agriculture,” Austen ([4], 14). Cattle domestication also seems to have had an independent origin, see Austen ([4], Chapter 1). Important independent achievements in mathematics and science also took place in America, see Mann ([60], 16-20 and 63-65), so a counting of achievements will not be conclusive in terms of development. Agriculture, the largest economic sector, will be discussed separately in the next sub-section.

patterns of city formation in Africa.) In order to provide a comparison in which factors out-of-Africa can be taken into account, we report different time periods (as the influence of Eurasia differed over time). We have also divided sub-Saharan Africa in three sub-regions. The cities in regions with high Arab influence are coded as Muslims while the Middle Nile and Ethiopia are regions with influence from trade through the Indian ocean and North Africa. The rest of sub-Saharan Africa is what we consider as indigenous formation. Our decomposition is consistent with the arguments in Connah [19].

Table 5. Urban formation in Africa and the Americas.

Year	North Africa	Sub-Saharan Africa			Total	North America	South and Central America
		Muslims	Middle Nile and Ethiopia	Rest (indigenous)			
A. Number of cities with populations over 20,000 inhabitants							
800	10	0	2	3	5	0	10
1000	13	0	1	4	5	0	9
1200	18	6	2	4	12	0	10
1300	18	8	2	5	15	0	11
1400	18	8	2	9	19	0	18
1500	16	13	3	8	24	1	16
B. Number of cities with populations over 40,000 inhabitants							
800	4	0	0	1	1	0	2
1500	7	4	0	2	6	0	6

Source: Chandler ([13], 39-57). The size of cities in the Americas in Modelski [63] is slightly smaller but there are no African cities for a comparison. The indigenous cities in sub-Saharan Africa cover mostly Ghana, Zimbabwe and the Bantus. The middle Nile corresponds to Dongola (modern Sudan) and Kaffa. North Africa includes cities in the Mediterranean (i.e., Arabian, Egypt, Spanish Africa, and Aloa) and the Maghreb. Meroë, is not included in the compilation but it had more than 20,000 inhabitants in 430 B.C. (Chandler [13], 461).

Up until 1460, when the Portuguese traveled down the coast of West Africa, the Islamic world was the main Eurasian influence in sub-Saharan Africa. Around the time Islam spread into Africa, after the seventh and eighth centuries, there was a total of 5 cities with more than 20 thousand inhabitants in Africa. In the Americas, in 800 A.D., there were already twice as many cities, 10. In the Americas, in fact, the number of cities was as large as the number of cities in North Africa,

Table 5. Large cities were also more common in the Americas. Our first comparison, before the first millennia, thus shows that Africa's population advantage over the Americas failed to materialize in city formation.

External trade with North Africa, or through the Mediterranean and the Indian ocean, can be argued as driving factors for urban formation in certain parts of Africa but the West African savannah and the West African forest were separated from the outside world by the Sahara desert and the Atlantic ocean; both highly isolating factors since navigation along the coast of the Sahara desert was only possible after the development of the caravel. Isolation was also common in Zimbabwe and external trade with Eurasia seems a less plausible explanation for those cities. The indigenous formation of cities in the previous regions was also much smaller in Africa as Table 5 shows.

After the first millennia, the Eurasian influence in Africa increased but in our decomposition of the cities with more than 20 thousand inhabitants in sub-Saharan Africa, more or less fifty percent can be attributed to indigenous formation with the rest due to external influences. From Table 5, South and Central America had about twice the number of cities with more than 20 thousand inhabitants in the sample. Cities with population sizes over 40 thousand were also more common in the Americas. Thus, the size of cities was more limited in Africa than in South and Central America and there were no urban complexes as the ones in the Near East or Mesoamerica.

While no mayor ruins or evidence of large empires exist for sub-Saharan Africa, the evidence of cities in South and Central America reveal large scale urban complexes. In 400 A.D., for example, Teotihuacán (currently Mexico city) was among the ten largest cities of the world, Chandler ([13], 464). In 1500, there were six cities with more than 40 thousand inhabitants in sub-Saharan Africa. Of those six, two could be credited as having an African origin while the rest can be credited as Eurasian's. In South and Central America, there were six large cities born in isolation of Eurasia.

In summary, beginning in 400 B.C., sub-Saharan Africa had a fast population growth as a

result of the spread of agricultural techniques in Bantu populations and the influence of crops from Eurasia. Population growth however failed to translate into higher technological sophistication as measured by rates of urbanization. There were multiple cities in Africa before the European expansion and societies exhibited elaborate patterns of organization, but even if the cities that resulted from external influences are taken into account, urban developments in sub-Saharan Africa were secondary to the developments in the Americas. In the formation of urban centers, the post-agricultural African advantage also failed to materialize in cities.

6 Some proposed explanations

There is a large list of explanations for the economic backwardness of Africa in the pre-colonial period often based on a primitive view of Africa. Pre-colonial backwardness has been associated with fundamental factors such as an unfavorable geography or climate and anticapitalist value systems or culture. Inadequate resource endowments or an inefficient agriculture are also considered, Hopkins ([30], 9-11).

While different from Eurasia's, climate and the geographical conditions for farming were similar between Africa and the Americas (i.e., the llama was not used as draught animal by the Incas). Yet, the Americas had a well developed foot plow (used by the Incas) and irrigation equipment not present in Africa (such as the Aztec's floating gardens). Means of navigation, transport, and distribution were also relatively backward in Africa although not because Africa south of the Sahara never invented the wheel, Hopkins ([30], 71); the Aztecs invented the wheel but it was never employed in transportation because it was not an appropriate technology. For example, despite the proximity to East Africa, the first human settlements of Madagascar came from Asia around 500 A.D. while the settlement of the islands of the Caribbean came from Central and South America starting as early as 500 B.C., see Diamond ([23], 341). Road infrastructure and agricultural terraces were also landmarks of the Inca empire which extended over a large geographic area, Mann ([60],

65).

In terms of differentials in values, Hopkins ([30], Chapter 2) and Austen ([4], Chapter 1) have shown that Africans were expert farm managers and their response to economic incentives is a typical one for traditional agriculture. For example, it is known that African farmers did not employ the European plow (despite knowing of its existence). Hopkins ([30], 36) argues that the plow was not an appropriate technology for West Africa because soils were not heavy and could be easily cleared by fire. Draught animals were also needed for plowing but they could not survive in the West African forest. (For an analysis of appropriate technologies see Basu and Weil [5].) In terms of institutional factors, because of the technical organization of production, African societies were organized around tribes or lineage groups while most of the Americas had a social order typical of large tributary empires.

Proximate aspects such as endowments and productive factors also have difficulties explaining Africa's underdevelopment. Compared to Eurasia, Africa's backwardness can be seen as the result of lower population levels and densities that prevented specialization and the division of labor as Boserup [7] suggested (see also Lee [55] and [56]). Compared to the Americas, such an explanation is less satisfactory because the Americas were the last continent ever to be populated by modern humans and it was not more densely populated than Africa. Africa was also clearly connected to Eurasia while technological progress in the Americas arose in isolation.

Similarly, land quality cannot be the explanation for African backwardness because non-indigenous crops were adopted by African farmers and now they are considered as "typical West African agriculture." After the European arrival, a number of South American crops such as "maize, cassava, groundnuts, tobacco and later cocoa, as well as a variety of fruits," were introduced and adopted, see Hopkins ([30], 30) and Austen ([4], 15-16). In fact, today, the majority of food eaten in sub-Saharan Africa is non-indigenous whereas in Asia, America and the temperate areas, diets are still based on the crops domesticated during the Neolithic agricultural revolution; rice, corn,

and wheat (Caldwell and Schindlmayr [9], 195).

As differentials in population size, land, and efficiency do not seem to be entirely responsible for the post-agricultural differences between Africa and the Americas, we next argue that differentials in technology creation and adoption played an important role in Africa's pre-colonial backwardness. We also examine potential causes for the differentials in technological change and claim that they arose not because of a disadvantage due to a relatively large population in Africa but because of a technological lock-in.

7 Backwardness, leapfrogging, and technological leadership

The economic backwardness of post-colonial Africa is commonly attributed to fundamental factors such as a natural resource curse, an unhealthy disease environment, and the legacy of colonization (including slavery and the political and social disruptions associated with it). Our findings suggest that even before the European expansion, Africa lagged behind comparable regions and that Africa's relative backwardness was not a consequence of a disadvantage in productive factors (i.e., population, land, or land quality), restricted access to international trade (as some contact with Eurasia existed), or in unfavorable geographical conditions (as the geography of the Americas is similar).

Africa was not always a backward region. In the origin of modern humans and in stone-tool manufacture Africa had a large advantage. The out-of-Africa migration of modern humans and the likely possibility of replacements of archaic humans out of Africa suggests important African achievements in population and technology in the long pre-agricultural period. The debate on human origins is not yet resolved in anthropology but the most central question nowadays seems to be the mode of dispersal of modern humans (Eswaran et al. [26]). The dispersal out of Africa could have generated a full replacement of archaic humans or an admixture out of Africa. Still, the mode of dispersal is not important for the role of population on induced innovation because

the movements out of Africa most likely would simply reflect a technological advantage in African populations as it is the case in other technological revolutions. In regards to the migrations out of Africa and the African advantage in tool making technologies, Mellars ([62], 9383) notes:

“[The] increased levels of technological efficiency and economic productivity in one small region of Africa could have allowed a rapid expansion of these populations to other regions and an associated competitive replacement (or absorption) of the earlier, technologically less “advanced,” populations in these regions.”

Despite Africa’s advantage in population size and tool making technologies, agriculture first originated in the Near East and China. Independently, agriculture also arose in the Americas and in Africa although at a later date. As a result of agriculture, population and technology in Asia leapt over Africa’s. Population in the Americas and in Africa also increased but despite a population advantage in Africa, large cities and complex political and social organizations were more prevalent in the isolated Americas.

Africa’s pre- and post-agricultural development is puzzling from a Boserupian point of view. A similar puzzle arises in the development of China since Chinese achievements are well documented in the post-agricultural period. For example, the technologies that made possible the Industrial Revolution in England were already in place many centuries before in China. The absence of an early industrialization in the most populous post-agricultural economy is one of the main mysteries in the history of technology (Mokyr [65]).

Europe was not a populous region at the time of the Industrial Revolution (especially England). Since Europe did not experience an independent origin of agriculture, Europe’s disadvantage in population and technology before industrialization (compared to China, say) resulted from a late adoption of agriculture. Past technological leadership, as Diamond [23] notes, would have radically failed to predict Europe’s rise:

A historian who had lived at anytime between 8500 B.C. and A.D. 1450, and who

had tried then to predict future historical trajectories, would surely have labeled Europe's eventual dominance as the least likely outcome, because Europe was the most backward of those three Old World regions for most of those 10,000 years.

Technological change responds to multiple forces but the previous paragraphs suggest that the backwardness of pre-agricultural Asia (relatively to Africa) and the backwardness of post-agricultural Europe (relatively to Asia) were important for their subsequent technological leadership. Agriculture failed to develop at an earlier date in Africa because their advantage in stone-tool manufacture made investments in agriculture less attractive. For a variety of reasons, Africa locked-in technologically. Similarly, once the techniques and organization of agricultural societies are mastered, as in pre-modern China, industrialization appears less profitable. In that sense, China also locked-in technologically. Finally, industrialization first took off in Europe and then transferred to North America and Australia. North America only had an incipient agriculture since no cereal was domesticated indigenously and the influence of Central America was inhibited by the Mexican deserts. While New Guinea seems to have had an incipient agriculture, Australia failed to develop agriculture independently. Thus, the agricultural disadvantage paid off in terms of industrialization.³²

As we have shown that leadership in a given technology tends to delay the adoption or the creation of additional innovations, our views on the paper are closely related to the economic and technological leapfrogging model of Brezis et al. [8]. A leapfrogging view is drastically different from endogenous growth models such as Kremer [52] and Jones [45] because endogenous growth models assume that past technologies complement future technologies and reinforce patterns of technological leadership. An endogenous growth model would have difficulties explaining the shifts in technological leadership described above or the change in leadership between the Dutch and the

³²The civilizations in the Indus Valley also failed to experience an independent origin of agriculture but the Indus valley is located between the Near East and China and that reduced the isolation (compared to Europe). The isolation of Australia and North America are also well established in comparison to Asia and South and Central America.

British early in the industrialization stage and between the rise of the United States and Germany over England during the twentieth century, Brezis et al. ([8], 1211).³³

To highlight the difference with the conventional view of endogenous growth models, consider Jones' [45] technology for the production of ideas: $\frac{dA(t)}{dt} = A(t)^\phi N(t)^\gamma$ with ϕ and γ taking values inside $[0, 1]$. An essential property of the previous expression is the complementarity between population and past technology in the production of ideas: $\frac{\partial^2}{\partial A(t) \partial N(t)} \left(\frac{dA(t)}{dt} \right) = \phi\gamma A(t)^{\phi-1} N(t)^{\gamma-1} > 0$. That is, past technological advantages reinforce leadership since an increase in population or in past technologies will generate a comparative advantage in innovation. Alternatively, ignoring the role of technology on population growth, knowledge or accumulated experience in Jones' [45] model can be seen as:

$$A(t; t_0) = A(t_0)(1 - \phi)^{1/(1-\phi)} \left[\int_{t_0}^t N(s)^\gamma ds \right]^{1/(1-\phi)}, \quad (5)$$

with $A(t_0)$ given.

A leapfrogging view considers that past technologies rather than generating an advantage, are a disadvantage when major technological change takes place. The main departure from endogenous growth models in the leapfrogging views of Brezis et al. [8] is that technological change is assumed of two kinds. A “normal” technical change that evolves as predicted by models of endogenous growth and a “radical” technical change represented by “major breakthroughs that change the nature of technology fundamentally.”³⁴ When new technologies are introduced, according to Brezis et al.

³³A well-known study is Alexander Gerschenkron's [34] theory of relative backwardness. Gerschenkron [34] argued that economic backwardness before industrialization in Europe (i.e., in Russia, Italy, and Germany) made their post-industrial growth faster. Theoretical models of experience-based overtaking and vested interests include Jovanovic and Nyarko [46] and Krusell and Ríos-Rull [53]. See also Chari and Hopenhayn [14], Motta et al. [64], and Ohyama and Jones [67]. Mokyr ([66], Chapter 6) presents an additional discussion of resistance to technology based on rigidities in the economic system, cultural, religious, and political factors. Abundant examples of barriers of adoption and innovation in economic history are also discussed in detail by Mokyr ([66], Chapter 6).

³⁴The idea of multiple kinds of technical change and drastic innovations is often associated with general purpose technologies (GPTs), see for example Helpman [39]. The examples more frequently discussed represent modern innovations such as the steam engine, electricity, and the computer although writing and tool-making technologies also represent GPTs, see Helpman ([39], Chapter 1). A dichotomy between different types of innovations is also featured in Mokyr [65] and [66], see also Helpman ([39], Chapter 2). In Mokyr's [65] views, microinventions refer to improvements on existing techniques while macroinventions are radical changes in technology. In the analysis of technological leadership in modern times, Mokyr ([65], 207) calls attention to Cardwell's Law or to the fact that

([8], 1212), their advantages over old technologies are not evident so leadership in a established technology creates an incentive for incremental investments in “normal” technical change but a disincentive for “radical” changes. Overtaking in technological leadership will take place because “radical” technological changes are more likely to arise in backward regions or in regions without much accumulated experience in “normal” technologies.

A simple way to organize the role of technological backwardness and leapfrogging is to assume that a new technology is made available at time $T > t_0$. Productivity in the old technology is given by $A(T; t_0)$ in equation (5). Productivity in the new technology is $A'(T)$ as there is no experience in such a technology. An advantage exists in favor of the new technology as long as $A'(t; T) > A(t; T)$, for $t > T$. (We can see the growth in A' as exogenously given or also as driven by endogenous decisions in which case we will need to specify a technology for the production of “radical” ideas.³⁵) If the use of the alternative technology is based on a simple comparative advantage principle, adoption will most likely take place in economies with less knowledge of the old technology. Formally, adoption will take place whenever $A'(\tau; T) \geq A(\tau; t_0)$, and since $A(t; t_0)$ is increasing in time or experience, adoption will take place in technologically backward economies first.

No other technological revolution has received more attention than agriculture and some inferences can be drawn from current observations of hunter-gatherers in support to the previous view. Whether current hunter-gatherers are representative of past populations is much debated issue in anthropology (Excoffier and Schneider [25]) but it is clear that present-day hunter-gatherers know how to cultivate crops. Agricultural systems, however, require more work for a unit of food and “neither agricultural nor industrial man has anything like the leisure time of hunters and

“no nation has been (technologically) creative for more than an historical short period.” A similar regularity can be found over longer horizons for the continents of the Old World.

³⁵Although we focused on adoption, leapfrogging differs from models in which backwardness is viewed as an advantage for catching-up with the technological leader. Beyond catching-up, the discussion above implies changes in technological leadership. (Two examples of technology adoption are Parente and Prescott [69] and Howitt [41].) Our estimates are a reduced form so we cannot test for the causes of backwardness. Our leapfrogging view and the disadvantages of agriculture for industrialization can also be related to the “reversal of fortune” described in Acemoglu et al. [1] for the countries colonized by European powers. The explanation offered by Acemoglu et al. [1] was one of reversals in institutional factors taking the European institutions as given.

gatherers,” see Harlan ([35], 40-43). One can argue that current hunter-gatherers have survived in the semi-tropical areas of Africa and the Americas because of their food procurement skills. Their accumulated experience, however, would make technologies for permanent farming much less attractive.

8 Concluding remarks

This paper argues that African populations were larger than populations in Eurasia through out most of human history and that despite a population advantage, sub-Saharan Africa invented agriculture later than any other region in the world with an independent origin. As there are no reliable sources capable of providing an accurate estimate of the human population in the past, we argue for a pre-agricultural population advantage in Africa based on genetic comparisons of living humans. We show that Africans are very diverse from a genetic point of view and that the high African diversity can be seen as a reliable signal of larger population size through out most of human existence.

We also studied cross sectional patterns of population growth in post-agricultural societies and showed that Africa had a population advantage over the Americas. Our cross sectional study compared Africa and the Americas because there are additional influences that could contaminate a comparison between Africa and Eurasia or between the Americas and Eurasia. For example, geography and the distribution of domesticable species were not randomly allocated between continents and as with size, they benefited Eurasian populations (Diamond [23]). Our cross sectional study also reveals a post-agricultural African puzzle as populations in Africa grew faster than in any other region of the world after 400 B.C. but failed to develop as the isolated Americas (i.e., to a large degree Africa failed to organize cities).

The relationship between population and technology is complex but since Deevey [21] the surges in human population growth have been related to changes in three fundamental technologies:

tool making, agriculture, and recently industrialization (see also Coale [17] and Livi-Bacci [57]). The consequences of those technological changes on population are somewhat well understood because in all cases populations have drastically increased. In broad terms, the population response to changes in the previous technologies gives support to Malthusian views. In order to explain the origin of the previous technological revolutions, we have argued that stone tool technologies generated an advantage for hunter-gatherers in Africa and produced dispersals over backward non-African regions. Agriculture originated initially in Asia and led to dispersals into Europe, a backward region compared to the Near East or China. Finally, industrialization first originated in Europe, one of the few regions in Eurasia in which agriculture did not originate independently. If a simple pattern is to be established, the innovators in one technology lost to the developers of the next technology as in models of technological lock-in. We are in favor of a technological lock-in because technological advances only appeared in peripheral populations of migrants from the originators of previous advances.

The relationship between population and technology described in the paper differs from Kremer's [52] synthesis because we fail to find strong support for the Boserupian side. While the initial African advantage in stone tool technologies weakly supports a population-induced innovation view, as Africa was the most populous region in the past, the pattern cannot be easily reconciled with an endogenous growth model in which innovations follow from increases in population.³⁶ Not only was population growth high, but Africa's continuous contact with Eurasia failed repeatedly to generate technological sophistication.

As stressed in endogenous growth models (or in Boserupian views in general), a population-induced innovation view generates a somewhat optimistic view of the relationship between population and technology since it suggests that an Industrial Revolution was inevitable. (See, for

³⁶In the paper we have also noted that the current time series patterns of population cannot be used to properly identify the effect of population on technology because the time series produced by Deevey [21], and other ecological sources such as Hassan [37], generate an increasingly increasing growth rate by construction. That is, the estimates assume that densities and occupied areas have expanded constantly since 1MYA. At this time, there is no definite support to both assumptions.

example, Galor and Weil [33] and Jones [45].) Without denying the importance of endogenous growth mechanisms and knowledge for the evolution of technological change, especially in ‘normal’ times, one cannot but recognize, as Hopkins ([30], 76), that “it is clear that pre-colonial Africa was not moving in the direction of an indigenous industrial revolution.”

Additional natural experiments could be exploited to understand the effect of population growth on technological change because an exogenous decline in population would have permanent adverse effects on long-run population and technological change. Such idea is discussed in a counterfactual described by Holland [40] as part of a series of “what if’s” in human history. She considers the fate of Europe if Ogadai Khan had not died on the eve of the Mongol siege of Vienna in 1242. The impact can be estimated using Bagdad as a control. According to Holland [40], for instance, European cities would have replaced learning with religious prejudice and would have fallen into the fundamentalism that the Islamic world experienced after the Mongols swept through Bagdad. Yet, if Ogadai Khan’s death saved Europe, the Black Death visited only a century after the Mongol’s retreat with short-term consequences fully in line with Malthusian views. The long-term effects of the Black Death are unknown but since Europe faced a severe population reduction by the Black Death, the advantage in population given by the Mongol’s retreat could not be easily seen as the cause behind Europe’s rise. If a candidate is needed to explain the geographic region in which major technological revolutions originate, the most likely one is the absence of precursors to that technology.

9 Appendix: Mathematical population explosions

Many fundamental problems in economics are described by well-behaved solutions to linear differential equations. Under nonlinearities, a solution may behave quite differently even if all the parameters in the economy are nicely behaved as nonlinear problems might be subject to *blow-up singularities*. That is, a solution of a nonlinear differential equation can escape to infinity in finite time because starting from any finite initial condition the solution (or in some cases its derivatives) becomes infinite due to the cumulative effect of the nonlinearities.

The simplest example of blow-up singularities occurs in a nonlinear (autonomous) differential equation given by:

$$\frac{dx(t)}{dt} = f(x(t)), \tag{6}$$

with $f(x) > 0$ for $x > 0$ and smooth; at least $\mathcal{C}^1([0, \infty))$. The necessary and sufficient conditions for the occurrence of blow-up for any solution of an autonomous differential equation above are described in the next Theorem (see Samarskii et al. [83] for further developments):

Theorem 1 *For any $x(t_0 = 0) > 0$, any solution of equation (6) is globally bounded (i.e., does not blow-up) if and only if the following (Osgood) condition*

$$\int_1^\infty \frac{ds}{f(s)} = \infty, \quad (7)$$

is satisfied.

Proof. Let $x(t_0 = 0) = M > 0$. $x(t)$ is determined by the following equation:

$$\int_M^{x(t)} \frac{ds}{f(s)} = t, \quad (8)$$

so if condition (7) is satisfied, $x(t)$ will be defined for all $t \in (0, \infty)$. That the previous condition is necessary can be seen as follows. Assume that (7) is not satisfied so that:

$$\int_M^\infty \frac{ds}{f(s)} < \infty.$$

Then, there exists a t^* given by:

$$t^* = \int_M^\infty \frac{ds}{f(s)} < \infty,$$

such that $x(t) \rightarrow \infty$ as $t \rightarrow t^*$. ■

In linear differential equations in which $f(x(t)) = Ax(t)$, (8) becomes

$$\int_1^{x(t)} \frac{ds}{s} = At \text{ but as } \ln(x(t)) = \int_1^{x(t)} \frac{ds}{s},$$

the general solutions are required to satisfy $\ln(x(t)) = At$ with $x(t) \rightarrow \infty$ only as $t \rightarrow \infty$. Hence, no blow-up will take place whenever A is bounded.

In Kremer [52], population changes as equation (1) suggests. Since the solution is equation (2), blow-up time is $t^* = N(t_0)^{1-\alpha}/n(\alpha-1)$, positive and finite whenever $\alpha > 1$. If population growth is proportional to population ($\alpha = 2$), the solution is $N(t) = N(t_0)/[1 - nN(t_0)t]$, which blows-up at $t^* = 1/nN(t_0)$.

Blow-ups are also featured in some endogenous growth models. As an example, consider the well-known Ak model of economic growth under positive productivity growth at a rate g ; that is, $dA(t)/dt = gA(t)$. The production function is given by: $y(t) = A(t)k(t)$ and the evolution of capital, under simple Solow savings rules, is:

$$\frac{dk(t)}{dt} = sA(t)k(t) - nk(t) > 0,$$

with constant population growth and savings rates as n and s . Income per-capita $y(t)$ will be $y(t) = y(t_0) \exp\{(g-n)t + sA(t_0)(\exp\{gt\} - 1)g^{-1}\}$. This function is hyperexponential (Varfolomeyev and Gurevich [95]) so income will increase at increasing rates. The Taylor expansion of the exponential with high order members being neglected, gives the following dependence

$$y(t) \simeq \frac{y(t_0)}{1 - [sA(t_0) + g - n]t},$$

with blow-up time: $t^* = [sA(t_0) + g - n]^{-1} < \infty$.

We next report nonlinear estimates of α in equation (2) in Table A1. The table also displays $|h|$ as a measure of undesirable nonlinear behavior. According to Ratkowsky ([72], 28), if $|h| \leq 0.1$, the estimators

of the individual parameters are close-to-linear so their standard errors and confidence intervals can be safely used for inferences.³⁷ Table A1 also includes an estimate of proportional growth restricting α to 2.

Table A1 suggests that α is statistically larger than one in the samples that include the modern demographic transition. Measured by the estimated value of population in the year zero, the restricted estimates are marginally better suggesting proportional growth in the human population. Population in the year 1 A.D. was 170 millions but the unrestricted model only predicts 90 millions. The restricted model predicts a population of 111.5 millions. Table A1 also shows that hyperbolic growth was consistent until 200 B.C. but it failed to appear again until modern times. For example, in column (4), the estimates of α are below one suggesting exponential and not hyperbolic growth. The unrestricted estimates of columns (1), (3) and (4) are the basis of Figure 2.

Table A1. Hyperbolic growth in the human population.

	(1)		(2)		(3)		(4)	
	1MYA $\leq t$		200 B.C. $\leq t$		1MYA $\leq t \leq 200$.B.C.		1MYA $\leq t \leq 1500$	
α	1.916	(rest.=2)	1.915	(rest.=2)	1.431	(rest.=2)	0.970	(rest.=1)
s.e.	(0.04)		(0.05)		(0.10)		(0.03)	
$ h $	0.019		0.0131		0.01		0.01	
n	8.72	4.41	8.78	4.40	1.76	0.14	0.79	0.69
s.e.	(3.11)	(0.09)	(3.76)	(0.11)	(0.81)	(0.01)	(0.12)	(0.03)
$ h $	1.089	0.049	1.284	0.057	1.61	0.23	0.44	0.08
$N(0)$	89.43	111.50	89.21	111.50	213.6	289.6	146.4	143.3
s.e.	(11.10)	(2.36)	(13.18)	(2.73)	(12.05)	(35.78)	(5.74)	(4.71)
$ h $	0.126	0.077	0.161	0.089	0.43	0.70	0.07	0.01
t^*	2,040	2,035	2,039	2,035	1,303	246	∞	∞
R^2	0.99	0.99	0.99	0.99	0.99	0.98	0.98	0.98
n_m	10.802		3.497		7.090		8.132	
Obs.	56	56	41	41	15	15	33	33

Note: MYA denotes million years ago, s.e. represent standard errors. $|h|$ computes the absolute value of the asymptotic skewness measure of Hougaard (i.e., Ratkowsky [72]). Estimates were obtained by Nonlinear Least Squares each employing the Marquardt-Levenberg method. The initial values used for the estimation in (1) and (2) were $\alpha = 2$, $n = n_m$ and $N(0) = 170$ which correspond to proportional growth, the exponential growth in the sample and the population in the year 1 A.D. The initial estimates for the samples 3 and 4 are: [0.95,0.0001,170]. Initial values of α below one were used since approximations from above failed to converge by the discontinuity of the model in $\alpha = 1$. We allow exponential growth as an approximation in the cases where convergence fails. n_m represents the exponential growth in every sample. n and its standard error multiplied by 1,000,000 in samples (1) and (2). In samples (3) and (4), n and its standard error multiplied by 10,000.

³⁷To evaluate the stability of the results we compute backward recursive estimates of α starting in the year 2,000. The results are not displayed in the paper but they show that it is not possible to reject the hypothesis of hyperbolic growth if the sample includes modern data points. We also computed recursive estimates of α and asymptotic 95 percent confidence intervals as the end of the sample increases from 200 B.C. to 2000. The estimates are available upon request. They show that hyperbolic growth was consistent until 200 B.C. but it failed to appear again until after 1500. Similar points of instability were identified by Kremer ([52], 706). Also, as in the post-Neolithic agricultural revolution, $\hat{\alpha}$ declines in the last 20 years in the sample as Kremer [52] first noted.

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