BROWN
Orlando Bravo Center
for Economic Research

The Ancient Origins of the Wealth of Nations*

Bravo Working Paper # 2020-022

Quamrul H. Ashraf   Oded Galor   Marc Klemp

Abstract: This essay explores the deepest roots of economic development. It underscores the significance of evolutionary processes in shaping fundamental individual and cultural traits, such as time preference, risk and loss aversion, and predisposition towards child quality, that have contributed to technological progress, human-capital formation, and economic development. Moreover, it highlights the persistent mark of the exodus of *Homo sapiens* from Africa tens of thousands of years ago on the degree of interpersonal population diversity across the globe and examines the impact of this variation in diversity for comparative economic, cultural, and institutional development across countries, regions, and ethnic groups.

Keywords: Comparative development, human evolution, natural selection, preference for child quality, time preference, loss aversion, entrepreneurial spirit, the "out of Africa" hypothesis, interpersonal diversity.

JEL codes: O11, N10, N30, Z10

---

*Ashraf: Department of Economics, Williams College, Schapiro Hall, 24 Hopkins Hall Drive, Williamstown, MA 01267 (email: qha1@williams.edu). Galor: Department of Economics, Brown University, Robinson Hall, 64 Waterman Street, Providence, RI 02912 (email: Oded Galor@brown.edu). Klemp: Department of Economics, University of Copenhagen, Øster Farimagsgade 5, Building 26, DK-1353 Copenhagen K, Denmark (email: marc.klemp@econ.ku.dk). Ashraf acknowledges research support from the Center for Development Economics at Williams College.

The Ancient Origins of the Wealth of Nations*

Quamrul H. Ashraf Oded Galor Marc Klemp

November 2020

Abstract

This essay explores the deepest roots of economic development. It underscores the significance of evolutionary processes in shaping fundamental individual and cultural traits, such as time preference, risk and loss aversion, and predisposition towards child quality, that have contributed to technological progress, human-capital formation, and economic development. Moreover, it highlights the persistent mark of the exodus of *Homo sapiens* from Africa tens of thousands of years ago on the degree of interpersonal population diversity across the globe and examines the impact of this variation in diversity for comparative economic, cultural, and institutional development across countries, regions, and ethnic groups.

Keywords: Comparative development, human evolution, natural selection, preference for child quality, time preference, loss aversion, entrepreneurial spirit, the "out of Africa" hypothesis, interpersonal diversity.

JEL codes: O11, N10, N30, Z10

*Ashraf: Department of Economics, Williams College, Schapiro Hall, 24 Hopkins Hall Drive, Williamstown, MA 01267 (email: qha1@williams.edu). Galor: Department of Economics, Brown University, Robinson Hall, 64 Waterman Street, Providence, RI 02912 (email: Oded_Galor@brown.edu). Klemp: Department of Economics, University of Copenhagen, Øster Farimagsgade 5, Building 26, DK-1353 Copenhagen K, Denmark (email: marc.klemp@econ.ku.dk). Ashraf acknowledges research support from the Center for Development Economics at Williams College.

1 Introduction

The past two centuries have borne witness to an extraordinary transformation in living standards across the globe. After stagnating for millennia preceding the Industrial Revolution, income per capita in the world economy has since undergone a remarkable 17-fold increase, bringing dramatic improvements in education, health, and wealth around the world. Nonetheless, the fruits of these improvements have not been equally shared across nations. Variation across societies in the timing of their take-off from the epoch of stagnation to the modern era of sustained economic growth has generated a great divergence in income per capita.[1] While global inequality in living standards was rather moderate across societies and regions until the nineteenth century, it has since intensified considerably, as reflected by a 5-fold increase in the income gap between the richest and poorest regions of the world.

Over the last two decades, an influential body of research has uncovered the ancient origins of the astounding transformation in the pattern of economic development across regions, countries, and ethnic groups. While early research focused on the proximate forces that contributed to the divergence in living standards in the era following the Industrial Revolution, attention has shifted toward ultimate, deep-rooted, prehistoric factors that may have affected the course of comparative development since the emergence of *Homo sapiens*. A significant portion of research on the long shadow of prehistory has highlighted the roles played by evolutionary forces since the Neolithic Revolution and the prehistoric "out of Africa" migration of humans in shaping the composition of individual and cultural traits as well as the degree of diversity among populations across the globe.

The exploration of the interaction between human evolution and the process of economic development has centered around two fundamental lines of inquiry. The first avenue examines the effect of the environment on the evolution of individual and cultural traits as well as the contribution of this evolutionary process to economic development in the long run. The central hypothesis in this research avenue suggests that in the era following the Neolithic Revolution, Malthusian pressures acted as a key determinant of the size of a population and conceivably shaped, via the forces of natural selection, its composition as well. Lineages of individuals whose traits were complementary to the economic environment generated higher levels of income and, thus, a larger number of surviving offspring.[2] The gradual increase in the representation of these growth-enhancing traits in the population contributed to the process of development and the emergence of modern growth.

This body of research has identified several traits that may have been subjected to positive selection during the Malthusian era due to their conduciveness to human-capital formation, technological progress, and economic development. In particular, these studies have examined the evolution of predisposition towards child quality, time preference, risk and loss aversion, and resistance to infectious diseases, highlighting the contribution of this evolutionary process to the transition from stagnation to growth.

The second research avenue on the interaction between human evolution and the process of economic development has explored the persistent effect of the prehistoric exodus of *Homo sapiens* from Africa on the diversity of human traits and, thus, on comparative economic development across societies from the dawn of civilization to the contemporary era. In particular, this line of research suggests that migratory distances from the cradle of humankind in East Africa to indigenous settlements across the globe diminished their levels of interpersonal diversity and, thereby, generated a persistent hump-shaped influence on development outcomes, reflecting a fundamental trade-off between beneficial and detrimental effects of diversity on productivity at the

[1] See Galor (2011).

[2] In contrast, due to the egalitarian nature of hunter-gatherer societies, the forces of evolutionary selection within a society were largely muted prior to the Neolithic Revolution and the emergence of the nuclear family.

societal level. Although diversity can reduce interpersonal trust and social cohesiveness, and can hence adversely affect the productivity of society, diversity can also foster the cross-fertilization of ideas for innovations and stimulate gains from specialization, and it can thus contribute to society's productivity. Therefore, in the presence of diminishing marginal effects of diversity and homogeneity on productivity, the economic performance of ethnic groups, countries, or regions possessing intermediate levels of diversity would be expected to be higher than that associated with more homogeneous or heterogeneous societies.

Consistent with each of the fundamental building blocks of this hypothesis, interpersonal population diversity has been shown to have contributed to ethnocultural heterogeneity, diminished interpersonal trust, and the emergence of social conflicts. Moreover, evidence suggests that interpersonal diversity has fostered innovative activity, occupational heterogeneity, and gains from specialization. Further, interpersonal diversity appears to have shaped the nature of both precolonial and contemporary political institutions. In particular, although diversity may have triggered the development of institutions for mitigating the adverse influence of population diversity on social cohesion, the contribution of diversity to economic inequality and class stratification may have ultimately led to the formation and persistence of extractive and autocratic institutions.

This essay surveys the existing literature on the role of evolutionary processes in comparative economic development. Section 2 is devoted to explorations of the effect of the environment on the evolution of individual and cultural traits—-predisposition towards child quality, time preference, loss aversion, and risk aversion, amongst others—-and the contribution of these evolutionary process to economic development in the long run. Section 3 focuses on the examination of the persistent impact of the prehistoric exodus of *Homo sapiens* from Africa on the global distribution of interpersonal population diversity and, consequently, on comparative economic development across societies. Section 4 provides some brief concluding remarks.

2 Evolutionary Processes and the Transition from Stagnation to Growth

Geographical characteristics have shaped the evolution of traits in a population as well as their lasting effects on the transition from stagnation to growth. These evolutionary processes and their contribution to the variation in preferences and cultural traits across countries, regions, and ethnic groups are therefore critical for understanding inequality across societies.

The impact of the environment on the evolution of individual and cultural traits as well as the contribution of this evolutionary process to economic development in the long run have been the subject of an intensive research program over the past two decades. The fundamental hypothesis in this body of research, originating in Galor and Moav (2002), suggests that in the era following the Neolithic Revolution, Malthusian pressures, which acted as a key determinant of the size of a population, shaped via the forces of natural selection, the composition of traits in society. Lineages of individuals whose traits were complementary to the economic or geographical environment generated higher levels of income and, thus, in this Malthusian environment, a larger number of surviving offspring. This reproductive success gradually increased the prevalence of growth-enhancing traits in the population, contributing to the process of development, and amplifying the pace of the transition from stagnation to growth across the globe.

Consistent with evidence regarding significant human evolutionary adaptations since the onset of the Neolithic Revolution, Galor and Moav (2002) additionally argue that, due to the egalitarian nature of hunter-gatherer societies and the resultant neutrality of economically productive traits for reproductive success, these forces of evolutionary selection of individual and cultural traits had been largely muted prior to the adoption of farming and the emergence of the nuclear family. The transition to sedentary agriculture and the emergence of property rights, however, reinforced the association between parental traits and reproductive success and, thus, boosted the pace of these evolutionary processes.

This section surveys evolutionary growth theories that have explored the evolutionary forces that emerged during the Malthusian epoch and have generated testable predictions that have been confirmed to be central for the understanding of the process of development and the transition from stagnation to growth. In particular, these theories have explored the evolution of various societal traits, such as predisposition toward child quality, the ability to delay gratification, as well as risk and loss aversion, that may have been subjected to positive selection during the Malthusian era due to their conduciveness to human-capital formation, technological innovations, and economic development.[3] Their testable predictions link ancestral geographical and climatic characteristics, as well as the stages of economic development, to the prevalence of these traits in a contemporary population.

2.1 Evolution of Preference for Child Quality

Predisposition towards investment in child quality has been instrumental for the process of human-capital formation, the onset of the demographic transition, and the take-off of the world economy from an epoch of Malthusian stagnation to an era of sustained economic growth.

Galor and Moav (2002) have advanced the hypothesis that during the Malthusian epoch, natural selection brought about a gradual increase in the prevalence of traits associated with stronger preferences for the quality rather than the quantity of offspring. The positive influence of this evolutionary process on investment in human capital stimulated technological progress and contributed to the reinforcing interaction between human-capital investment and technological progress, ultimately triggering the demographic transition and accelerating the shift to a state of sustained economic growth. However, the onset of the demographic transition reversed this evolutionary process and generated an evolutionary advantage to individuals with a predisposition toward higher fertility and lower investment in human capital, thereby limiting the rates of human-capital accumulation and economic growth in the long run.[4]

2.1.1 Theory

Consider a society during the Malthusian epoch. It consists of two types of individuals: the Quantity type and the Quality type. The Quantity type allocate their limited resources between consumption and child rearing, whereas the Quality type additionally allocate some resources to the quality (human capital) of their offspring.

Although a quantity-biased preference has a positive effect on fertility rates and may appear to generate a direct evolutionary advantage, it adversely affects the quality of offspring, their income, and their fitness, and it may therefore generate an evolutionary disadvantage. In contrast, the Quality type will generate higher income and, therefore, to the extent that their quality bias is moderate, enjoy higher reproductive success. Thus, the prevalence of this growth-enhancing trait will gradually increase in the population and will contribute to the formation of human capital, the onset of the demographic transition, and the transition to modern growth.

[3]This interaction between human evolution and the process of development may capture cultural and, possibly, genetic propagation mechanisms for the intergenerational transmission of individual and societal traits (Bisin and Verdier, 2000, 2001, 2011; Weibull and Salomonsson, 2006; Bowles and Gintis, 2011; Robson and Samuelson, 2011; Sacerdote, 2011; Doepke and Zilibotti, 2014).

[4]The quantitative analysis of Collins, Baer, and Weber (2014) corroborates this hypothesis.

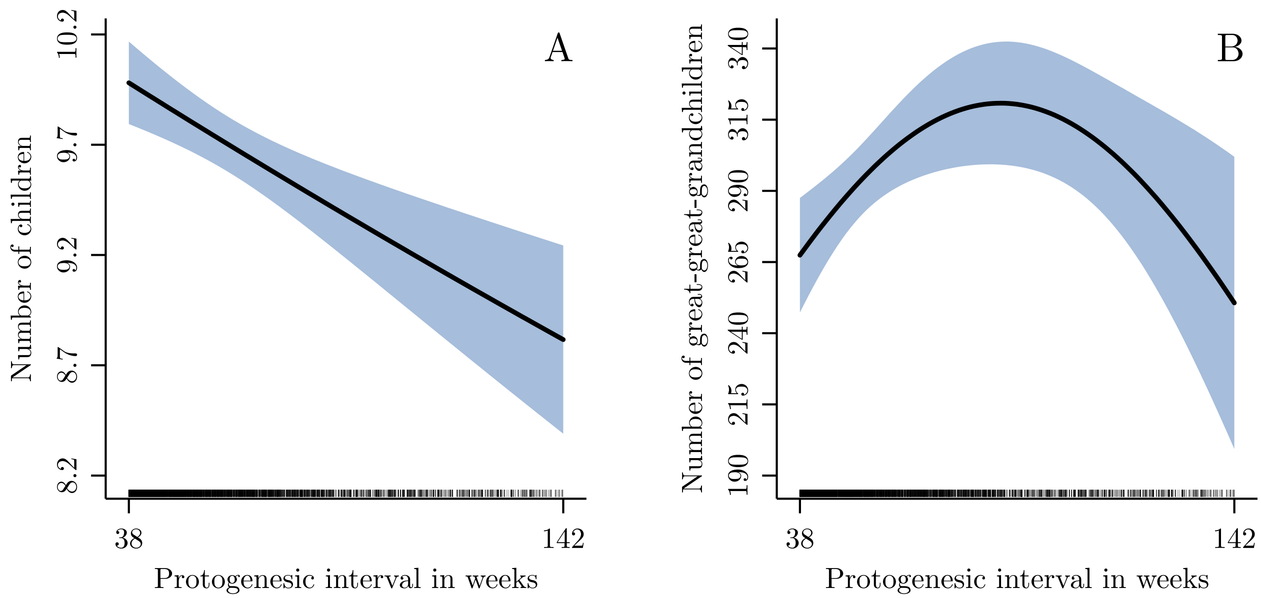

Figure 1: Fecundity and Long-Run Reproductive Success

Notes: This figure depicts the predicted number of children (panel A) and of great-great-grandchildren (panel B) as functions of the level of fecundity of 3,798 heads of lineages, where fecundity is inversely captured by the protogenesic interval (i.e., the time interval between the date of marriage and the first live birth). The shaded areas represent 95 percent confidence bands, and the rugs at the bottom of each panel represent the distribution of observations. *Source*: Galor and Klemp (2019).

However, in the post-demographic-transition era, as higher income no longer translates to greater reproductive success, the Quantity type is favored by evolutionary forces. Namely, as technological progress brings about increases in income and relaxes Malthusian pressures, the importance of income in fertility decisions is diminished, and the inherent advantage of higher valuation of quantity in reproduction starts to dominate. As individuals whose preferences are biased toward child quantity gain the evolutionary advantage, human-capital formation subsides, diminishing the long-run growth potential of the economy.

2.1.2 Evidence

The selection of greater predisposition towards child quality in a Malthusian environment has been explored by Galor and Klemp (2019). Using an extensive data set of genealogical records for nearly half a million individuals in Quebec between the 16th and 18th centuries, the study establishes that while higher fecundity was associated with a larger number of children, perhaps paradoxically, moderate fecundity maximized the number of descendants after several generations, reflecting the beneficial effects of lower fecundity on various measures of child quality (e.g., marriageability and literacy) and, thus, on the reproductive success of each child (Fig. 1).[5] Moreover, the analysis further suggests that over this period, evolutionary forces decreased the level of fecundity and, thus, increased the prevalence of predisposition towards child quality in the population.

[5]Evidence from England in the 1541–1851 time period reveals a similar pattern. Middle-class families that tended to invest in their childrens human capital had the largest number of children surviving to adulthood (de la Croix, Schneider, and Weisdorf, 2019). These data also indicate the negative impact of high fecundity on offspring quality (Klemp and Weisdorf, 2019).

Interestingly, the conditions that were faced by the founder population of Quebec during this time period of high fertility may have resembled the environment that anatomically modern humans confronted during their migration from Africa, as they settled new territories where the carrying capacity of the environment was an order of magnitude greater than the size of the founder population. Thus, the findings suggest that during the high-fertility regime of the Malthusian epoch, in which evolutionary forces could have had a significant impact on the composition of the population (e.g., during the Neolithic transition and the formation of sedentary agricultural communities), natural selection favored individuals with stronger predisposition towards child quality, contributing to the formation of human capital, the onset of the demographic transition, and the evolution of societies from an epoch of stagnation to sustained economic growth.

While Galor and Klemp (2019) uncover evidence in line with Galor and Moav's (2002) theoretical predictions for the pre-demographic-transition Malthusian epoch, the findings of Kong et al. (2017) are consistent with their predictions for the post-demographic-transition era. Specifically, based on data for Icelandic individuals born between 1910 and 1990, Kong et al. (2017) uncover evidence for an evolutionary disadvantage of parental genomic variants associated with children's educational attainment.

2.2 Evolution of Time Preference

Future-oriented behavior, as reflected by the ability to delay gratification and the rate of time preference, has been pivotal for the growth process and long-run prosperity. Long-term orientation has governed the pace of human- and physical-capital formation, technological advancement, and economic growth, and has been widely considered as a fundamental determinant of the wealth of nations.

Galor and Özak (2016) has advanced the hypothesis and established empirically that the trait of long-term orientation, reflecting individual characteristics as well as societal norms, has evolved over the course of human history in a process of adaptation to local geographical environments. Pre-industrial agroclimatic characteristics that were conducive to higher crop returns, triggered an evolutionary process of adaptation, as well as learning to delay gratification, that contributed to the prevalence of long-term orientation in the contemporary era. In line with this hypothesis, variation in the degree of long-term orientation across individuals, as well as across countries and regions, have been traced to variation in the natural return to agricultural investment across the ancestral environments of these individuals and societies.

2.2.1 Theory

Consider farmers during the Malthusian epoch who are contemplating between two strategies regarding the use of their land. The first strategy is to exploit the entire plot for gathering, fishing, and hunting, in order to guarantee a modest, yet stable, year-round food supply. The second strategy is to use only part of the land for ongoing consumption while planting crops on the remaining segment. This investment strategy would generate a larger food supply in the long run, but it would require a capacity for delayed gratification, since it would involve sacrificing short-term consumption for the sake of greater consumption in the future.

According to the theory, the investment strategy was more profitable in regions in which crops generated a higher rate of return (higher average daily yield) over the required period from planting to harvesting. In areas with relatively high returns on harvestable crops, farmers that chose to engage in crop cultivation, forgoing consumption units in the present for additional ones in the future, enjoyed higher income and, in the Malthusian era, higher reproductive success. Their rewarding experience reinforced their outlook about the virtues of delayed gratification, and this enhanced capacity was transmitted to their offspring and diffused to society at large. The capacity for delayed gratification, therefore, gradually spread in the population, and this essential trait for the growth process became more prevalent in those regions.

The ability to delay gratification might have spread through a process of biological or cultural evolution. Since this trait contributed to higher earnings and, thus, a larger number of children, if this ability is transmitted genetically from parent to child, the number of carriers of this trait would have increased over time, and it would inevitably become more prevalent in the population. In addition, the ability to delay gratification could have plausibly diffused through a process of cultural evolution. Parents could have taught their children about the virtues of delayed gratification, and society as a whole could have emulated farmers that amassed wealth due to their ability to delay gratification, increasing the representation of this trait in the population.

The theory generates several testable predictions regarding the effect of the natural rate of return to agricultural investment on the rate of time preference. First, in societies in which the ancestral population was exposed to a higher crop yield (for a given growth cycle), the rewarding experience of agricultural investment triggered selection, adaptation, and learning processes that gradually increased the representation of the trait of stronger long-term orientation in the population. Thus, individuals, countries, and regions whose ancestral populations resided in environments with higher natural return to agricultural investment would be expected to possess stronger long-term orientation. Second, societies that benefited from an expansion in the spectrum of suitable crops in the post-1500 period, and could therefore have adopted crops with higher rates of return, would be expected to experience further gains in the degree of long-term orientation.

2.2.2 Evidence

Potential crop returns, as measured by the maximal average daily calories that can be generated by an acre of land, over the period from planting to harvesting, are distributed rather unevenly across the globe (Fig. 2). In particular, the dominating crops in Europe (barley) and Asia (rice) yield nearly twice as many calories as the corresponding crop in sub-Saharan Africa (peas), while requiring two-thirds of the duration between planting and harvesting. Consistent with the proposed theory, individuals, countries, and regions whose ancestral populations originated in areas with higher potential caloric returns tend to be more forward-looking.

Clearly, the positive relationship between caloric return and the ability to delay gratification is not necessarily indicative of an evolutionary process. It might instead reflect the choice of farmers, with a greater ability to delay gratification, to adopt crops with higher caloric returns that require longer-term investment. However, *potential* caloric return, as predicted by agroclimatic characteristics that are orthogonal to human cultivation, is shown by Galor and Özak (2016) to impart a positive impact on the ability to delay gratification, reaffirming the influence of these geographical attributes on the evolution of the ability to delay gratification.

Nevertheless, the association across regions between potential caloric return and the ability to delay gratification could have reflected the selective migration of individuals that were able to delay gratification into regions better-suited for high-yield crops that required long-term investment. However, the findings show that the potential for adoption of high-yield New World crops (such as maize and the potato) following the Columbian Exchange had a significant impact on the capacity for delayed gratification among the already settled populations of Europe and Asia, mitigating the potential role of selective migration in this relationship and lending further credence to the evolutionary mechanism.

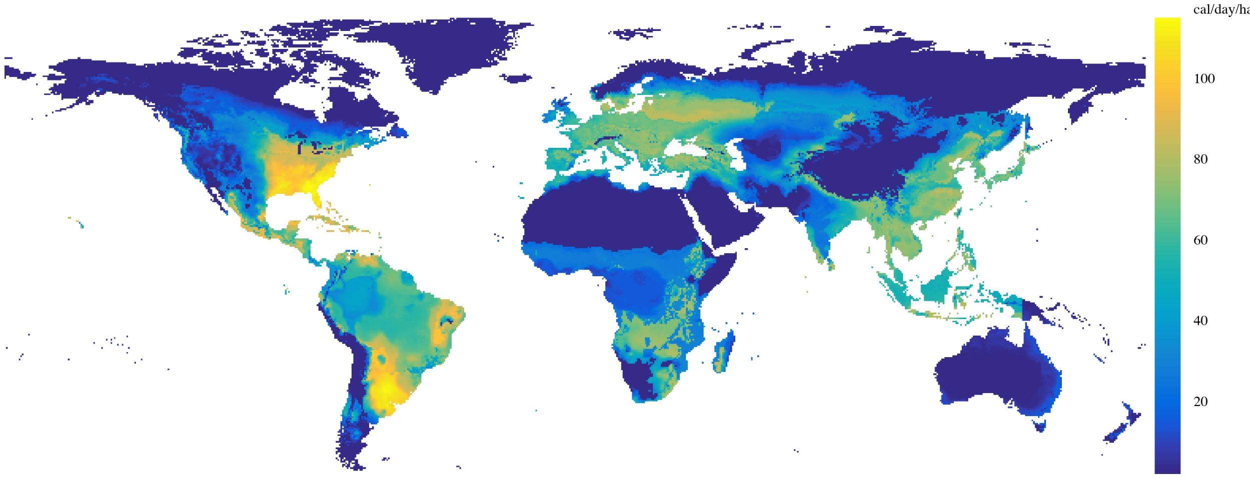

FIGURE 2: The Global Distribution of the Potential Caloric Return of Native Crops Before AD 1500

Notes: This figure depicts the worldwide distribution of daily crop yields, as measured by the ratio of total crop yields to crop growth cycles, for crops that were native to a location before AD 1500. Higher (lower) daily crop yield values are indicated by pixels closer to the yellow (blue) end of the color spectrum. *Source*: Based on data from Galor and Özak (2016).

Exploiting a natural experiment associated with the expansion of suitable crops for cultivation in the course of the Columbian Exchange (i.e., the pervasive exchange of crops between the New and Old World), Galor and Özak (2016) establish that pre-industrial agroclimatic characteristics that were conducive to generating higher returns to agricultural investments, indeed triggered selection, adaptation, and learning processes that have had a persistent positive influence on the prevalence of long-term orientation in the contemporary era. This suggests that the evolutionary process has taken place in both the pre- and the post-1500 time periods. Furthermore, these agroclimatic characteristics have had a culturally-embodied impact on economic behavior such as technological adoption, human-capital formation, the propensity to save, and the inclination to smoke.

The empirical analysis is robust to the use of distinct samples and to examining patterns at different units of analysis, exploiting variation in preferences and behavior across individuals, countries, and ethnic groups, based on data from the European Social Survey (ESS), the General Social Survey (GSS), a cross-country sample, the World Values Survey (WVS), the Ethnographic Atlas (EA), and the Standard Cross-Cultural Sample (SCCS).

This evidence therefore suggests that crop yields have shaped humans' capacity for delayed gratification through a process of adaptation. The evidence further suggests that the capacity for delayed gratification among second-generation immigrants that currently reside in Europe and the United States is linked to potential crop yields in their parental homelands rather than in the adopted countries where they were born and raised. In other words, the capacity for delayed gratification was determined by cultural attributes that had evolved in the distant past and were passed down intergenerationally.

2.3 Evolution of Loss Aversion

Entrepreneurship is a significant determinant of economic prosperity in the modern world. One of its main determinants—the degree of loss aversion—has evolved over the course of human history in a process of adaptation to the climatic environment. Thus, the evolutionary origins of this intriguing phenomenon of loss aversion—the tendency of people to attach disproportionate weight to losses than to comparable gains (Tversky and Kahneman, 1991)—has critical implications for the understanding of human behavior and the growth process.

In light of existing evidence that resources per capita during the Malthusian era were near the subsistence-consumption level, lineages of individuals that were subjected to significant adverse transitory productivity shocks during this period became extinct, while lineages of individuals that experienced favorable climatic realizations enjoyed higher reproductive success only temporarily. In other words, unfavorable climatic conditions could have driven entire populations to extinction, while transitory favorable conditions bestowed only temporary gains in productivity and modest and temporary gains in reproductive success.

The potential for catastrophes arising from adverse climatic fluctuations made it advantageous from an evolutionary viewpoint to minimize losses even on the account of forgoing expected potential gains. Thus, in the present day, the tendency of humans to attribute greater importance to losses than comparable gains may reflect the formation of natural instincts shaped in an evolutionary process that unfolded during an epoch when losses often drove populations to extinction.

Galor and Savitskiy (2020) explore the origins of loss aversion and the variation in its prevalence across regions, nations, and ethnic groups. They advance the hypothesis and establish empirically that the evolution of loss aversion in the course of human history can be traced to the adaptation of humans to the asymmetric effects of climatic shocks on reproductive success during the epoch in which subsistence consumption was a binding constraint. Regions with greater climatic volatility and lower spatial correlation in climatic shocks experienced an evolutionary process that contributed to the prevalence of lower degrees of loss aversion in the contemporary era.

2.3.1 Theory

Consider a continuum of loss-averse individuals on the edge of the subsistence consumption constraint during the Malthusian epoch. They deliberate between two agricultural modes of production: a safe one and a risky one. The safe mode of production is climatically insensitive, assuring a subsistence level of consumption as well as one surviving offspring. The risky mode, in contrast, is vulnerable to climatic volatility, but it generates an expected consumption above subsistence, and, thus, expected reproductive success above replacement in this Malthusian environment, although it may lead to extinction following unfavorable climatic realizations.

Ex ante, individuals who are loss averse may favor the safe agricultural practices that would assure their subsistence consumption and reproductive success, minimizing the risk for catastrophic realizations that would inevitably make their dynasties extinct. In contrast, individuals who are loss neutral may favor the riskier agricultural practices that are associated with a higher expected return, higher reproductive success, but a higher risk of extinction.

In a Malthusian environment characterized by aggregate productivity shocks, loss-neutral individuals who were engaged in risky agricultural practices would have eventually been affected by a catastrophic climatic realization and would have become extinct. Hence, in an environment characterized by aggregate productivity shocks, the trait of loss aversion, and the associated choice of the safer production mode, would have been favored by the forces of natural selection and would have dominated in the population in the long run.

However, in a Malthusian environment characterized by idiosyncratic shocks, although the trait of loss aversion would have still maximized the survival probability of each individual, some loss-neutral dynasties would have experienced a long realization of favorable climatic conditions and, thus, significantly higher reproductive success, and would have ultimately dominated in the population in the long run.

The theory generates two fundamental testable predictions about the climatic origins of the observed variation in predisposition toward loss-aversion. It suggests that individuals, as well as societies, that originate from regions of the world in which climatic shocks tended to be spatially correlated, and thus aggregate in nature, should be characterized by a greater intensity of loss aversion. In contrast, descendants of populations indigenous to regions of the world that had been characterized by greater climatic volatility should tend to exhibit a higher degree of loss neutrality.

2.3.2 Evidence

Empirical evidence based on historical climate data and contemporary survey and experimental data on loss aversion are in line with the theory. Exploiting regional variations in vulnerability to climatic shocks, as well as their exogenous changes over the course of the Columbian Exchange, the analysis of Galor and Savitskiy (2020) suggests that individuals and ethnic groups that originate from regions marked by greater climatic volatility have a higher predisposition toward loss neutrality, while descendants of populations native to regions where climatic conditions tended to be spatially correlated, and where shocks were, thus, aggregate in nature, are characterized by a greater intensity of loss aversion. These findings are robust to the use of distinct samples and to exploiting variations at different units of analysis (i.e., individuals, ethnic groups, and countries).

Remarkably, populations retain their predisposition to loss aversion even when they depart from their native homelands. Among European-born and American-born children of immigrants, the degree of loss aversion reflects the climatic conditions of their *parental* countries of origin, rather than the climate, institutions, or economic incentives in the location where they were born and raised. That is, the critical determinants of individuals' loss aversion are the climatic conditions in their ancestral homelands and the contribution of these historical factors to the evolution and intergenerational transmission of cultural traits over centuries or millennia.

2.4 Causes and Consequences of Other Evolutionary Processes

2.4.1 Evolution of Entrepreneurial Spirit

Galor and Michalopoulos (2012) have explored the coevolution of entrepreneurial spirit and the process of long-run economic development. Their analysis suggests that Darwinian selection of entrepreneurial traits may have played a significant role in the process of economic development and influenced the dynamics of inequality both within and across societies. Specifically, they argue that entrepreneurial spirit evolved nonmonotonically over the course of human history. In early stages of development, risk-tolerant growth-promoting traits possessed an evolutionary advantage, and their increased representation in the population over time accelerated the pace of technological progress and, thereby, the process of economic development. In mature stages of development, however, risk-averse traits gained an evolutionary advantage, diminishing the growth potential of advanced economies and contributing to convergence in economic growth across countries.

The predictions of the theory are in line with the recent findings of Bouchouicha and Vieider (2019). In particular, their findings indicate the existence of a positive association between risk tolerance and the number of children in early stages of development, and a negative association in later stages of development, as reflected by a negative impact of the interaction between income per capita and risk tolerance on the fertility rate across countries. Moreover, consistent with the theory, the analysis suggests that risk tolerance is less prevalent in richer societies.

2.4.2 Evolution of Physical and Biological Traits

The evolutionary origins of worldwide variations in resistance to infectious diseases have been examined by Galor and Moav (2007). This research hypothesizes and provides empirical evidence that the socioeconomic transformations associated with the Neolithic Revolution triggered an evolutionary process that imparted positive selective pressures on disease resistance. Consequently, heterogeneity across societies in their length of exposure to this evolutionary process, as captured by their differential timing of the transition to sedentary agriculture, may have significantly shaped the contemporary global distribution of human longevity. Cook (2015) further links this evolutionary process to the degree of intrapopulation genetic diversity in the human leukocyte antigen (HLA) system.

In related research, Lagerlöf (2007) has argued that resource depletion associated with technological progress and rising population density during the Malthusian epoch may have triggered a shift in reproductive advantage from large to small body sizes, thereby generating an endogenous reversal of the long-run time trend in human body mass.[6]

2.4.3 Barrier Effects

Differential evolutionary processes across societies and regions may have contributed to their cultural and biological divergence, creating biocultural and institutional barriers to the diffusion of development across countries and regions.

In line with such "barrier effects" associated with cultural and biological divergence, this research program, pioneered by Spolaore and Wacziarg (2009), has established a reduced-form contribution of pairwise F_{ST} genetic distance between societies to dyadic differences in income per capita, technology adoption, and institutional quality, amongst other outcomes. The exploited measure predominantly captures the time elapsed since two societies diverged from a common ancestral population and, therefore, the time over which intersocietal cultural and biological differences could have accumulated due to the forces of cultural and genetic drift, differential selection, and divergent gene-culture coevolution (Spolaore and Wacziarg, 2014).[7]

2.5 Evolutionary Processes in Genetic Traits since the Neolithic Revolution

Existing scientific evidence suggests that the composition of genetic traits within a population has evolved rather swiftly in the course of human history and that differential evolutionary processes have transpired in human populations since the onset of the Neolithic Revolution, lending credence to the nature and intensity of the evolutionary forces highlighted by evolutionary growth theories.[8] The transition from hunting and gathering to sedentary agriculture apparently triggered selection at genetic loci associated with skin pigmentation, resistance to infectious diseases, height, and diet.

[6] The long-run codetermination of human physiology and economic development is explored further by Dalgaard and Strulik (2015, 2016).

[7] The study by Becker, Enke, and Falk (2020) is another example of the application of pairwise F_{ST} genetic distance as a measure of the temporal divergence between societies. Specifically, the authors uncover evidence linking this measure with dyadic intersocietal differences in economic preferences, particularly risk aversion and the prosocial traits of altruism, positive reciprocity, and trust.

[8] Voight et al. (2006) detected about 700 regions of the human genome in which genetic loci appear to have been reshaped by natural selection within the past 5,000 to 15,000 years. Moreover, Mekel-Bobrov et al. (2005) reports that a variant of the *ASPM* gene (a specific regulator of brain size in the lineage leading to *Homo sapiens*) arose in humans merely about 5,800 years ago and has since swept into high frequency under strong positive selection. Additional evidence on recent human adaptive evolution is provided by Sabeti et al. (2006), Hawks et al. (2007), and Nielsen et al. (2007).

The differential onset of the Neolithic transition across regions has therefore contributed to the emergence of variations across populations in their composition of genetic traits.

Lactase persistence emerged among European and Near Eastern populations due to their early domestication of dairy-producing animals during the Neolithic Revolution, whereas in regions that experienced a delayed exposure to these domesticates, a larger fraction of the contemporary adult population continues to experience lactose intolerance (Bersaglieri et al., 2004; Burger et al., 2007; Tishkoff et al., 2007). Similarly, genetic immunity to malaria provided by the sickle cell trait is highly prevalent among the descendants of African populations whose early engagement in agriculture provided fertile breeding grounds for mosquitoes and, thus, elevated the incidence of malaria, whereas this trait is largely absent among descendants of populations that did not practice early agriculture (Livingstone, 1958; Wiesenfeld, 1967; Tishkoff et al., 2001).

Moreover, evidence based on comparing the genomes of ancient West Eurasians, dated to have lived between 6500 BCE and 300 BCE, with the genomes of present-day Europeans indicates that adaptive immunity was apparently favored by natural selection due to the rise in population density and the associated increase in the prevalence of infectious diseases over the course of the Neolithic Revolution. In addition, lactase persistence, reduced blood plasma triglyceride levels, and regulators of vitamin D levels were selected to provide protection against the ergothioneine deficiency associated with the shift from hunter-gatherer to agricultural diets. Furthermore, lighter skin pigmentation (and to a lesser extent, lighter eye color) was subject to strong positive selection in some regions of the world: early Neolithic migrants to southern Europe were under selection pressures that favored decreased height, while the selection of increased height operated on the steppe populations that ultimately migrated to northern Europe (Mathieson et al., 2015).[9]

3 The "Out of Africa" Hypothesis of Comparative Development

3.1 The Main Hypothesis

An emergent body of research on the deep roots of comparative development has advanced the hypothesis that migratory distances from the cradle of humankind in East Africa to the ancestral populations of contemporary societies affected the worldwide distribution of interpersonal diversity and generated a persistent hump-shaped effect on development outcomes, reflecting the trade-off between the beneficial and detrimental effects of diversity on productivity at the societal level.[10]

This research program, originating in Ashraf and Galor (2013a), suggests that interpersonal diversity may have opposing effects on aggregate productivity. It can enhance economic development by widening the spectrum of individual traits (e.g., skills, abilities, and approaches to problem-solving), thus fostering specialization, stimulating the cross-fertilization of ideas in innovative activities, and facilitating more rapid adaptation to changing technological environments. Conversely, by widening the spectrum of individual values, beliefs, preferences, and predispositions in social interactions, diversity can reduce trust and social cohesion, generate social conflicts, and introduce inefficiencies in the provision of public goods, thus adversely affecting economic performance.

Therefore, so long as the beneficial effects of diversity and homogeneity on productivity are diminishing, the degree of interpersonal diversity would be expected to confer a hump-shaped effect on economic development. In particular, the economic performance of ethnic groups, countries, or

[9] Independently of the Neolithic Revolution, natural selection led to the emergence of hemoglobin-regulating high-altitude adaptations among Tibetans, allowing carriers to survive in low-oxygen conditions (Simonson et al., 2010).

[10] The discussion in these sections partly draw on Ashraf and Galor (2018) and Arbatlı et al. (2020).

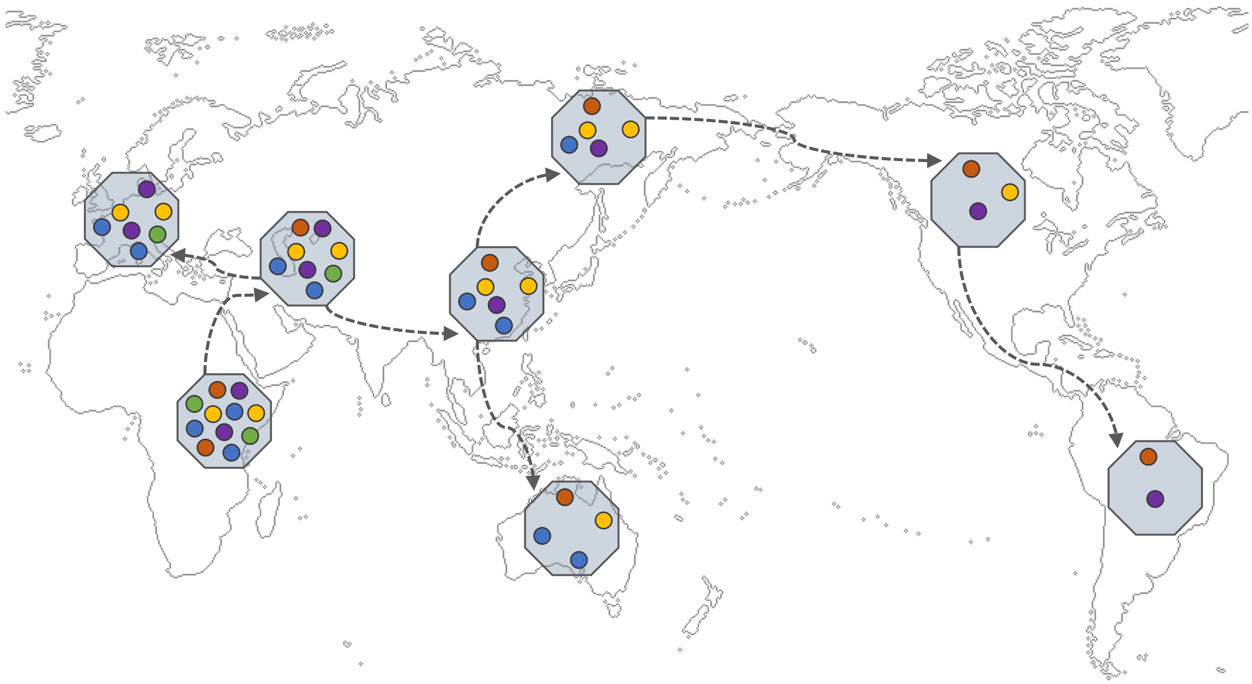

Figure 3: The "Out of Africa" Migration and the Associated Serial Founder Effect

Notes: This figure depicts the "out of Africa" migration pattern of *Homo sapiens*, while illustrating its impact on the worldwide distribution of interpersonal population diversity. With each outward migration event, the departing (founder) population carries with it only a subset of the diversity of its parental colony, as reflected by the decline in the representation of the different variants of a hypothetical trait in the founder population, relative to its source population. The dashed arrows represent approximate migration paths, and the small colored circles represent the variants of the hypothetical trait. *Source*: Ashraf and Galor (2018).

regions that are characterized by intermediate levels of diversity would be expected to be higher than that associated with largely homogenous or heterogeneous societies.

3.2 The Origins of Worldwide Variations in Human Population Diversity

The expansion of anatomically modern humans from the cradle of humankind in Africa has imparted a deep and indelible mark on the worldwide variation in the degree of interpersonal diversity across populations. According to the widely accepted "out of Africa" hypothesis of human origins, the human species, having evolved to its anatomically modern form in East Africa nearly 300,000 years ago, embarked on populating the entire globe in a stepwise migration process commencing 90,000–70,000 BP. The world map in Fig. 3 depicts the approximate migration routes that characterized this prehistoric process of human expansion from Africa.

The "out of Africa" migration was inherently associated with a reduction in the extent of diversity in populations that settled at greater migratory distances from Africa. In particular, as follows from a *serial founder effect* akin to that illustrated in Fig. 3, since the spatial diffusion of humans to the rest of the world occurred in a series of discrete steps, where in each step a subgroup of individuals left their parental colony to establish a new settlement farther away, carrying with them only a subset of the traits of their parental colony, the extent of diversity observed *within* a geographically indigenous contemporary ethnic group decreases with distance

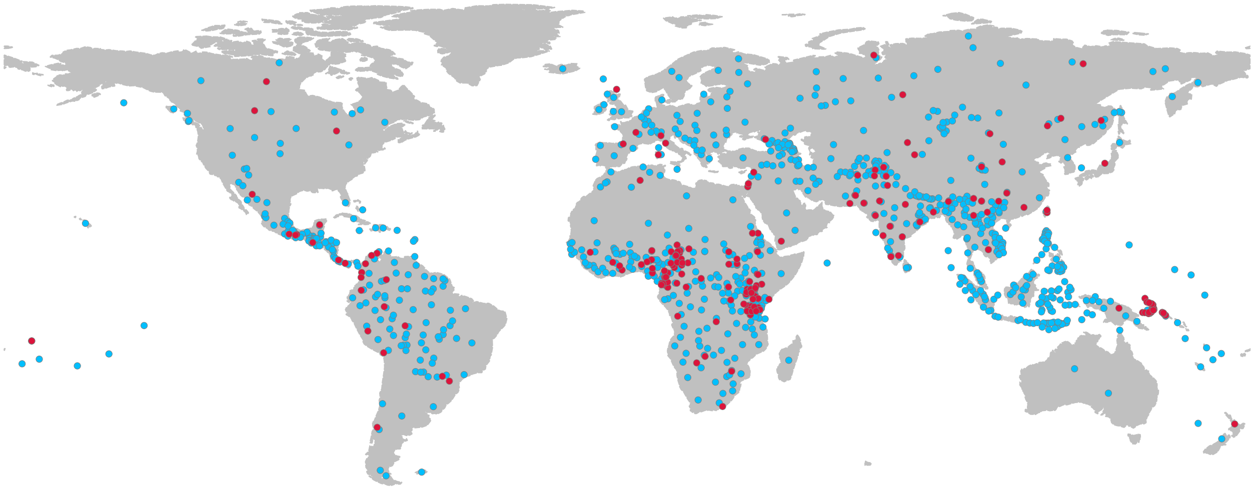

FIGURE 4: The Global Distribution of Ethnic Groups with Observed or Predicted Population Diversity

Notes: This figure depicts the worldwide distribution of ethnic groups for which interpersonal population diversity is either observed or predicted based on migratory distance from East Africa. Each point represents the centroid of the historical homeland of an ethnic group. Red points depict homelands for which population diversity is observed, whereas blue points depict homelands for which it is predicted. *Source*: Arbatlı et al. (2020).

along ancient migratory paths from East Africa (e.g., Harpending and Rogers, 2000; Ramachandran et al., 2005; Prugnolle, Manica, and Balloux, 2005; Ashraf and Galor, 2013a).

Reflecting this chain of ancient population bottlenecks originating in East Africa, the scatter plot in Fig. 4 depicts the negative influence of migratory distance from the cradle of humankind on intrapopulation genetic diversity in a sample comprising 207 globally representative ethnic groups examined in the literature on human population genetics (Pemberton, DeGiorgio, and Rosenberg, 2013; Arbatlı et al., 2020).[11] According to population geneticists, these groups are both indigenous to their current geographical locations and have been largely isolated from genetic flows from other ethnic groups. The spatial distribution of these ethnic groups is depicted on the world map in Fig. 5.

In order to measure the extent of diversity in genetic material across individuals in a given population (e.g., an ethnic group), population geneticists employ an index known as expected heterozygosity, which captures the probability that two individuals, selected at random from the relevant population, are genetically different from one another with respect to a given spectrum of genetic traits. In particular, a gene-specific expected heterozygosity index (i.e., the probability that two randomly selected individuals differ with respect to a given genetic trait) is first constructed, based on the proportional representations of different alleles or variants of this trait in the population, and upon measuring heterozygosity for a large number of genes or DNA loci, this information is averaged across loci to yield the overall expected heterozygosity for the relevant population.

[11] This sample of 207 ethnic groups consists of all observations from the data set of Pemberton, DeGiorgio, and Rosenberg (2013) that can be mapped to distinct ethnic homelands, excluding the Surui of South America, who are viewed by population geneticists as an extreme outlier in terms their measured level of expected heterozygosity (Ramachandran et al., 2005). Nevertheless, including this outlier observation in the sample does not qualitatively affect the results.

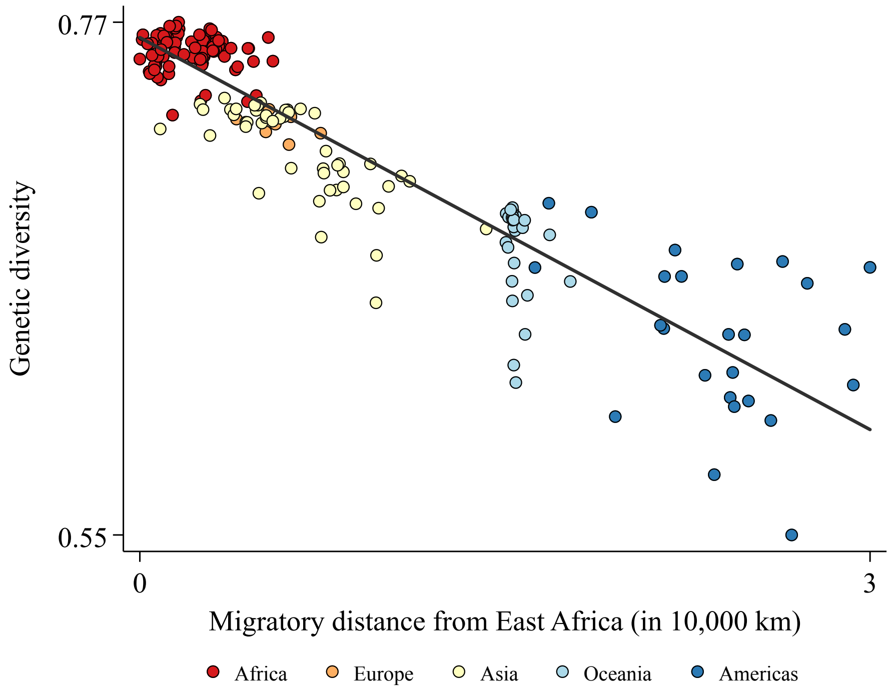

FIGURE 5: Expected Heterozygosity and Migratory Distance from East Africa

Notes: This figure depicts the negative impact of migratory distance from East Africa on expected heterozygosity in a sample of 207 ethnic groups, drawn from the data set of Pemberton, DeGiorgio, and Rosenberg (2013). *Source*: Arbatlı et al. (2020).

Thus, expected heterozygosity for a population, H_{exp}, takes the form:

$$H_{\text{exp}} = 1 - \frac{1}{m} \sum_{l=1}^{m} \sum_{i=1}^{k_l} (p_i)^2,$$

where m is the number of genes or DNA loci being considered, k_l is the number of naturally occurring variants or alleles of gene l, and p_i is the proportional representation (or frequency of occurrence) of allele i of gene l in the population.

The measure of expected heterozygosity for geographically indigenous ethnic groups is constructed by population geneticists using data on allelic frequencies for a particular class of DNA loci known as microsatellites. These DNA loci reside in non-protein-coding regions of the human genome (i.e., regions that do not directly result in phenotypic expression) and are therefore viewed as selectively neutral. For the purposes of examining the influence of interpersonal diversity on socioeconomic outcomes across populations, this measure possesses a key advantage of not being tainted by any unobserved heterogeneity in the forces of natural selection that may have operated on these populations since their exodus from Africa; forces that could have obscured the relationship predicted by an ancient serial founder effect. In addition, differential selection and its underlying forces could have also influenced socioeconomic outcomes, thus making it difficult to identify the causal socioeconomic influence of interpersonal diversity.

Nevertheless, to be conceptually meaningful for socioeconomic outcomes, the measure of neutral genetic diversity ought to serve as a valid proxy for diversity in phenotypically and behaviorally expressed traits. Indeed, mounting evidence from the fields of physical and cognitive anthropology suggests the existence of an ancient serial founder effect originating in East Africa on the observed worldwide patterns in various forms of intragroup morphological and cognitive diversity (Henn, Cavalli-Sforza, and Feldman, 2012), including interpersonal diversity in skeletal features pertaining to cranial characteristics (Manica et al., 2007; von Cramon-Taubadel and Lycett, 2008; Betti et al., 2009), dental attributes (Hanihara, 2008), pelvic traits (Betti et al., 2013), and birth canal morphology (Betti and Manica, 2018), as well as intralingual phonemic diversity (Atkinson, 2011).[12] Thus, as argued by Ashraf and Galor (2013a, 2018) and discussed in the next section, a proxy measure of population diversity *predicted* by the migratory distance of the ancestral populations of a society from East Africa would indeed capture the latent impact of interpersonal diversity in phenotypically and behaviorally expressed traits on societal outcomes. Importantly, in light of gene-culture coevolution and transgenerational epigenetic inheritance, the socioeconomic influence of population diversity may be interpreted as reflecting the impact of interpersonal diversity in traits rooted in both "nature" and "nurture" as well as the interaction between the two.[13]

In addition to giving rise to the worldwide variation in interpersonal diversity *within* human societies, the prehistoric "out of Africa" dispersal also imparted a deep and long-lasting influence on the extent of genetic differentiation *between* societies, as measured by population geneticists using an index called F_{ST} genetic distance. For any two populations, this index captures the extent of their combined genetic diversity that is *unexplained* by the population-weighted average of their respective expected heterozygosities. Thus, the F_{ST} genetic distance between populations i and j is given by:

$$F_{\mathrm{ST}}^{ij} = 1 - \frac{\theta_i H_{\mathrm{exp}}^{i} + \theta_j H_{\mathrm{exp}}^{j}}{H_{\mathrm{exp}}^{ij}},$$

where H_{exp}^{i} and H_{exp}^{j} are the individual expected heterozygosity indices of i and j, θ_i and θ_j are the population shares of i and j in the combined population, and H_{exp}^{ij} is the expected heterozygosity of the combined population comprising i and j.

Following the splitting up of populations from one another during the "out of Africa" migration process, the residual genetic variation between populations, as captured by F_{ST} genetic distance, arose from (i) random mutations that caused genetic drift within each population over time; and (ii) heterogeneity in environmentally driven selective pressures across their different eventual habitations. In particular, since migratory distance between a pair of populations partly reflects the length of time elapsed since they diverged from their common ancestral population, and because it also reduces the likelihood that they would have subsequently come into contact with one another, a direct implication of the "out of Africa" hypothesis is that pairwise F_{ST} genetic distance increases with the pairwise migratory distance between populations. Using a measure of F_{ST} genetic distance based on selectively neutral genetic markers (i.e., distance that only captures genetic drift due to random mutations), the scatter plot in Fig. 6 depicts the aforementioned relationship arising

[12] Moreover, a serial founder effect associated with the initial expansion of humans across Polynesian islands has been shown to exist in the context of intrapopulation diversity in functional markers pertaining to material culture (Rogers, Feldman, and Ehrlich, 2009).

[13] For instance, introducing the concept of "genetic nurture," Kong et al. (2018) find that parental genotype associated with the educational attainment of parents in turn affects the educational attainment of children even when the latter do not carry the relevant allelic variants, thus suggesting the intergenerational propagation of traits that may initially be rooted in "nature" through the transmission mechanism of "nurture."

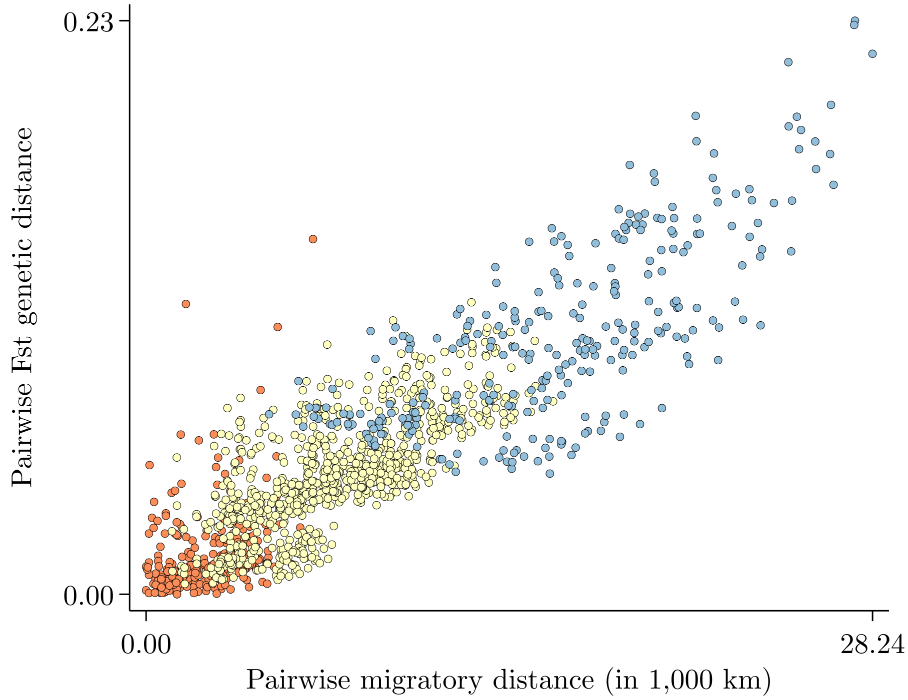

FIGURE 6: Pairwise F_{ST} Genetic Distance and Pairwise Migratory Distance

Notes: This figure depicts the positive impact of pairwise migratory distance on pairwise F_{ST} genetic distance across all 1,378 ethnic group pairs from the set of 53 ethnic groups that constitute the HGDP–CEPH Human Genome Diversity Cell Line Panel. Orange points represent observations in which the two ethnic groups in the pair belong to the same world region (i.e., both come from either Africa, the Middle East, Europe, Central and South Asia, East Asia, Oceania, or the Americas). Yellow points represent pairs in which the two groups belong to different world regions, involving neither Oceania nor the Americas. Blue points represent pairs in which the two groups belong to different world regions, with at least one group representing Oceania or the Americas. *Source*: Ashraf and Galor (2013a, 2018).

from "isolation by distance" across all pairs of populations in a sample of 53 ethnic groups from the HGDP-CEPH Human Genome Diversity Cell Line Panel (Cann et al., 2002; Ramachandran et al., 2005; Ashraf and Galor, 2013a).

3.3 Predicted Population Diversity

3.3.1 Measurement and Identification at the Country Level

In light of the absence of measures of interpersonal diversity for national populations, as well as the scarcity of such measures for ethnic groups, one can exploit the strong negative impact of migratory distance from East Africa on interpersonal diversity in observable traits to generate an index of population diversity levels for every country, region, or ethnic group, based on the migratory distances of their respective *ancestral* populations from East Africa. In particular, following the association depicted in Fig. 4, the interpersonal diversity of an indigenous population can be *predicted* based on the distance that its ancestors had traveled over the course of their migration from East Africa. The discussion to follow provides an elaboration of this insight.

A nave approach to measuring interpersonal diversity at the country level would be to simply aggregate the *observed* expected heterozygosity measure, as calculated by population geneticists, across the ethnic groups belonging to a given country. However, such an approach faces several major shortcomings. First, although the ethnic groups for which observed population diversity is available are globally representative in terms of their spatial distribution across continents and world regions, they span only a modest fraction of nations. As such, the nave approach would yield observed population diversity for a limited sample of countries. Second, a simple (or even population-weighted) averaging of the expected heterozygosity index across ethnic groups in a national population would fail to account for the additional diversity that results from the pairwise biocultural distances among the constituent groups. This issue would be particularly salient for the New World, where contemporary national populations are comprised of groups that can trace their ancestries to world regions that were once geographically rather isolated from one another. Third, the potential endogeneity of observed population diversity with socioeconomic outcomes at the ethnic-group level would imply that, under the nave approach to measurement, the country-level diversity measure would also be tainted by concerns regarding reverse causality and omitted variables.

To overcome sample limitations, dependence on neutral genetic markers, and potential concerns about endogeneity in the use of an *observed* population diversity measure under the nave approach, the research program originated by Ashraf and Galor (2013a) adopts the strategy of exploiting the strong explanatory power of migratory distance from East Africa for the worldwide variation in observed expected heterozygosity across ethnic groups, similar to that depicted in Fig. 4. Specifically, in a first step, the coefficients from a regression of expected heterozygosity on migratory distance from East Africa across 53 ethnic groups in the HGDP-CEPH sample are employed to generate a measure of *predicted* interpersonal diversity for all precolonial societies spanning the globe, based on their respective geographical locations in AD 1500.[14] Importantly, prior to the discovery of the New World and the great intercontinental migrations of the colonial era, the geographical locations of historical societies largely reflected the locations to which their ancestral populations had arrived at the end of their prehistoric "out of Africa" migration, and as such, the diversity of a precolonial society was presumably determined overwhelmingly by the ancient serial founder effect originating in East Africa. As corroborated by the discussion in the next section, the plausible exogeneity of distance along the ancient "out of Africa" migratory paths implies that the measure of predicted population diversity generated in this step is appropriate for identifying the impact of interpersonal diversity on comparative economic and institutional development across societies in the precolonial era.

Nevertheless, to identify the impact of diversity on comparative economic development and comparative sociopolitical institutions across countries in the modern world, it is necessary to construct a measure of predicted population diversity that incorporates the additional diversity arising from the multiethnic ancestries of modern national populations, reflecting the great intercontinental and interregional migrations over the past half millennium. Thus, the measure of predicted diversity for a contemporary national population as developed by Ashraf and Galor (2013a) is based on (i) the proportional representation of each ethnic group in the national population[15]; (ii) the population diversity of each of these group, as *predicted* by its ancestral migratory distance from East Africa; and (iii) the pairwise biocultural distances among these ethnic groups, as *predicted* by the migratory distance between the ancestral populations of each pair.

[14] Exploiting the more recent and larger data set of Pemberton, DeGiorgio, and Rosenberg (2013), rather than the HGDP-CEPH sample, would generate nearly identical results.

[15] The data on the population shares of these subnational groups are obtained from the *World Migration Matrix, 1500–2000* of Putterman and Weil (2010), who compiled, for each country in their data set, the share of a country's population in 2000 that is descended from the population of every other country in 1500.

In particular, following the definition of F_{ST} genetic distance presented earlier, and considering the hypothetical case of a contemporary national population comprised of two ethnic groups, whose ancestors originate from different locations, A and B, the overall diversity of this national population is calculated as:

$$\widehat{H}_{\exp}^{AB} = \frac{\theta_A \widehat{H}_{\exp}^{A}(d_A) + \theta_B \widehat{H}_{\exp}^{B}(d_B)}{1 - \widehat{F}_{\mathrm{ST}}^{AB}(d_{AB})},$$

where, for $i \in \{A, B\}$, $\widehat{H}_{\exp}^{i}(d_i)$ denotes the expected heterozygosity predicted by migratory distance, d_i, of ancestral location i from East Africa (i.e., the predicted population diversity of the precolonial population native to location i), and θ_i is the proportional representation (in the national population being considered) of the ethnic group whose ancestors immigrated from location i since the onset of the colonial era in AD 1500. Moreover, $\widehat{F}_{\mathrm{ST}}^{AB}(d_{AB})$ is the biocultural distance predicted by the migratory distance between ancestral locations A and B, obtained by applying the coefficients associated with a regression line similar to that depicted in Fig. 6. In practice, since contemporary national populations are typically composed of more than two ethnic groups, the procedure above is applied recursively for national populations with a larger number of constituent groups.

The fact that the measure of population diversity for contemporary national populations incorporates both within-group diversity and between-group distances makes it particularly valuable for identifying the impact of population diversity on cross-country comparative economic development and comparative sociopolitical institutions in the modern era. In contrast, other commonly used measures of diversity that aim to capture variation in the degree of ethnic fragmentation across national populations typically do not exploit information beyond the proportional representations of ethnolinguistically differentiated groups in the national population—namely, they implicitly assume that these groups are internally homogenous and bioculturally equidistant from one another.[16] Aside from accounting for both intragroup diversity and intergroup distances, the use of plausibly exogenous migratory distances (of a nation's ancestral populations from East Africa and from one another) to predict within-group diversity and between-group distances makes it possible for the measure to identify the impact of national population diversity on contemporary outcomes, even for countries for which observed expected heterozygosity and F_{ST} genetic distance data are unavailable for their constituent ethnic groups.

Further, insofar as interregional migrations since AD 1500 and, thus, the proportional representation of ethnic groups within each national population may have been affected by historically persistent spatial patterns of comparative development and conflict, contemporary national population diversity may be endogenous to these societal outcomes. To confront this issue, two alternative empirical strategies have been implemented by previous works in this research program. The first strategy confines the empirical analysis to variations in a sample of countries that only belong to the Old World (i.e., Africa, Europe, and Asia), where the diversity of contemporary national populations predominantly reflects the diversity of indigenous populations that became native to their current locations well before the colonial era. This strategy rests on the observation

[16] More sophisticated measures of ethnic fragmentation—such as (i) the Greenberg index of "cultural diversity," as measured by Fearon (2003) and Desmet, Weber, and Ortuño-Ortín (2009), or (ii) the ethnolinguistic polarization index, as measured by Desmet, Weber, and Ortuño-Ortín (2009) and by Esteban, Mayoral, and Ray (2012)—do incorporate information on pairwise linguistic distances, wherein pairwise linguistic proximity monotonically increases in the number of shared branches between any two languages in a hierarchical linguistic tree. This information, however, is constrained by the nature of a hierarchical linguistic tree, where languages residing at the same level of branching of the tree are necessarily equidistant from one another.

that population movements since AD 1500 within the Old World did not result in the significant admixture of populations that were very distant from one another. The second strategy exploits variations in a globally representative sample of countries using a two-stage estimator, in which the migratory distance of a country's prehistorically native population from East Africa is employed as an instrumental variable for the diversity of its contemporary national population. It rests on the identifying assumption that the migratory distance of a country's prehistorically native population from East Africa is plausibly exogenous to economic and sociopolitical outcomes of the country's overall population in the contemporary era.

3.3.2 Measurement and Identification at the Ethnic-Group Level

The research program on the role of population diversity in comparative economic development and comparative sociopolitical institutions employs several strategies to mitigate concerns about reverse causality, omitted cultural, geographical, and human characteristics, as well as selection bias from sorting, in the observed association between population diversity and economic, political, and social outcomes at the ethnic-group level. Over the course of human history, differential patterns across ethnic groups in their levels of economic development and in the incidence of internal conflicts may have altered the degree of *observed* interpersonal diversity within these groups. Thus, the association between the observed population diversity of an ethnic group and outcomes such as group productivity or internal conflicts may partly reflect reverse causality. Furthermore, these associations at the ethnic-group level could be partly governed by omitted cultural, geographical, and human characteristics. To mitigate these concerns, empirical analyses in this research program have exploited the strong negative association between the observed population diversity of an indigenous contemporary ethnic group and its migratory distance from East Africa—arising from the previously highlighted ancient serial founder effect (e.g., Harpending and Rogers, 2000; Ramachandran et al., 2005; Prugnolle, Manica, and Balloux, 2005; Ashraf and Galor, 2013a)—to generate a measure of *predicted* population diversity for a globally representative sample of over 900 ethnic groups.

Nevertheless, several scenarios could a priori weaken the credibility of this methodology. First, selective migration out of Africa, or natural selection along the ancient migratory paths, could have affected human traits and, therefore, group-level outcomes independently of the impact of migratory distance from East Africa on the degree of *diversity* in human traits. However, while migratory distance from East Africa has a significant negative association with the degree of diversity in human traits, it appears uncorrelated with the *mean* levels of different traits in a population, such as height, weight, and skin reflectance, conditional on distance from the equator (Ashraf and Galor, 2013a). Second, migratory distance from East Africa could be correlated with distances from important historical locations (e.g., technological frontiers) and could, therefore, capture the effect of these other distances on the process of development and the incidence of conflicts, rather than its impact that operates through population diversity. Nevertheless, conditional on migratory distance from East Africa, distances from historical technological frontiers in AD 1, AD 1000, and AD 1500 do not qualitatively alter the impact of predicted diversity on either group productivity or internal conflicts (Ashraf and Galor, 2013a; Arbatlı et al., 2020), further justifying the reliance on the serial founder effect associated with the "out of Africa" migration of humans for identifying the influence of population diversity on various group-level outcomes.

Moreover, a threat to identification would emerge if the actual migratory paths from Africa would have been correlated with geographical characteristics (e.g., soil quality, ruggedness, climatic conditions, and propensity to trade) that can directly influence both innovative activities and internal conflicts. This would have involved, however, that the favorability of these geographical factors for these outcomes would be aligned along the main root of the migratory path from Africa as well as along each of the main forks that emerge from this primary path. Specifically, in several important forks of this migration process (e.g., the Fertile Crescent and the associated eastward migration into Asia versus the westward migration into Europe), geographical factors that are conducive to these outcomes would have to diminish symmetrically along these divergent secondary migratory paths, a requirement that appears implausible in reality. Nevertheless, analyses in this research program show that the influence of predicted population diversity on group-level outcomes remain qualitatively unaffected when accounting for a host of potentially confounding geographical characteristics of ethnic homelands, spatial dependence, as well as time-invariant unobserved heterogeneity across regions, identifying the association between interpersonal diversity and outcomes across ethnic societies in the same world region.

The observed associations between population diversity and outcomes at the ethnic-group level may further reflect the sorting of less diverse populations into geographical niches that carry lower conflict risk but are also less conducive to innovative activities. While sorting would not affect the existence of a positive association between population diversity and either conflicts or innovative activities, it would weaken the proposed interpretation of these associations. However, such sorting would require that the spatial distribution of ex ante conflict risk and innovation potential would have to be negatively correlated with migratory distance from East Africa, and the conduciveness of geographical characteristics to conflicts and innovations would have to be negatively aligned with the primary migratory path out of Africa as well as with each of the main subsequent forks and their associated secondary paths. Despite the implausibility of these requirements in nature, concerns pertaining to sorting are further mitigated by accounting for heterogeneity in a wide range of geographical characteristics across ethnic homelands, spatial autocorrelation, and world region fixed effects.

3.4 Empirical Findings

3.4.1 Population Diversity and Comparative Development across Countries

Exploiting the country-level measures of interpersonal diversity discussed in Section 3.3.1, Ashraf and Galor (2013a) empirically examine their prediction regarding the trade-off between the beneficial and detrimental effects of the degree of diversity on productivity at the societal level. Consistent with their hypothesis, they find that interpersonal diversity, as determined predominantly by a serial founder effect associated with the prehistoric "out of Africa" migration process, does indeed confer a significant hump-shaped influence on income per capita, explaining 16 percent of the worldwide cross-country variation in the standard of living in the year 2000.

Although Ashraf and Galor's main focus is on *contemporary* comparative development, they confirm the hump-shaped influence of diversity on economic development in both historical and contemporary time periods, demonstrating that diversity within societies has shaped their comparative development since well before the advent of the Industrial Revolution. In the preindustrial era, comparative development was characterized by Malthusian forces—namely, gains in productivity at the societal level were channeled primarily towards population growth rather than growth in income per capita. During this era, more developed societies were therefore characterized by higher population density, rather than a higher standard of living (Ashraf and Galor, 2011). Thus, Ashraf and Galor's historical analysis focuses on explaining variation across societies in their population density in AD 1500.

Employing the measure of predicted diversity for precolonial societies, the authors document a hump-shaped influence of interpersonal diversity on productivity in AD 1500, as captured by

Table 1: Population Diversity and Comparative Development across Countries

	Log population density in AD 1500		Log urbanization rate in AD 1500		Log income per capita, 2010–18		Log luminosity per capita, 1992–2013	
	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)
Population diversity	277.7***	288.9***	408.0***	364.8***	328.8**	416.1***	467.8***	431.5***
	(86.7)	(90.7)	(73.2)	(57.1)	(128.0)	(124.2)	(170.9)	(163.5)
Population diversity (squared)	-190.2***	-207.0***	-298.4***	-271.1***	-231.9**	-292.5***	-336.4***	-308.8***
	(63.5)	(67.1)	(57.6)	(44.2)	(92.9)	(88.5)	(123.2)	(116.2)
Baseline controls	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes
World region FE	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes
Additional controls (past)	No	Yes	No	Yes	No	Yes	No	Yes
Additional controls (present)	No	No	No	No	No	Yes	No	Yes
Number of observations	140	140	80	80	132	132	134	134
Adjusted R^2	0.64	0.68	0.58	0.67	0.65	0.86	0.71	0.84

Notes: This table presents OLS regressions demonstrating the hump-shaped impact of interpersonal population diversity on historical and contemporary economic development across countries, conditional on relevant covariates noted below. Columns 1–4 examine the impact of predicted diversity (based on migratory distance from East Africa) on economic development in AD 1500, as reflected by either log population density (columns 1–2) or log urbanization rate (columns 3–4). Columns 5–8 examine the impact of predicted ancestry-adjusted diversity (i.e., population diversity predicted by the migratory distances of a country's ancestral populations from East Africa, as well as the pairwise migratory distances among them) on economic development in the contemporary era, as reflected by either log income per capita during the 2010–18 time period (columns 5–6) or log nighttime luminosity per capita during the 1992–2013 time period (columns 7–8). The baseline controls in all columns include time since the Neolithic Revolution, time since initial human settlement, absolute latitude, the mean and standard deviation of caloric suitability, the percentage of land in tropical climate zones, a measure of disease richness, distance to coasts or rivers, and an island nation dummy. The world region fixed effects in all columns are captured by dummies for Sub-Saharan Africa, Middle East and North Africa, Europe and Central Asia, South Asia, East Asia and the Pacific, North America, and Latin America and the Caribbean. Columns 2 and 4 additionally control for an index of state antiquity. Columns 6 and 8 add even further controls for the percentage of the population at risk of contracting malaria, the percentages of the population that fall into four religious categories (Protestant, Catholic, Muslim, and other denominations), ethnic fractionalization, an index of the degree of democracy, measures of dependence on oil and gas exports, an ex-colony dummy, and dummies for different legal origins (British, French, Socialist, German, and Scandinavian). Heteroskedasticity-robust standard errors are reported in parentheses. *** denotes statistical significance at the 1 percent level, ** at the 5 percent level, and * at the 10 percent level, all for two-sided hypothesis tests.

population density, in a sample of observations spanning the entire globe. Notably, the relationship accounts for potentially confounding effects due to heterogeneity across societies in the timing of the Neolithic Revolution and in various geographical factors relevant for their historical development, as well as confounding effects arising from unobserved time-invariant cross-continental differences. This finding is robust to a large number of sensitivity checks, including "placebo tests" showing that a similar hump-shaped pattern does not exist when employing either aerial distance from East Africa or migratory distances from other geographical locations.

Columns 1 and 2 of Table 1 reproduce this finding using updated specifications that account for variations in a sizable vector of geographical, climatic, and historical institutional characteristics, the timing of the Neolithic Revolution and of initial human settlement, and world region fixed effects. The full specification for examining population density in column 2 reveals a significant hump-shaped relationship, which predicts population density at the diversity level associated with the inflection point to be 3.3 and 0.9 log points higher than at the minimum and maximum levels of diversity, respectively. This relationship is depicted on the scatter plot in panel A of Fig. 7. In addition, using a similar pair of specifications, columns 3 and 4 of Table 1 demonstrate that the hump-shaped influence of interpersonal diversity on preindustrial productivity holds when the rate of urbanization in AD 1500 is employed as an alternative measure of comparative development

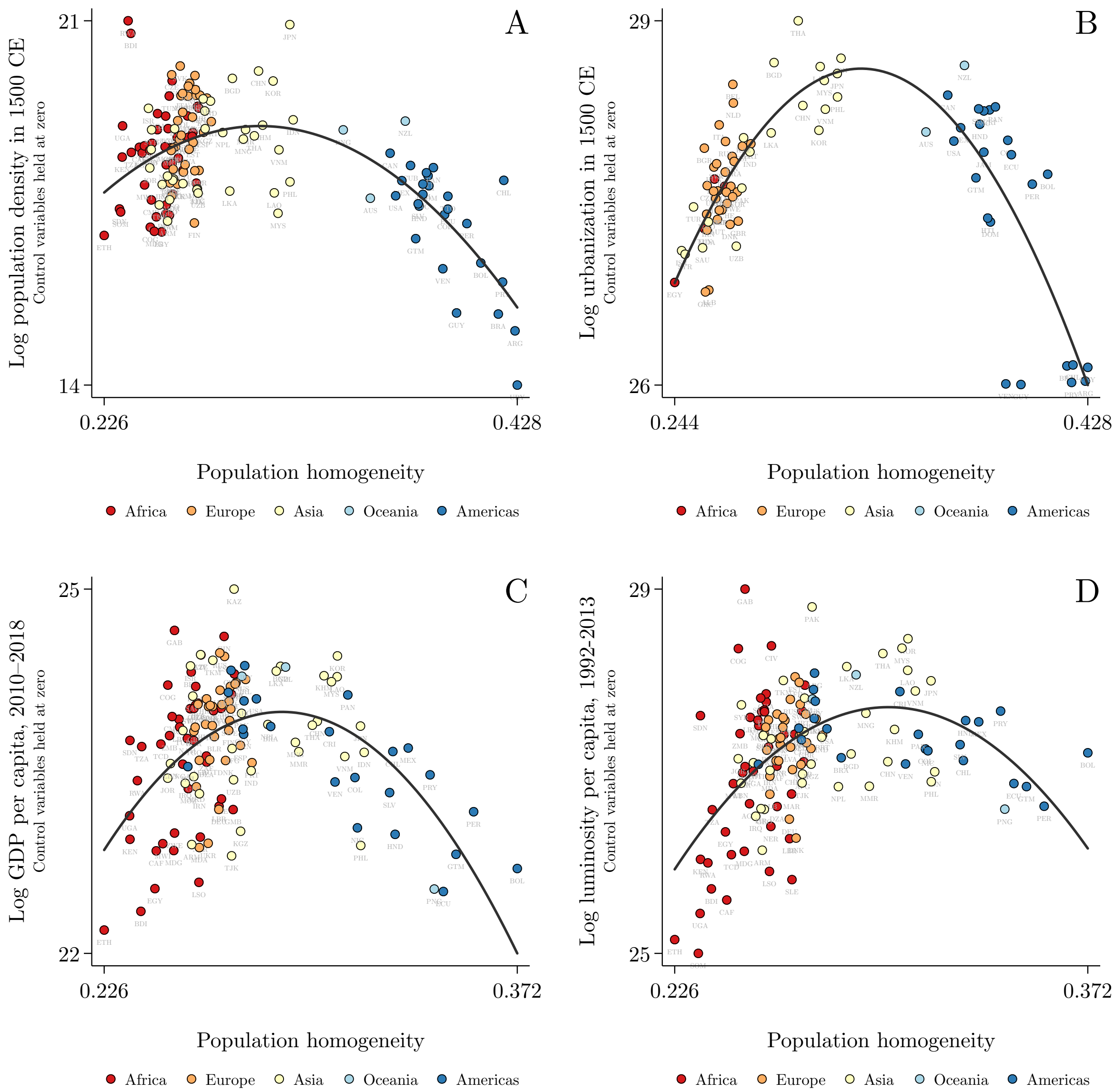

Figure 7: Population Diversity and Comparative Development across Countries

Notes: This figure depicts the hump-shaped impact of interpersonal population diversity on historical and contemporary economic development across countries, conditional on geographical, climatic, cultural, and institutional characteristics, the timing of the Neolithic Revolution and of initial human settlement, and world region fixed effects. The top panels depict the impact of predicted population homogeneity (i.e., 1 minus population diversity predicted by migratory distance from East Africa) on economic development in AD 1500, as reflected by either log population density (panel A) or log urbanization rate (panel B). The bottom panels depict the impact of predicted ancestry-adjusted homogeneity (i.e., 1 minus population diversity predicted by the migratory distances of a country's ancestral populations from East Africa, as well as the pairwise migratory distances among them) on economic development in the contemporary era, as reflected by either log income per capita during the 2010–18 time period (panel C) or log luminosity per capita during the 1992–2013 time period (panel D). Each panel presents an augmented-component-plus-residual plot with a quadratic fit, corresponding to the relevant even-numbered column of Table 1.

across preindustrial societies. The scatter plot in panel B of Fig. 7 shows the hump-shaped relationship estimated by the regression in column 4.

Applying the measure of diversity for contemporary national populations, Ashraf and Galor (2013a) find a significant hump-shaped influence of diversity on income per capita in the year 2000. This finding accounts for cross-country heterogeneity in the timing of the Neolithic Revolution, various geographical, cultural, and institutional correlates of contemporary economic development, and unobserved time-invariant continent-specific characteristics. The relationship is additionally robust to controlling for population density in AD 1500, indicating that the hump-shaped influence of diversity does not merely reflect long-run persistence in economic development. Moreover, it continues to hold when limiting the sample to countries in which the overwhelming majority of the population has remained geographically native since the precolonial era, thus alleviating concerns regarding the endogeneity of interregional population flows over the past half millennium.

The significant hump-shaped impact of interpersonal diversity at the country level on contemporary comparative development is reproduced in columns 5 and 6 of Table 1, using updated specifications that augment those from earlier columns of the table with contemporary malaria risk and a considerable set of cultural and institutional covariates relevant for modern-day outcomes, while exploiting average income per capita during the 2010–18 time period as the dependent variable. As depicted on the scatter plot in panel C of Fig. 7, the full specification for examining income per capita in column 6 predicts income per capita at the diversity level associated with the inflection point to be 2.1 and 1.2 log points higher than at the minimum and maximum levels of diversity, respectively.

Confronting the possibility that income per capita in the modern world could be noisily measured, especially for less-developed economies, Ashraf, Galor, and Klemp (2014) find that the hump-shaped influence of diversity on contemporary comparative development additionally holds when relative prosperity is measured by the cross-country variation in per-capita adjusted nighttime luminosity, as observed by satellites from outer space, averaged over the 1992–2013 time period. Their analysis of nighttime luminosity is reproduced in columns 7 and 8 of Table 1, using the updated specifications employed for examining income per capita in the preceding two columns. The significant hump-shaped relationship estimated by the full specification in column 8 is depicted on the scatter plot in panel D of Fig. 7. These findings mitigate the potential concern that the estimated costs of high diversity on aggregate productivity could be biased upward when productivity is measured using income per capita, because the shadow economy may well be larger in more diverse societies in light of the adverse influence of diversity on social cohesion.

The Relative Importance of Population Diversity and Other Fundamental Determinants

This section provides an assessment of the relative contribution of interpersonal population diversity and of six other fundamental channels—geoclimatic factors, political institutions, ethnocultural composition, historical determinants, disease ecology, and legal environment—to the contemporary disparity in economic prosperity across nations, as reflected by the cross-country variation in average income per capita during the 2010–18 time period. Specifically, as presented in Table 2, the analysis explores the *added* explanatory power (partial R^2 statistic) associated with distinct groups of covariates that correspond to these various channels.

The analysis commences with a baseline specification in column 1 in which each of the six alternative fundamental channel is represented by a core set of covariates. However, in order to assure a balanced assessment of all channels, the analysis then proceeds in subsequent specifications (columns 2–7) with a one-at-a-time expansion of the set of covariates representing each alternative

Table 2: Explanatory Power of Population Diversity and Other Determinants for Contemporary Comparative Development across Countries

	Baseline	Expanded Geoclimatic Controls	Expanded Historical Controls	Expanded Disease Controls	Expanded Ethnocultural Controls	Expanded Legal Envi. Controls	Expanded Institutional Controls	Full Specification
	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)
Population diversity	360.0***	403.8***	430.1***	356.8***	362.4***	364.0***	356.3***	492.1***
	(91.9)	(93.5)	(95.5)	(91.8)	(92.0)	(92.3)	(90.2)	(92.3)
Population diversity (squared)	-251.7***	-284.8***	-301.2***	-249.0***	-253.2***	-254.7***	-249.6***	-347.0***
	(65.7)	(67.1)	(68.2)	(65.6)	(65.8)	(66.0)	(64.5)	(66.1)
Number of Observations	129	129	129	129	129	129	129	129
Adjusted R^2	0.86	0.87	0.86	0.86	0.86	0.86	0.86	0.88
	Partial R^2 (in percent) by channel							
Population diversity	16.5	18.1	20.4	17.1	17.1	16.7	16.3	26.3
Geoclimatic factors	27.2	34.2	27.3	25.8	27.6	27.4	27.9	38.9
Historical determinants	3.4	7.4	8.3	2.3	3.5	3.5	3.3	12.8
Disease ecology	15.6	9.5	17.7	16.7	16.2	15.1	15.6	14.6
Ethnocultural composition	20.5	20.0	22.5	20.7	21.1	20.6	19.1	21.9
Legal environment	24.6	27.0	17.3	24.7	25.1	25.0	16.1	13.0
Political institutions	2.8	1.6	3.4	2.4	2.3	2.3	7.2	8.1

Notes: This table employs OLS regressions to explore the added explanatory power of the hump-shaped impact of interpersonal population diversity for log income per capita across countries during the 2010–18 time period, along with the added explanatory power of each of six covariate groups that represent other determinants of comparative development. The six covariate groups, along with the baseline set of variables in each group (as employed in column 1), include: (a) geoclimatic factors: absolute latitude, caloric suitability, distance to coasts or rivers, the percentage of land in tropical climate zones, and terrain ruggedness; (b) historical determinants: time since the Neolithic Revolution and time since initial human settlement; (c) disease ecology: the percentage of the population at risk of contracting malaria; (d) ethnocultural composition: the percentages of the population that belong to each of four religious denominations, including Protestant, Catholic, Muslim, and "other"; (e) legal environment: dummies for each of three legal origins, including British, French, and Socialist; and (f) political institutions: an index of the degree of executive constraints during the 1960–2000 time period. Relative to the baseline specification, (a) column 2 additionally controls for the arable percentage of land, average monthly temperature and average monthly precipitation during the 1961–1990 time period, and an island nation dummy; (b) column 3 additionally controls for an index of state antiquity and an ex-colony dummy; (c) column 4 additionally controls for a measure of disease richness; (d) column 5 additionally controls for the degree of ethnic fractionalization; (e) column 6 additionally controls for dummies for each of two legal origins, including German and Scandinavian; and (f) column 7 additionally controls for an index of the degree of democracy during the 1960–2000 time period. The set of covariates in the full specification of column 8 represents the union of the sets from all preceding columns. The added explanatory power of a given covariate group in a specification is represented by the partial R^2 of the set of independent variables representing that group in the specification. The specifications in all columns control for the full set of world region fixed effects, as captured by dummies for Sub-Saharan Africa, Middle East and North Africa, Europe and Central Asia, South Asia, East Asia and the Pacific, North America, and Latin America and the Caribbean. Heteroskedasticity-robust standard errors are reported in parentheses. *** denotes statistical significance at the 1 percent level, ** at the 5 percent level, and * at the 10 percent level, all for two-sided hypothesis tests.

channel, relative to the set employed in the baseline specification. The analysis concludes with examining a full specification in which all channels are represented by their respective augmented set of covariates considered in earlier columns.[17]

Turning to the results, the partial R^2 statistic associated with the reported hump-shaped impact of interpersonal population diversity suggests that, across specifications, this channel explains between 16% and 26% of the residual variation in contemporary income per capita, conditional on the other fundamental channels. Amongst the other fundamental channels, the geoclimatic one possesses partial R^2 values in the range of 26%–39%, whereas the channels capturing the

[17] See the notes section of Table 2 for the list of variables employed in the baseline and expanded representations of each channel examined by the analysis.

legal environment, ethnocultural composition, and disease ecology respectively possess partial R^2 values in the range of 13%–27%, 19%–23%, and 10%–18%. On the other hand, the channels capturing historical determinants (i.e., time since the Neolithic Revolution, time since initial human settlement, state antiquity, and colonial history) and the extent to which political institutions can minimize expropriation risk (i.e., executive constraints and the degree of democracy) appear to possess partial R^2 values in the range of 2%–13% and 2%–8% respectively. Finally, focusing on the full specification in column 8 that includes all the covariates for each channel, population diversity enters with an added explanatory power of 26%, geoclimatic factors with 39%, ethnocultural composition with 22%, disease ecology with 15%, legal environment and historical determinants with 13% each, and political institutions with 8%.

3.4.2 Population Diversity and Comparative Development across Ethnic Homelands

Ashraf, Galor, and Klemp (2020a) have empirically examined the influence of population diversity on productivity at the ethnic group level, while accounting for potentially confounding effects arising from observed heterogeneity in various ethnicity-specific geographical, cultural, and institutional factors, as well as unobserved heterogeneity in time-invariant region-specific characteristics. This research finds that observed diversity in a worldwide sample of 207 ethnic groups (Pemberton, DeGiorgio, and Rosenberg, 2013), as well as predicted diversity (based on migratory distance from East Africa) in a global sample of over 900 ethnic groups, has imparted a significant hump-shaped influence on economic prosperity throughout the course of human history since the onset of the Neolithic Revolution in the Fertile Crescent. The results demonstrate that the variation in interpersonal diversity across ethnic homelands has contributed to variations in their economic development in the very long run, as captured by their historical population densities at various points in time, corresponding to the initial year of every thousand-year time interval between 10,000 BC and AD 1500, as well as by their per-capita adjusted nighttime luminosities in the contemporary era.

Table 3 highlights a modest subset of the findings of Ashraf, Galor, and Klemp (2020a). Exploiting variations across ethnic homelands, the regressions reveal the significant hump-shaped influence of interpersonal diversity on population density in 5000 BC (columns 1–2), 3000 BC (columns 3–4), 1000 BC (columns 5–6), and AD 100 (columns 7–8), as well as a qualitatively similar impact on per-capita adjusted nighttime luminosity during the 1992–2013 time period (columns 9–10), using either observed diversity (odd-numbered columns) or predicted diversity (even-numbered columns). The regressions examining historical population densities account for the timing of initial human settlement and a host of geographical and climatic factors, along with world region fixed effects, whereas those examining contemporary nighttime luminosity additionally control for contemporary malaria risk and contemporary cultural and institutional covariates.

To interpret a subset of the significant hump-shaped patterns revealed in Table 3, the regression in column 5 predicts historical population density at the diversity level associated with the inflection point to be 5.4 and 1.9 log points higher than at the minimum and maximum levels of diversity, respectively. Moreover, the regression in column 9 predicts contemporary nighttime luminosity at the diversity level associated with the inflection point to be 1.2 and 2.5 log points higher than at the minimum and maximum levels of diversity, respectively. The hump-shaped influence of observed diversity on comparative development across ethnic homelands in the different time periods, as revealed by the regressions in odd-numbered columns of Table 3, are depicted sequentially on the scatter plots in the different panels of Fig. 8.

The ethnic-group-level analysis of Ashraf, Galor, and Klemp (2020a) provides the first-best setting for confirming the robustness of the main prediction of Ashraf and Galor's hypothesis to

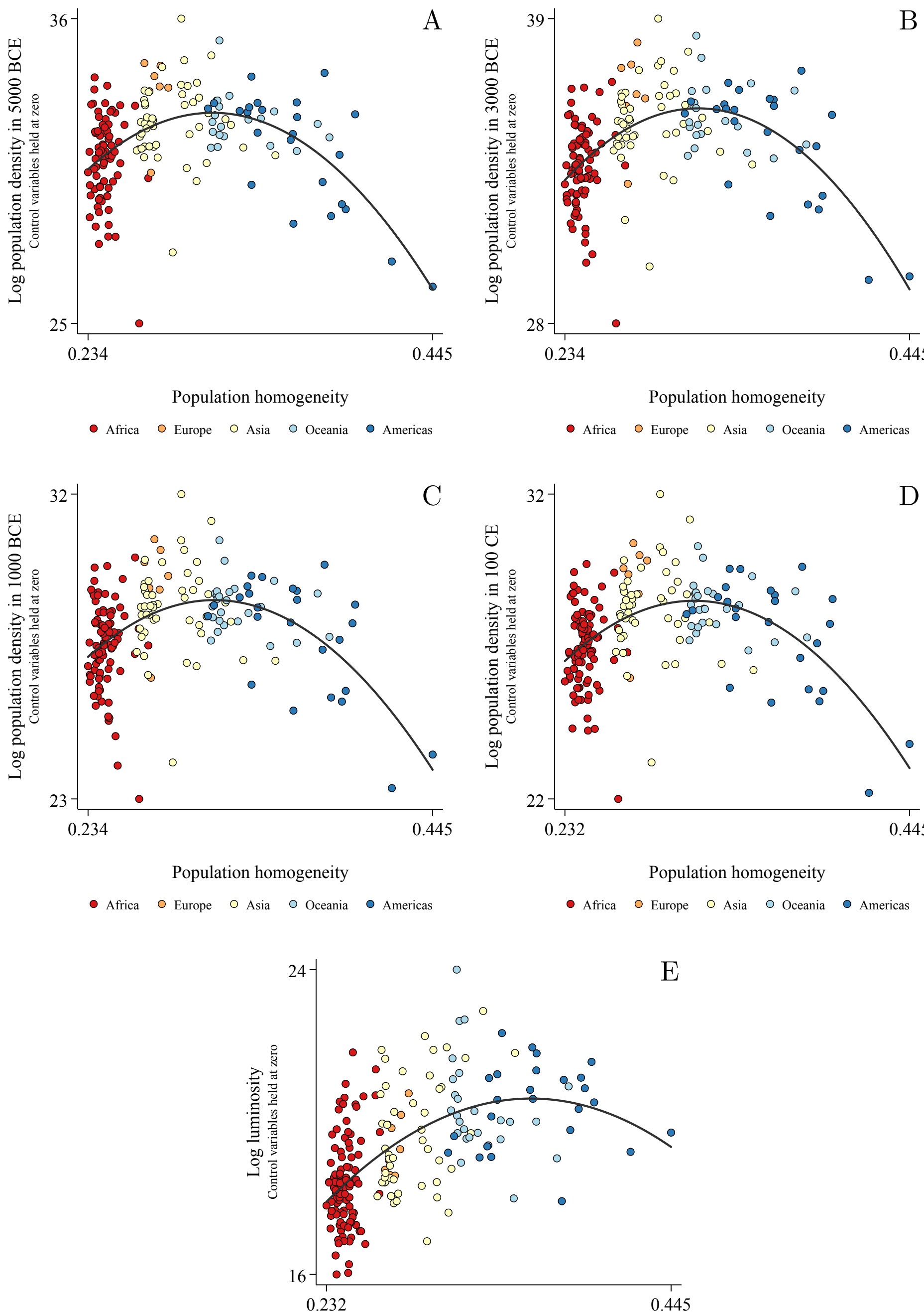

Figure 8: Population Diversity and Comparative Development across Ethnic Homelands

Notes: This figure depicts the hump-shaped impact of interpersonal population diversity on historical and contemporary economic development across ethnic homelands, conditional on geographical, climatic, cultural, and institutional characteristics, the timing of initial human settlement, and world region fixed effects. The first four panels depict the impact of observed population homogeneity (i.e., 1 minus observed population diversity) on long-run historical economic development, as reflected by log population density in 5000 BC (panel A), 3000 BC (panel B), 1000 BC (panel C), and AD 100 (panel D), whereas the last panel depicts its impact on contemporary economic development, as reflected by a per-capita adjusted measure of log luminosity during the 1992–2013 time period. Each panel presents an augmented-component-plus-residual plot with a quadratic fit, corresponding to the relevant odd-numbered column of Table 2.

Table 3: Population Diversity and Comparative Development across Ethnic Homelands

	Log population density in 5000 BC		Log population density in 3000 BC		Log population density in 1000 BC		Log population density in AD 100		Log luminosity per capita, 1992–2013	
	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)
Population diversity	470.5***	294.9***	490.0***	274.9***	411.1***	378.8***	404.8***	676.2**	203.1***	199.0***
	(70.0)	(110.6)	(71.5)	(104.2)	(74.8)	(93.0)	(76.0)	(306.5)	(74.5)	(71.7)
Population diversity (squared)	-341.0***	-193.8**	-357.9***	-179.8**	-298.4***	-263.0***	-294.2***	-471.8**	-158.3***	-134.2***
	(53.0)	(78.0)	(53.3)	(73.6)	(55.6)	(65.8)	(56.1)	(215.5)	(57.0)	(50.6)
World region FE	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes
Baseline controls	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes
Additional controls	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes
Sample	Observed	Predicted	Observed	Predicted	Observed	Predicted	Observed	Predicted	Observed	Predicted
Number of observations	173	838	184	849	196	873	199	877	207	909
Adjusted R^2	0.50	0.39	0.53	0.41	0.55	0.42	0.57	0.42	0.65	0.69

Notes: This table presents OLS regressions demonstrating the hump-shaped impact of interpersonal population diversity on historical and contemporary economic development across ethnic homelands, conditional on relevant covariates noted below. The odd-numbered columns examine the impact of observed population diversity, whereas the even-numbered ones explore the impact of diversity predicted by migratory distance from East Africa. Columns 1–8 examine the impact of population diversity on long-run historical economic development, as reflected by log population density in 5000 BC (columns 1–2), 3000 BC (columns 3–4), 1000 BC (columns 5–6), and AD 100 (columns 7–8), whereas columns 9–10 examine its impact on contemporary economic development, as reflected by a per-capita adjusted measure of log nighttime luminosity during the 1992–2013 time period. The baseline controls in all columns include time since initial human settlement, absolute latitude, the mean and standard deviation of caloric suitability, distance to coasts or rivers, mean elevation, and ruggedness. Columns 1–8 additionally control for the means and standard deviations of temperature and precipitation, the range of temperature, and the percentage of land in tropical climate zones. Columns 9–10 add even further controls for contemporary malaria risk and ethnic fractionalization. In columns 1–8, the world region fixed effects are captured by dummies for the "New World" (i.e., the Americas and Oceania) and for Sub-Saharan Africa, whereas in columns 9–10 they are captured by separate dummies for each continent. Heteroskedasticity-robust standard errors are reported in parentheses. *** denotes statistical significance at the 1 percent level, ** at the 5 percent level, and * at the 10 percent level, all for two-sided hypothesis tests.

using Pemberton, DeGiorgio, and Rosenberg's (2013) data on observed diversity in the extended sample of 200+ ethnic groups (relative to the HGDP-CEPH sample of 53 groups employed by Ashraf and Galor's original analysis). Nevertheless, the results for the influence of interpersonal diversity on comparative development in both precolonial and modern periods are robust in a second-best country-level setting. In particular, following Ashraf and Galor's (2013a) methodology, one can generate measures of *predicted* population diversity for a *globally representative* sample of countries, based on their respective migratory distances from East Africa. Since the coefficients of the estimated relationship between migratory distance and observed diversity are virtually identical in the HGDP-CEPH sample versus the extended sample of ethnic groups, the hump-shaped influence of predicted diversity on both historical and contemporary cross-country comparative development remains unaffected.[18]

[18] A third-best approach would be to conduct a preliminary (non-inferential) exploration of the association between observed diversity and economic prosperity at the country level. This is the approach of Rosenberg and Kang (2015), who argue that the hump-shaped pattern between observed diversity and historical population density is statistically insignificant in a thirty-nine-country sample, constructed by averaging expected heterozygosity across the subset of ethnic groups that are observed within each country. However, their attempt to use this approach to test for the hump-shaped influence of interpersonal diversity on economic prosperity is fundamentally flawed for two major reasons. First, because the subset of only observed ethnic groups in a country is not necessarily representative of the country's entire population, and since the ethnic groups from their extended sample span only thirty-nine (globally nonrepresentative) countries, their study is severely marred by sample selection bias *at the country level*. Specifically, the actual presence of a hump-shaped cross-country association between observed diversity and economic prosperity cannot be confirmed or rejected based on a nonrepresentative sample of countries. Second, observed diversity may reflect past socioeconomic outcomes such as intra-regional social conflicts and migrations that are themselves driven by past economic prosperity. Thus, Rosenberg and Kang's explorative analysis is afflicted by issues of reverse causality and omitted variables that serve to mask the existence of a hump-shaped relationship between diversity and economic prosperity. Indeed, even in the context of their nonrepresentative sample of country populations, Ashraf, Galor, and

3.4.3 Mechanisms of the Influence of Population Diversity

The reduced-form hump-shaped influence of interpersonal diversity on productivity suggests several mechanisms through which diversity can influence economic performance, reflecting various elements of the trade-off between the costs and benefits of diversity. This section reviews the evidence on these mechanisms, as uncovered by various works in this research program.

Mechanisms Capturing the Adverse Impact of Diversity on Social Cohesiveness

Impact on Internal Conflicts. Intra-societal conflicts capture a fundamental mechanism though which the interpersonal diversity of a population can lead to its economic underperformance.[19] Exploiting variations across countries and ethnic groups, Arbatlı et al. (2020) demonstrate that population diversity, as determined primarily by the ancient migration of humans from East Africa, has been a pivotal contributor to the risk and intensity of both historical and contemporary internal conflicts, conditional on various geographical, cultural, and institutional correlates of conflict, outcomes of economic development, and unobserved time-invariant continent- or region-specific characteristics. Importantly, unlike commonly used measures of ethnic fractionalization and polarization, because interpersonal diversity captures both intergroup and *intragroup* differences in individual traits, the latter possesses explanatory power for not only intergroup conflicts but *intragroup* conflicts as well. This research additionally finds that interpersonal diversity may have contributed to internal conflicts in society through the channels of greater ethnic fragmentation at the country level, reduced interpersonal trust, and sharper divergence in preferences for public goods and redistributive policies. As established by Arbatlı et al. (2020), the scatter plots in Fig. 9 depict (i) the positive influence of observed population diversity on the prevalence of civil conflicts across ethnic homelands over the 1989–2008 time period (panel A); and (ii) the positive influence of contemporary national population diversity on the annual frequency of civil conflict onsets across countries during the 1960–2017 time period (panel B).

Impact on Ethnocultural Fragmentation. A previous literature (e.g., Easterly and Levine, 1997; Alesina et al., 2003; Alesina and La Ferrara, 2005) has shown that ethnic diversity at the national level, as measured by the degree of fractionalization and polarization across ethnic groups, is associated with various dimensions of economic underperformance. Examining the deeper roots of this causal chain, the evidence uncovered by Ashraf and Galor (2013b) suggests that prehistorically determined interpersonal diversity could be an underlying cause of different manifestations of the ethnolinguistic fragmentation of national populations. Specifically, their hypothesis suggests that following the ancient "out of Africa" migration, the initial endowment of population diversity in a given location may have catalyzed the formation of distinct groups at that location through a process of endogenous group selection, reflecting the trade-off associated with the scale and internal cohesion of each group. Although a larger group can benefit from economies of scale, it is more likely to be less cohesive due to costly coordination. Thus, in light of the added contribution of interpersonal diversity to the lack of cohesiveness of a group, a larger initial endowment of population diversity in a given location may have given rise to a larger number of groups. Over time, due to the forces of "cultural drift" and "biased transmission" of cultural markers that serve to

Klemp (2020b) find that a significant hump-shaped association emerges between observed diversity and historical population density once a sufficient set of potential geographical confounders is accounted for. Moreover, as shown by Ashraf, Galor, and Klemp (2020a), conditional on employing a *valid* statistical methodology, the main prediction of Ashraf and Galor's hypothesis is fully robust to exploiting genetic data from the extended sample of ethnic groups.

[19] For a comprehensive review of the multifaceted links between conflict and economic underdevelopment, see Ray and Esteban (2017).

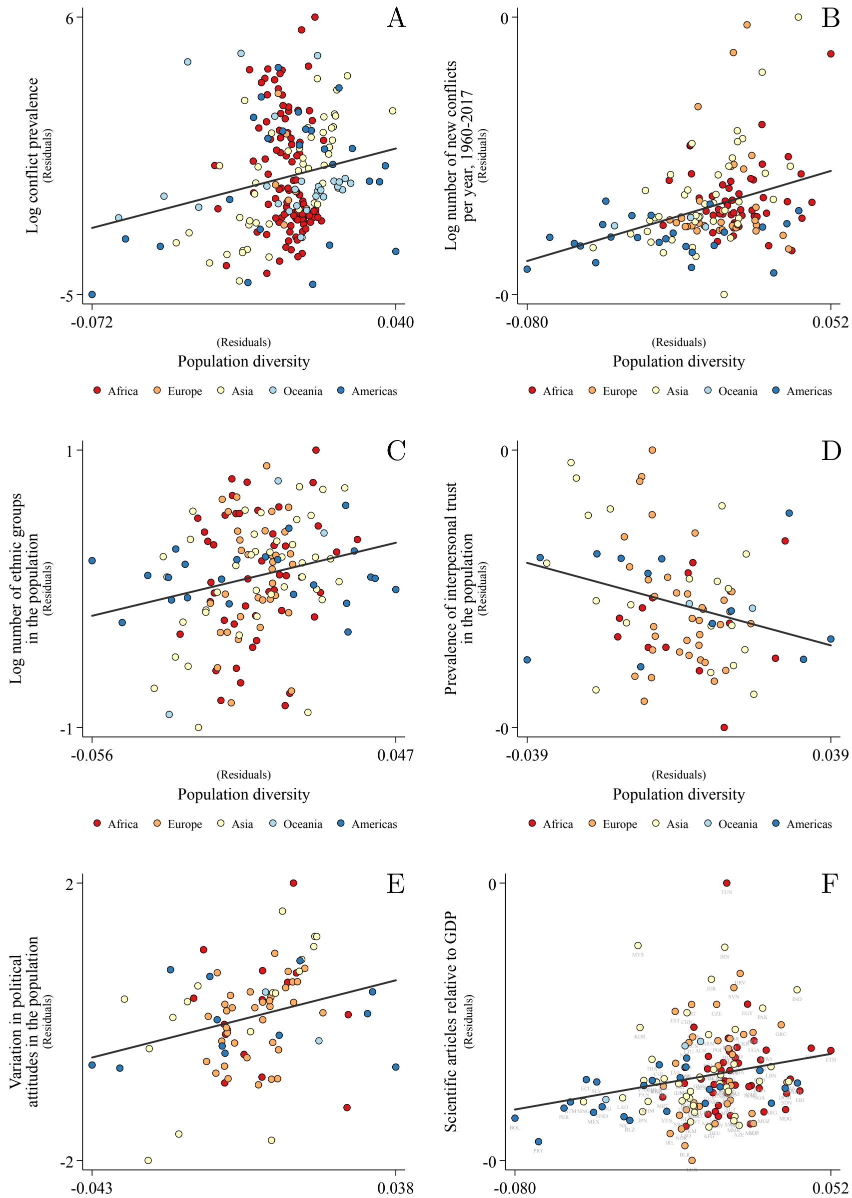

Figure 9: Mechanisms of the Impact of Population Diversity on Aggregate Productivity

Notes: This figure depicts the impact of interpersonal population diversity across either ethnic homelands or countries on various outcomes that capture the mechanisms through which diversity can influence aggregate productivity. Panel A depicts the impact of observed population diversity across ethnic homelands on the prevalence of civil conflicts over the 1989–2008 time period. The remaining panels depict the impact of predicted ancestry-adjusted diversity across countries on (i) the annual frequency of civil conflict onsets across countries during the 1960–2017 time period (panel B); (ii) the number of ethnic groups (panel C); (iii) the prevalence of interpersonal trust in data covering the 1981–2008 period from the World Values Survey (panel D); (iv) the intra-country dispersion in individual political attitudes (expressed on a politically "left"–"right" categorical scale) in data covering the 1981–2008 period from the World Values Survey (panel E); and (v) the number of scientific articles per real GDP dollar over the 2010–18 time period (panel F). Each panel presents an added-variable plot, capturing a relationship that is conditioned on a sizeable vector of control variables relevant for explaining the outcome of interest. *Source*: Ashraf and Galor (2013a, 2013b, 2018), Arbatlı et al. (2020).

distinguish “insiders” from “outsiders” of a group (e.g., language dialects, customs and traditions, norms of social conduct), intergroup divergence in such markers became more pronounced, leading to the formation of distinct collective identities along ethnic lines.

In line with this hypothesis, interpersonal diversity at the national level is found to impart a strong positive influence on various alternative measures of ethnolinguistic diversity, while accounting for the potentially confounding influence of the timing of the Neolithic Revolution, the time elapsed since initial human settlement, colonial history, the geographical determinants of ethnic diversity, and unobserved time-invariant continent-specific factors. Further, to address the issue of causality, the findings are shown to hold in a sample restricted to only countries from the Old World, which were largely immune from the potentially endogenous intercontinental migrations of the colonial era. In the same vein, the findings are also shown to be robust to employing the prehistoric migratory distance of the indigenous (precolonial) population of a country from East Africa as a plausibly exogenous source of variation of contemporary population diversity in a global sample of countries. The positive influence of interpersonal diversity on the number of ethnic groups at the national level, as uncovered by Ashraf and Galor (2013b) and further examined by Arbatlı et al. (2020), is depicted by the scatter plot in panel C of Fig. 9.

Impact on Reduced Interpersonal Trust. Consistent with the hypothesis that interpersonal diversity can reduce social capital, and thus economic development, by widening the spectrum of individual values, beliefs, preferences, and predispositions, Ashraf and Galor (2013a) and Arbatlı et al. (2020) demonstrate that contemporary population diversity imparts a significant negative influence across countries on the prevalence of generalized interpersonal trust, based on data covering the 1981–2008 time period from the World Values Survey.[20] As depicted on the scatter plot in panel D of Fig. 9, the relationship accounts for cross-country heterogeneity in various geographical correlates of economic development and of ethnic diversity, as well as unobserved world region fixed effects.

Further, Arbatlı et al. (2020) employ two distinct analyses that exploit variations across individuals to show that the prevalence of mistrust at the individual level is significantly linked to the degree of interpersonal diversity in the individual’s ancestral population.

- The first analysis connects the level of mistrust across individuals from the Afrobarometer surveys with the observed population diversity of their respective ancestral ethnic homelands in Africa, regardless of whether the surveyed individuals currently reside in their respective ancestral homelands or have or have migrated to a different location. The relationship is robust to accounting for a sizable vector of potential confounders, including (i) country-of-residence fixed effects, (ii) individual-level characteristics (age, gender, education, occupation, living condition, and religion), (iii) the degree of exposure of the ancestral homeland to slave exports, (iv) district-of-residence characteristics (i.e., presence of school, electricity, piped water, sewage, health clinic, and urban status), (v) ancestral-country fixed effects, and (vi) the current levels of ethnolinguistic diversity in both the district of residence and the ancestral homeland.

- The second analysis links the level of mistrust across second-generation U.S. immigrants from the General Social Survey with the contemporary national population diversity of their respective parental countries of origin. The focus on immigrants to a single country permits

[20]See Algan and Cahuc (2014) for a review of the empirical literature that has established the causal impact of generalized trust on economic performance and examined the various mechanisms through which this impact is manifested in the data.

the analysis to implicitly account for unobserved time-invariant host-country characteristics (in geographical, cultural, and institutional dimensions). Moreover, the analysis explicitly accounts for a considerable set of potential individual-level confounders, as well as geographical characteristics, world region fixed effects, and the degree of ethnolinguistic fractionalization and polarization, all with respect to the individual's parental country of origin.

Impact on Divergence in Political Preferences. Interpersonal diversity in values, beliefs, and preferences in general can capture heterogeneity in preferences over types of public goods in particular, as well as divergence in individual dispositions towards economic inequality and redistributive government policies, thereby leading to social conflicts and economic underperformance by contributing to political polarization and related institutional distortions. In line with this mechanism, Ashraf and Galor (2018) and Arbatlı et al. (2020) document that contemporary population diversity imparts a significant positive influence across countries on the degree of heterogeneity in political preferences, as captured by the intra-country dispersion in self-reported individual positions on a politically "left"−"right" categorical scale, based on data covering the 1981–2008 time period from the World Values Survey. The scatter plot in panel E of Fig. 9 depicts this relationship, conditional on various geographical correlates of development and political economy, as well as unobserved world region fixed effects.

Impact on Extractive Institutions. The emergence and persistence of autocratic forms of societal governance is another crucial mechanism through which interpersonal diversity may have given rise to contemporary economic underperformance. Specifically, Galor and Klemp (2017) advance the hypothesis that although prehistorically determined interpersonal diversity may have raised society's demand for formal institutions that mitigated the adverse influence of diversity on social cohesion, the contribution of diversity to economic inequality and class stratification within societies may have also shaped institutional development toward more extractive and autocratic forms of governance. Exploiting variations across precolonial ethnic homelands, the authors find that conditional on the potentially confounding effects of a host of geographical factors and unobserved time-invariant continent-specific characteristics, interpersonal diversity imparts a positive influence on the prevalence of precolonial autocratic institutions, plausibly reflecting the dual impact of diversity on the demand for formal institutions and the emergence of social stratification. Furthermore, the research documents that the spatial variation in interpersonal diversity across the globe may have contributed to the cross-country variation in contemporary autocracy, partly reflecting the persistence of institutional, cultural, and compositional characteristics of populations over time.

Mechanisms Capturing the Beneficial Impact of Diversity on Productivity

Impact on Innovative Activities. Consistent with their hypothesis that interpersonal diversity can foster innovative activity by expanding the domain of distinct varieties of complementary cognitive approaches to problem-solving and knowledge production, Ashraf and Galor (2013a) demonstrate that contemporary population diversity bears a significant positive association across countries with the average annual number of scientific articles per capita in the 1981–2000 time period. Their finding accounts for potentially confounding variation across countries in the timing of the Neolithic Revolution, various geographical, cultural, and institutional correlates of contemporary economic development, and unobserved time-invariant continent-specific factors. The scatter plot in panel F of Fig. 9 depicts a similar positive influence of contemporary population diversity across countries on the total number of scientific articles per real GDP dollar over the 2010–18 time period, conditional on geographical and climatic factors as well as unobserved time-invariant regional characteristics.[21]

Impact on the Division of Labor and Gains from Trade. In a recent paper, Depetris-Chauvin and Özak (2020) empirically examine Ashraf and Galor's (2013a) hypothesis that interpersonal diversity could have fostered the division of labor in society by widening the spectrum of individual skills, abilities, and cognitive approaches. Exploiting variations observed across precolonial ethnic homelands, they document that, consistently with Ashraf and Galor's original hypothesis, prehistorically determined interpersonal diversity may have conferred a positive influence on the degree of economic specialization in different production activities in a society, thereby fostering its proclivity to engage in and reap the economic benefits of market-based exchange.[22] The authors additionally show that ethnic homelands that were characterized by a higher degree of precolonial economic specialization, partly due to their higher levels of interpersonal population diversity, tend to exhibit significantly higher levels of both precolonial and contemporary economic development.

Impact via Cross-Fertilization of Ideas in Cognitive and Human Capital Development. Interestingly, the beneficial impact of interpersonal diversity on productivity has also been documented at a much lower level of aggregation than countries or ethnic groups. Specifically, exploiting variations across ethnically homogenous high schools in the state of Wisconsin, Cook and Fletcher (2018) find that the expected heterozygosity of the student body of a high school in 1957 may have conferred a significant positive influence on the economic performance of the school's graduates later in life, as captured by completed years of schooling, measures of occupational prestige of the graduate's first job, and family income in 1974 and 1992. The authors additionally provide evidence in line with a novel behavioral mechanism—namely, that exposure to more diverse schooling environments may have shaped individual personality traits towards greater creativity and openness to new ideas and, thus, behaviorally conditioned the individual for greater socioeconomic success later in life. Importantly, because the high-school student bodies in the authors' data set were entirely composed of individuals of European ancestry, the cultural homogeneity and social cohesiveness within these groups assure that the analysis overwhelmingly captures the benefits of diversity, rather than its costs. Further, because the findings are established by exploiting variations within a single state, they are immune to cross-country (and even within-country, cross-state) confounders.

[21]The beneficial effects of interpersonal diversity on economic development are also documented empirically by Ager and Brueckner (2018). Exploiting variations across counties in the United States in the late nineteenth century, these authors find that county-level populations that experienced a larger initial increase in their diversity due to the arrival of European immigrants also subsequently experienced higher rates of growth in both income and scientific patents per capita during the 1870–1920 time horizon. In another interesting study by Delis et al. (2017), the authors exploit panel variations across firms listed in the stock markets of North America and the United Kingdom to show that adding members to a firm's board of directors from countries of origin with differing levels of genetic diversity increases its corporate performance. The authors hypothesize that their finding reflects the productivity-enhancing benefits of interpersonal differences in cultural, psychological, physiological, and other traits that cannot be captured by alternative measured indices of diversity.

[22]Interestingly, as one would expect from preindustrial production activities, in which characteristics of the physical environment and individual abilities behave as complementary inputs, the research also documents that the degree of agro-ecological and agro-climatic heterogeneity reinforces the positive influence of interpersonal diversity on the emergence of economic specialization in precolonial societies.

3.5 Policy Implications

Ashraf and Galor (2013a) and Ashraf, Galor, and Klemp (2020a) document a fundamental trade-off associated with the influence of interpersonal diversity, as reflected by predicted population diversity, on economic performance. Nevertheless, the finding that predicted diversity, based on migratory distance from East Africa, has been a deep *determinant* of economic development does not imply that the composition of heritable traits in a population governs its economic *destiny*. Migratory distance from East Africa affected interpersonal diversity via the interaction of geographical, biological, and cultural attributes, and policies could thus be aimed at conditioning the intervening channels.

In particular, the influence of diversity on productivity implies that a society can shape the context in which the *existing* diversity of its population influences socioeconomic outcomes, by enacting policies to harness the beneficial effects of the existing level of diversity and mitigate its potentially detrimental consequences. Overly diverse societies could focus on fostering interpersonal trust and mediating the potential for social conflict, by encouraging civic participation, improving the quality of political institutions, and mitigating inefficiencies and distortions in the provision of public goods. Overly homogenous societies, on the other hand, could aim to increase diversity in skills, occupations, and training programs in order to foster specialization and innovative activity. In both cases, the orientation of the educational system appears to be the most promising avenue: education can help instill the values of tolerance needed in overly diverse societies, and it can promote cultural receptiveness to different types of productivity-enhancing knowledge that may be lacking in overly homogenous societies.

3.6 Common Misconceptions

The literature on the influence of interpersonal diversity on comparative development across societies has attracted the attention of the scholarly community beyond the discipline of economics and, given methodological divisions, perhaps unsurprisingly generated unfounded criticisms. Three main criticisms have been raised by scholars from other disciplines, predominantly, cultural anthropologists. As discussed below, they reflect a basic misunderstanding of the conceptual framework, the statistical methodology, the scope of the analysis, and its policy implications.

3.6.1 Potential Underestimation of Population Density in pre-Columbian Americas

Some have argued that the hump-shaped relationship between population diversity and aggregate productivity is an artifact of imperfections in the measure of population sizes during the precolonial era. In particular, they contend that the underestimation of population sizes for precolonial Amerindian societies contributed to the documented relationship.

In fact, the historical analysis of Ashraf and Galor (2013a) accounts for the possibility that the data on population density from the precolonial era could indeed be afflicted by measurement errors, establishing through various methods that this issue has no bearing on the validity of their empirical findings:

- Since population density is the *dependent* variable, classical measurement error in this variable does not generate bias in the estimates of the hump-shaped influence of diversity on historical development. In fact, in the absence of classical measurement error, the statistical significance of the estimates would be even higher.

- If there are *systematic* differences across continents in the measurement of historical population density (e.g., if historical population density in the Americas is indeed consistently underestimated), then the estimated effects could have been biased. However, the use of continent fixed effects in the statistical analysis of Ashraf and Galor (2013a), assures that the influence of diversity on historical development is identified based on intersocietal variations within continents, rather than across continents, and hence systematic under-estimation of population levels in the Americas would have no bearing on the results.

- Employing an alternative measure of historical development based on the extent of urbanization in AD 1500, rather than population density, does not qualitatively alter the hump-shaped influence of interpersonal diversity on historical development, as shown by the regressions in columns 3 and 4 of Table 1 and by the scatter plot in panel B of Fig. 7.[23]

- The significant hump-shaped impact of interpersonal population diversity on historical population density at various points in time between 10,000 BC and AD 1500 is established across ethnic homelands (derived from the extended sample of ethnic groups in Pemberton, DeGiorgio, and Rosenberg, 2013) by Ashraf, Galor and Klemp (2020a). A subset of their findings are highlighted in columns 1–8 of Table 3 and illustrated in panels A–D of Fig. 8.

- The main analysis of Ashraf and Galor (2013a) focuses on *contemporary* comparative development, in which the dependent variable is income per capita in the year 2000 (rather than historical population density). Further, the significant hump-shaped impact of interpersonal population diversity on an updated measure of contemporary comparative development, captured by average income per capita during the 2010–18 time period, is apparent in the regression results presented in columns 5–6 of Table 1 and in the scatter plot in panel C of Fig. 7.

- As shown by regressions in columns 7–8 of Table 1 and columns 9–10 of Table 3, and depicted in the scatter plots presented in panel D of Fig. 7 and panel E of Fig. 8, the hump-shaped impact of interpersonal population diversity is robust to the use of an alternative measure of contemporary economic development, captured by per-capita adjusted nighttime luminosity, either across countries or across the ethnic homelands based on the extended sample of groups in Pemberton, DeGiorgio, and Rosenberg (2013).

Thus, concerns about the potential underestimation of populations in the Americas in the pre-Columbian era and its impact on the analysis are based on a fundamental misunderstanding of the statistical methodology employed by this research program. Moreover, the presence of a hump-shaped impact of interpersonal population diversity on: (i) the rate of urbanization in AD 1500, (ii) the population density of ethnic groups at various points in the considerable expanse of time between 10,000 BC and AD 1500, and (iii) contemporary measures of income per capita (for which potential mismeasurements of population density in the pre-Columbian period are entirely irrelevant), further highlight the uninformed nature of this criticism.

3.6.2 The Mapping from Diversity in Neutral Genetic Markers to Social Outcomes

Some have questioned the research program by arguing that expected heterozygosity in neutral genetic markers, employed to proxy for the degree of interpersonal diversity within individual ethnic groups, does not reflect diversity in functional (phenotypic) markers and, therefore, cannot influence behavioral and social interactions.

[23] It may be noted that the data source for urbanization rates in AD 1500 is independent of the source for historical population density.

The measure of observed genetic diversity for the 53 ethnic groups in the HGDP-CEPH sample, as well as for the 200+ groups in the extended data set of Pemberton, DeGiorgio, and Rosenberg (2013) are indeed based neutral genetic markers and, thus, do not *directly* reflect diversity in functional (phenotypic) markers. However, the core analysis of Ashraf and Galor (2013a) is based not on *observed* genetic diversity but rather on *predicted* diversity, implied predominantly by the migratory distances from East Africa of the ancestral populations of contemporary nations. In particular, as discussed in Section 3.3.1, in order to overcome sample limitations and potential concerns about reverse causality associated with the use of *observed* genetic diversity, Ashraf and Galor (2013a) exploit the pronounced impact of migratory distance from East Africa on observed genetic diversity across ethnic groups in the HGDP-CEPH sample in order *predict* interpersonal diversity for all societies, based on the geographical locations of their precolonial ancestral populations, relative to East Africa and to one another.

Importantly, since migratory distance from East Africa has a negative influence on various forms of intragroup phenotypic diversity, *predicted* interpersonal diversity is a valid proxy for diversity in phenotypically and behaviorally expressed traits. As noted earlier in Section 3.2, evidence from the fields of physical and cognitive anthropology suggest that an ancient serial founder effect originating in East Africa has influenced observed worldwide patterns in various forms of intragroup morphological and cognitive diversity, including interpersonal diversity in skeletal features pertaining to cranial characteristics (Manica et al., 2007; von Cramon-Taubadel and Lycett, 2008; Betti et al., 2009), dental attributes (Hanihara, 2008), pelvic traits (Betti et al., 2013), and birth canal morphology (Betti and Manica, 2018), as well as intralingual phonemic diversity (Atkinson, 2011).

Hence, the assertion that inferences cannot be made regarding the impact of interpersonal diversity on socioeconomic outcomes, because the measure of diversity in the HGDP-CEPH sample is based on neutral genetic markers reflects a misunderstanding of the empirical strategy of Ashraf and Galor (2013a). Since migratory distance from Africa affects diversity in neutral genetic markers as well as diversity in phenotypically expressed morphological and cognitive traits, the empirical strategy of exploiting *predicted* population diversity is well positioned to capture the effect of interpersonal diversity on socioeconomic outcomes.

3.6.3 Potential Misuse

Some critics have raised concerns that the finding that productivity tends to be maximized at intermediate levels of diversity could be used to justify disturbing policies, such as the forcible movement or "engineering" of populations, designed to achieve the desirable diversity level in a population.

This view, however, reflects a misunderstanding of the most fundamental insight of this research agenda and its main policy implications. The influence of diversity on productivity operates through various mechanisms, and policies can thus be targeted on these mediating forces, allowing societies to shape the context in which their *existing* levels of diversity can further promote productivity. For instance, as noted in Section 3.5, education policies geared towards pluralism can advance cultural receptiveness to different types of productivity-enhancing knowledge (that may be lacking in overly homogenous societies) while instilling cultural values of trust and tolerance (that may be lacking in overly diverse societies).

4 Concluding Remarks

The past two decades have witnessed the emergence of an influential body of research that has focused on uncovering the ancient roots of economic development across countries, regions, and ethnic groups. This line of inquiry has been exploring the influence of evolutionary processes in the transition from stagnation to growth, as well as the impact of the diversity of human traits on comparative economic development across societies, highlighting the role of the prehistoric "out of Africa" migration of anatomically modern humans in shaping variations in the composition of human traits among populations across the globe.

This exploration of the interaction between evolutionary processes and long-run economic development has centered around two major lines of inquiry. The first suggests that in the era following the Neolithic Revolution, Malthusian pressures not only acted as a key determinant of the size of a population but conceivably shaped, via the forces of natural selection, its composition as well. Lineages of individuals whose traits were complementary to the economic environment generated higher levels of income and, thus, a larger number of surviving offspring. Consequently, the gradual increase in the representation of these growth-enhancing traits in the population over time contributed to the process of development and the emergence of modern growth.

The second line of research advances the hypothesis that migratory distances from the cradle of humankind in East Africa to indigenous settlements across the globe diminished their levels of interpersonal diversity and, thereby, generated a persistent hump-shaped influence on development outcomes, reflecting a fundamental trade-off between beneficial and detrimental effects of diversity on productivity at the societal level. Although diversity can reduce interpersonal trust and social cohesiveness, and can hence adversely affect the productivity of society, diversity can also foster the cross-fertilization of ideas for innovations and stimulate gains from specialization, and it can thus contribute to society's productivity. Therefore, in light of diminishing marginal effects of diversity and homogeneity on productivity, intermediate levels of diversity have contributed to economic prosperity across countries, regions, and ethnic groups.

References

Ager, Philipp, and Markus Brueckner. 2018. "Immigrants' Genes: Genetic Diversity and Economic Development in the United States." *Economic Inquiry*, 56(2): 1149–1164.

Alesina, Alberto, Arnaud Devleeschauwer, William Easterly, Sergio Kurlat, and Romain Wacziarg. 2003. "Fractionalization." *Journal of Economic Growth*, 8(2): 155–194.

Alesina, Alberto, and Eliana La Ferrara. 2005. "Ethnic Diversity and Economic Performance." *Journal of Economic Literature*, 43(3): 762–800.

Algan, Yann, and Pierre Cahuc. 2014. "Trust, Growth, and Well-Being: New Evidence and Policy Implications." In *Handbook of Economic Growth, Volume 2A*, edited by Philippe Aghion and Steven N. Durlauf, 49–120. Amsterdam and Boston: Elsevier, North-Holland.

Arbatlı, Cemal Eren, Quamrul H. Ashraf, Oded Galor, and Marc Klemp. 2020. "Diversity and Conflict." *Econometrica*, 88(2): 727–797.

Ashraf, Quamrul, and Oded Galor. 2011. "Dynamics and Stagnation in the Malthusian Epoch." *American Economic Review*, 101(5): 2003–2041.

Ashraf, Quamrul, and Oded Galor. 2013a. "The 'Out of Africa' Hypothesis, Human Genetic Diversity, and Comparative Economic Development." *American Economic Review*, 103(1): 1–46.

Ashraf, Quamrul, and Oded Galor. 2013b. "Genetic Diversity and the Origins of Cultural Fragmentation." *American Economic Review*, 103(3): 528–533.

Ashraf, Quamrul H., and Oded Galor. 2018. "The Macrogenoeconomics of Comparative Development." *Journal of Economic Literature*, 56(3): 1119–1155.

Ashraf, Quamrul, Oded Galor, and Marc Klemp. 2014. "The 'Out of Africa' Hypothesis of Comparative Development Reflected by Nighttime Light Intensity." Brown University Department of Economics Working Paper 2014-4.

Ashraf, Quamrul H., Oded Galor, and Marc Klemp. 2020a. "Population Diversity and Differential Paths of Long-Run Development since the Neolithic Revolution." Unpublished.

Ashraf, Quamrul H., Oded Galor, and Marc Klemp. 2020b. "Interpersonal Diversity and Societally Important Disparities across Populations: A Reply to Rosenberg and Kang." Unpublished.

Atkinson, Quentin D. 2011. "Phonemic Diversity Supports a Serial Founder Effect Model of Language Expansion from Africa." *Science*, 332(6027): 346–349.

Becker, Anke, Benjamin Enke, and Armin Falk. 2020. "Ancient Origins of the Global Variation in Economic Preferences." *AEA Papers and Proceedings*, 110: 319–323.

Bersaglieri, Todd, et al. 2004. "Genetic Signatures of Strong Recent Positive Selection at the Lactase Gene." *American Journal of Human Genetics*, 74(6): 1111–1120.

Betti, Lia, and Andrea Manica. 2018. "Human Variation in the Shape of the Birth Canal is Significant and Geographically Structured." *Proceedings of the Royal Society B: Biological Sciences*, 285(1889): 20181807.

Betti, Lia, François Balloux, William Amos, Tsunehiko Hanihara, and Andrea Manica. 2009. "Distance from Africa, Not Climate, Explains Within-Population Phenotypic Diversity in Humans." *Proceedings of the Royal Society B: Biological Sciences*, 276(1658): 809–814.

Betti, Lia, Noreen von Cramon-Taubadel, Andrea Manica, and Stephen J. Lycett. 2013. "Global Geometric Morphometric Analyses of the Human Pelvis Reveal Substantial Neutral Population History Effects, Even across Sexes." *PLoS ONE*, 8(2): e55909.

Bisin, Alberto, and Thierry Verdier. 2000. "'Beyond the Melting Pot': Cultural Transmission, Marriage, and the Evolution of Ethnic and Religious Traits." *Quarterly Journal of Economics*, 115(3): 955–988.

Bisin, Alberto, and Thierry Verdier. 2001. "The Economics of Cultural Transmission and the Dynamics of Preferences." *Journal of Economic Theory*, 97(2): 298–319.

Bisin, Alberto, and Thierry Verdier. 2011. "The Economics of Cultural Transmission and Socialization." In *Handbook of Social Economics, Volume 1A*, edited by Jess Benhabib, Alberto Bisin, and Matthew O. Jackson, 339–416. Amsterdam and Boston: Elsevier, North-Holland.

Bouchouicha, Ranoua, and Ferdinand M. Vieider. 2019. "Growth, Entrepreneurship, and Risk-Tolerance: A Risk-Income Paradox." *Journal of Economic Growth*, 24(3): 257–282.

Bowles, Samuel, and Herbert Gintis. 2011. *A Cooperative Species: Human Reciprocity and Its Evolution*. Princeton and Oxford: Princeton University Press.

Burger, Joachim, Martina Kirchner, Barbara Bramanti, Wolfgang Haak, and Mark G. Thomas. 2007. "Absence of the Lactase-Persistence-Associated Allele in Early Neolithic Europeans." *Proceedings of the National Academy of Sciences*, 104(10): 3736–3741.

Cann, Howard M., et al. 2002. "A Human Genome Diversity Cell Line Panel." *Science*, 296(5566): 261–262.

Collins, Jason, Boris Baer, and Ernst Juerg Weber. 2014. "Economic Growth and Evolution: Parental Preference for Quality and Quantity of Offspring." *Macroeconomic Dynamics*, 18(8): 1773–1796.

Cook, C. Justin. 2015. "The Natural Selection of Infectious Disease Resistance and Its Effect on Contemporary Health." *Review of Economics and Statistics*, 97(4): 742–757.

Cook, C. Justin, and Jason M. Fletcher. 2018. "High School Genetic Diversity and Later-Life Student Outcomes: Micro-Level Evidence from the Wisconsin Longitudinal Study." *Journal of Economic Growth*, 23(3): 307–339.

Dalgaard, Carl-Johan, and Holger Strulik. 2015. "The Physiological Foundations of the Wealth of Nations." *Journal of Economic Growth*, 20(1): 37–73.

Dalgaard, Carl-Johan, and Holger Strulik. 2016. "Physiology and Development: Why the West is Taller Than the Rest." *Economic Journal*, 126(598): 2292–2323.

de la Croix, David, Eric B. Schneider, and Jacob Weisdorf. 2019. "Childlessness, Celibacy and Net Fertility in Pre-Industrial England: The Middle-Class Evolutionary Advantage." *Journal of Economic Growth*, 24(3): 223–256.

Delis, Manthos D., Chrysovalantis Gaganis, Iftekhar Hasan, and Fotios Pasiouras. 2017. "The Effect of Board Directors from Countries with Different Genetic Diversity Levels on Corporate Performance." *Management Science*, 63(1): 231–249.

Depetris-Chauvin, Emilio, and Ömer Özak. 2020. "The Origins of the Division of Labor in Pre-Industrial Times." *Journal of Economic Growth*, 25(3): 297–340.

Desmet, Klaus, Shlomo Weber, and Ignacio OrtuñoOrtín. 2009. "Linguistic Diversity and Redistribution." *Journal of the European Economic Association*, 7(6): 1291–1318.

Doepke, Matthias, and Fabrizio Zilibotti. 2014. "Culture, Entrepreneurship, and Growth." In *Handbook of Economic Growth, Volume 2A*, edited by Philippe Aghion and Steven N. Durlauf, 1–48. Amsterdam and Boston: Elsevier, North-Holland.

Easterly, William, and Ross Levine. 1997. "Africa's Growth Tragedy: Policies and Ethnic Divisions." *Quarterly Journal of Economics*, 112(4): 1203–1250.

Esteban, Joan, Laura Mayoral, and Debraj Ray. 2012. "Ethnicity and Conflict: An Empirical Study." *American Economic Review*, 102(4): 1310–1342.

Fearon, James D. 2003. "Ethnic and Cultural Diversity by Country." *Journal of Economic Growth*, 8(2): 195–222.

Galor, Oded. 2011. *Unified Growth Theory.* Princeton and Oxford: Princeton University Press.

Galor, Oded, and Marc Klemp. 2017. "The Roots of Autocracy." National Bureau of Economic Research Working Paper 23301.

Galor, Oded, and Marc Klemp. 2019. "Human Genealogy Reveals a Selective Advantage to Moderate Fecundity." *Nature Ecology & Evolution*, 3(4): 853–857.

Galor, Oded, and Stelios Michalopoulos. 2012. "Evolution and the Growth Process: Natural Selection of Entrepreneurial Traits." *Journal of Economic Theory*, 147(2): 759–780.

Galor, Oded, and Omer Moav. 2002. "Natural Selection and the Origin of Economic Growth." *Quarterly Journal of Economics*, 117(4): 1133–1191.

Galor, Oded, and Omer Moav. 2007. "The Neolithic Revolution and Contemporary Variations in Life Expectancy." Brown University Department of Economics Working Paper 2007-14.

Galor, Oded, and Ömer Özak. 2016. "The Agricultural Origins of Time Preference." *American Economic Review*, 106(10): 3064–3103.

Galor, Oded, and Viacheslav Savitskiy. 2020. "Climatic Roots of Loss Aversion." National Bureau of Economic Research Working Paper 25273.

Hanihara, Tsunehiko. 2008. "Morphological Variation of Major Human Populations Based on Nonmetric Dental Traits." *American Journal of Physical Anthropology*, 136(2): 169–182.

Harpending, Henry, and Alan Rogers. 2000. "Genetic Perspectives on Human Origins and Differentiation." *Annual Review of Genomics and Human Genetics*, 1: 361–385.

Hawks, John, Eric T. Wang, Gregory M. Cochran, Henry C. Harpending, and Robert K. Moyzis. 2007. "Recent Acceleration of Human Adaptive Evolution." *Proceedings of the National Academy of Sciences*, 104(52): 20753–20758.

Henn, Brenna M., L. Luca Cavalli-Sforza, and Marcus W. Feldman. 2012. "The Great Human Expansion." *Proceedings of the National Academy of Sciences*, 109(44): 17758–17764.

Klemp, Marc, and Jacob Weisdorf. 2019. "Fecundity, Fertility and the Formation of Human Capital." *Economic Journal*, 129(618): 925–960.

Kong, Augustine, et al. 2017. "Selection Against Variants in the Genome Associated with Educational Attainment." *Proceedings of the National Academy of Sciences*, 114(5): E727–E732.

Kong, Augustine, et al. 2018. "The Nature of Nurture: Effects of Parental Genotypes." *Science*, 359(6374): 424–428.

Lagerlöf, Nils-Petter. 2007. "Long-Run Trends in Human Body Mass." *Macroeconomic Dynamics*, 11(3): 367–387.

Livingstone, Frank B. 1958. "Anthropological Implications of Sickle Cell Gene Distribution in West Africa." *American Anthropologist*, 60(3): 533–562.

Manica, Andrea, William Amos, François Balloux, and Tsunehiko Hanihara. 2007. "The Effect of Ancient Population Bottlenecks on Human Phenotypic Variation." *Nature*, 448(7151): 346–348.

Mathieson, Iain, et al. 2015. "Genome-Wide Patterns of Selection in 230 Ancient Eurasians." *Nature*, 528(7583): 499–503.

Mekel-Bobrov, Nitzan, et al. 2005. "Ongoing Adaptive Evolution of *ASPM*, a Brain Size Determinant in *Homo sapiens*." *Science*, 309(5741): 1720–1722.

Nielsen, Rasmus, Ines Hellmann, Melissa Hubisz, Carlos Bustamante, and Andrew G. Clark. 2007. "Recent and Ongoing Selection in the Human Genome." *Nature Reviews Genetics*, 8(11): 857–868.

Pemberton, Trevor J., Michael DeGiorgio, and Noah A. Rosenberg. 2013. "Population Structure in a Comprehensive Genomic Data Set on Human Microsatellite Variation." *G3: Genes, Genomes, Genetics*, 3(5): 891–907.

Prugnolle, Franck, Andrea Manica, and François Balloux. 2005. "Geography Predicts Neutral Genetic Diversity of Human Populations." *Current Biology*, 15(5): R159–R160.

Putterman, Louis, and David N. Weil. 2010. "Post-1500 Population Flows and the Long-Run Determinants of Economic Growth and Inequality." *Quarterly Journal of Economics*, 125(4): 1627–1682.

Ramachandran, Sohini, Omkar Deshpande, Charles C. Roseman, Noah A. Rosenberg, Marcus W. Feldman, and L. Luca Cavalli-Sforza. 2005. "Support from the Relationship of Genetic and Geographic Distance in Human Populations for a Serial Founder Effect Originating in Africa." *Proceedings of the National Academy of Sciences*, 102(44): 15942–15947.

Ray, Debraj, and Joan Esteban. 2017. "Conflict and Development." *Annual Review of Economics*, 9: 263–293.

Robson, Arthur J., and Larry Samuelson. 2011. "The Evolutionary Foundations of Preferences." In *Handbook of Social Economics, Volume 1A*, edited by Jess Benhabib, Alberto Bisin, and Matthew O. Jackson, 221–310. Amsterdam and Boston: Elsevier, North-Holland.

Rogers, Deborah S., Marcus W. Feldman, and Paul R. Ehrlich. 2009. "Inferring Population Histories using Cultural Data." *Proceedings of the Royal Society B: Biological Sciences*, 276(1674): 3835–3843.

Rosenberg, Noah A., and Jonathan T. L. Kang. 2015. "Genetic Diversity and Societally Important Disparities." *Genetics*, 201(1): 1–12.

Sabeti, Pardis C., et al. 2006. "Positive Natural Selection in the Human Lineage." *Science*, 312(5780): 1614–1620.

Sacerdote, Bruce. 2011. "Nature and Nurture Effects on Children's Outcomes: What Have We Learned from Studies of Twins and Adoptees?" In *Handbook of Social Economics, Volume 1A*, edited by Jess Benhabib, Alberto Bisin, and Matthew O. Jackson, 1–30. Amsterdam and Boston: Elsevier, North-Holland.

Simonson, Tatum S., et al. 2010. "Genetic Evidence for High-Altitude Adaptation in Tibet." *Science*, 329(5987): 72–75.

Spolaore, Enrico, and Romain Wacziarg. 2009. "The Diffusion of Development." *Quarterly Journal of Economics*, 124(2): 469–529.

Spolaore, Enrico, and Romain Wacziarg. 2014. "Long-Term Barriers to Economic Development." In *Handbook of Economic Growth, Volume 2A*, edited by Philippe Aghion and Steven N. Durlauf, 121–176. Amsterdam and Boston: Elsevier, North-Holland.

Tishkoff, Sarah A., et al. 2001. "Haplotype Diversity and Linkage Disequilibrium at Human *G6PD*: Recent Origin of Alleles That Confer Malarial Resistance." *Science*, 293(5529): 455–462.

Tishkoff, Sarah A., et al. 2007. "Convergent Adaptation of Human Lactase Persistence in Africa and Europe." *Nature Genetics*, 39(1): 31–40.

Tversky, Amos, and Daniel Kahneman. 1991. "Loss Aversion in Riskless Choice: A Reference-Dependent Model." *Quarterly Journal of Economics*, 106(4): 1039–1061.

Voight, Benjamin F., Sridhar Kudaravalli, Xiaoquan Wen, Jonathan K. Pritchard. 2006. "A Map of Recent Positive Selection in the Human Genome." *PLoS Biology*, 4(3): e72.

von Cramon-Taubadel, Noreen, and Stephen J. Lycett. 2008. "Brief Communication: Human Cranial Variation Fits Iterative Founder Effect Model with African Origin." *American Journal of Physical Anthropology*, 136(1): 108–113.

Weibull, Jörgen W., and Marcus Salomonsson. 2006. "Natural Selection and Social Preferences." *Journal of Theoretical Biology*, 239(1): 79–92.

Wiesenfeld, Stephen L. 1967. "Sickle-Cell Trait in Human Biological and Cultural Evolution: Development of Agriculture Causing Increased Malaria is Bound to Gene-Pool Changes Causing Malaria Reduction." *Science*, 157(3793): 1134–1140.