

Ashraf, Quamrul H.; Galor, Oded

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# The Macrogenoeconomics of Comparative Development\*

Quamrul H. Ashraf<sup>†</sup>      Oded Galor<sup>‡</sup>

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## Abstract

A vibrant literature has emerged in recent years to explore the influences of human evolution and the genetic composition of populations on the comparative economic performance of societies, highlighting the roles played by the Neolithic Revolution and the prehistoric “out of Africa” migration of anatomically modern humans in generating worldwide variations in the composition of genetic traits across populations. The recent attempt by Nicholas Wade’s *A Troublesome Inheritance: Genes, Race and Human History* to expose the evolutionary origins of comparative economic development to a wider audience provides an opportunity to review this important literature in the context of his theory.

**Keywords:** Comparative development, natural selection, human evolution, Malthusian era, Neolithic Revolution, genes, race

**JEL classification codes:** O11, N10, N30, Z10

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<sup>†</sup>Department of Economics, Williams College, Schapiro Hall, 24 Hopkins Hall Drive, Williamstown, MA 01267 (email: Quamrul.H.Ashraf@williams.edu).

<sup>‡</sup>Department of Economics, Brown University, Robinson Hall, 64 Waterman Street, Providence, RI 02912 (email: Oded.Galor@brown.edu).

## 1 Introduction

The past two decades have witnessed the emergence of a large and influential body of research that has focused on uncovering the roots of comparative economic development across regions, countries, and ethnic groups (Diamond, 1997; Galor, 2011; Acemoglu and Robinson, 2012). A significant portion of this line of inquiry has been exploring the influences of human evolution and the genetic composition of populations on comparative economic performance across societies, emphasizing the roles played by the Neolithic Revolution and the prehistoric “out of Africa” migration of anatomically modern humans in generating variations in the composition of genetic traits across populations around the globe (Galor and Moav, 2002; Ashraf and Galor, 2013a).

Explorations of the interaction between human evolution and the process of economic development have centered around two fundamental lines of inquiry. The first avenue uncovers the effect of the economic environment on the evolution of human traits and 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 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 traits in the population contributed to the process of development, the pace of the transition from stagnation to growth, and comparative economic development across societies. Moreover, 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 (Galor and Moav, 2002).

Subjecting hypothetical evolutionary processes to the scrutiny of evolutionary growth models, 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 and economic development. In particular, these studies have highlighted the selection of innate preferences for quality rather than quantity of offspring (Galor and Moav, 2002), resistance to infectious diseases (Galor and Moav, 2007), human body size (Lagerlöf, 2007), predisposition towards entrepreneurial spirit (Galor and Michalopoulos, 2012), time preference (Galor and Özak, 2014), lactase persistence (Cook, 2014), and conspicuous consumption (Collins, Baer and Weber, 2015).

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 composition of genetic traits within human populations and, thus, on comparative economic development across societies from the dawn of civilization to the contemporary era. In particular, this line of research has advanced the hypothesis and empirically established that migratory distances from the cradle of mankind in East Africa to indigenous settlements across the globe adversely affected their levels of genetic diversity and, thereby, generated a persistent hump-shaped influence on development outcomes, reflecting the fundamental trade-off between the

beneficial and detrimental effects of diversity on productivity at the societal level (Ashraf and Galor, 2013a; Ashraf, Galor and Klemp, 2014, 2015). Although diversity diminishes interpersonal trust, cooperation, and economic coordination, adversely affecting the productivity of society, complementarity across diverse productive traits stimulates innovations and gains from specialization, thus contributing to society's economic performance. In the presence of diminishing marginal returns to diversity and homogeneity, the aggregate productivity of ethnic groups, countries, or regions that are characterized by intermediate levels of diversity is therefore expected to be higher than that associated with excessively homogenous or heterogeneous societies.

Consistent with the fundamental elements of this hypothesis, genetic diversity has been established as a central determinant of observed ethnic and cultural heterogeneity, as reflected by the number of ethnic groups and the degree of ethnolinguistic fractionalization in a society (Ashraf and Galor, 2013b), and as a major force in the emergence of civil conflicts (Arbath, Ashraf and Galor, 2015). Genetic diversity has also been shown to contribute to diminished interpersonal trust and more intensive innovative activity (Ashraf and Galor, 2013a), as well as greater occupational heterogeneity and gains from specialization (Depetris-Chauvin and Özak, 2015). Moreover, it has been argued that genetic diversity has shaped the nature of both precolonial and contemporary political institutions. In particular, although diversity triggered the development of institutions for mitigating the adverse influence of diversity on social cohesion, the contribution of diversity to economic inequality and class stratification ultimately led to the formation and persistence of extractive and autocratic institutions (Galor and Klemp, 2015).

The recent attempt by Nicholas Wade's *A Troublesome Inheritance: Genes, Race and Human History* to expose evolutionary forces in comparative development to a wider audience could have a priori complemented other books that have focused on the root causes of the wealth and poverty of nations (e.g., Diamond, 1997; Galor, 2011; Acemoglu and Robinson, 2012) and, in particular, existing paradigms of research on the macrogenetic origins of comparative development. Unfortunately, the main elements of Wade's thesis rest on largely unsubstantiated suppositions, making it unlikely to inspire considerable general interest in this important topic or stimulate further academic research.

Wade advances a modified evolutionary theory of long-run economic development, based on regional variation in the intensity of positive selection of traits that are conducive to growth-enhancing institutions. His theory suggests that variation in the duration of selective pressures on genetic traits across regions form the basis of differences in social behaviors across racial groups, thereby shaping variations in the nature of institutions and, thus, the level of economic development across the globe. Although at the outset, the broad outline of this argument appears plausible and largely consistent with existing evolutionary theories of comparative development, there is currently no compelling evidence for supporting the actual mechanisms proposed by Wade. Furthermore, Wade's focus on genetic differentiation *between* societies and its hypothesized ramifications for comparative development entirely overlooks the significant role that interpersonal genetic diversity

*within* populations has played in generating differential processes of economic development across societies.

The two fundamental building blocks of Wade's theory are rather speculative. In particular, his narrative relies on unsubstantiated selection mechanisms and on empirically unsupported conjectures regarding the determinants of institutional variation across societies. In line with the earlier insights of Galor and Moav (2002), the first building block of Wade's theory plausibly argues that following the Neolithic Revolution, natural selection favored long-run growth-enhancing traits during the Malthusian era, a stage of economic development when temporary gains in income were primarily channeled towards population growth. Nevertheless, the specific evolutionary process that he proposes is unsubstantiated. Rather than subjecting his hypothesized mechanism to the scrutiny of evolutionary growth theory, Wade follows the speculative supposition of Clark (2007), merely positing that in historically densely populated regions of the world that were characterized by early statehood, there existed a class of rich elites, endowed with genetic traits (e.g., nonviolence, cooperation, and thrift) conducive to growth-enhancing institutions, whose evolutionary advantage increased the prevalence of these favorable traits in the populations of those regions over time. It is far from evident, however, that the traits emphasized by Wade necessarily generated higher incomes in a Malthusian environment and were, thus, necessarily favored by the forces of natural selection. Moreover, Wade provides no evidence on how variations across societies in their geographical setting or historical experience could have given rise to differential selective pressures on these traits and, thus, generated variation in the growth-promoting genetic makeup of their populations. Furthermore, there is currently little scientific consensus on the extent to which the key behavioral traits of nonviolence, cooperation, and thrift, as emphasized by Wade's theory, are genetically determined.

The second building block of Wade's theory that links genetic traits to institutions is equally speculative. In particular, there is little evidence to support the claim that the variation in institutions across societies is driven by differences in their endowment of specific genetic traits that might govern key social behaviors. In addition, Wade's hypothesized association between genetic traits and institutions is based on the untested assertion that since a society's institutions tend to be highly persistent over time, the variation in institutions across societies must be rooted in differences in their endowment of favorable genetic traits. This proposition, however, disregards the role of cultural persistence and the well-documented role of economic incentives in shaping institutional persistence. Further, in contrast to Wade's theory, existing findings in the economics literature support the contribution of the interpersonal *diversity* of traits (rather than the *prevalence* of any *specific* traits) within a society to the emergence and persistence of institutions.

Setting aside the scientific fragility of the main building blocks in Wade's theory, Wade's conjecture suggests that national populations occupying the global technological frontier are endowed with genetic traits that are most conducive for economic development. Thus, populations that are genetically more distant from the technological frontier would be expected to underperform economically. Nevertheless, a novel empirical assessment conducted by this review refutes the

predictions of Wade’s theory and supports the significant role of genetic diversity in shaping comparative development. In particular, exploiting worldwide variations across modern national populations, the analysis documents that conditional on cross-country heterogeneity in various geographical, historical, cultural, and unobserved regional factors, genetic diversity does indeed confer a significant hump-shaped influence on income per capita, as established by the existing literature, but genetic distance to the frontier possesses no statistically discernible relationship with the level of economic development.

The remainder of this review is organized as follows. For readers unfamiliar with the topic, Section 2 provides some background on basic concepts and empirical facts from the field of human population genetics, complementing the material in the remainder of the review. Section 3 provides an overview of the literature on the macrogenoeconomics of comparative development, highlighting the role genetic diversity in generating differential development trajectories across societies. It also discusses some of the elaborate theories of evolutionary processes during the Malthusian epoch that could shed light on the observed disparity in the process of development across societies.<sup>1</sup> Section 4 summarizes Wade’s thesis and provides a conceptual critique of his arguments. Section 5 reveals empirical findings that support the significant role that genetic diversity within national populations plays in comparative economic development, while establishing the insignificant role of genetic distance to the global technological frontier. Section 6 concludes.

## 2 Background on Human Population Genetics

### 2.1 The “Out of Africa” Origins of Worldwide Variations in Human Genetic Diversity

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 200,000 years ago, embarked on populating the entire globe in a stepwise migration process beginning around 90,000–60,000 BP and ending no later than 17,000 BP. The world map in Figure 1 depicts the approximate migration routes that characterized this prehistoric demic diffusion process, with the land connectedness of the migratory paths being determined by a set of key intercontinental waypoints.

The “out of Africa” migration, however, was inherently associated with what population geneticists refer to as a serial founder effect, which had a profound and long-lasting influence by way of generating variations in the macrogenetic structure of human populations across the globe. Specifically, because the spatial diffusion of humans to the rest of the world occurred in a

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<sup>1</sup>The current review focuses on research that has been exploring the interaction of human evolution and the process of development at the societal level as well as the influence of the macrogenetic structure of human populations on comparative economic development across societies. It may be noted, however, that there exists a distinct but tangentially related literature that has been employing “genome-wide association studies” to explore the potential links between molecular genetics and either individual social behaviors in experimental settings or individual economic outcomes in observational data, including dispositions of fairness in ultimatum games (Wallace et al., 2007), cooperative behavior in trust games (Cesarini et al., 2008), risk preferences and giving behavior in dictator games (Cesarini et al., 2009), risk-taking in observed financial decisions (Cesarini et al., 2010), and observed levels of educational attainment (Rietveld et al., 2013). The reader is referred to Beauchamp et al. (2011), Sacerdote (2011), and Benjamin et al. (2012) for reviews of this literature.

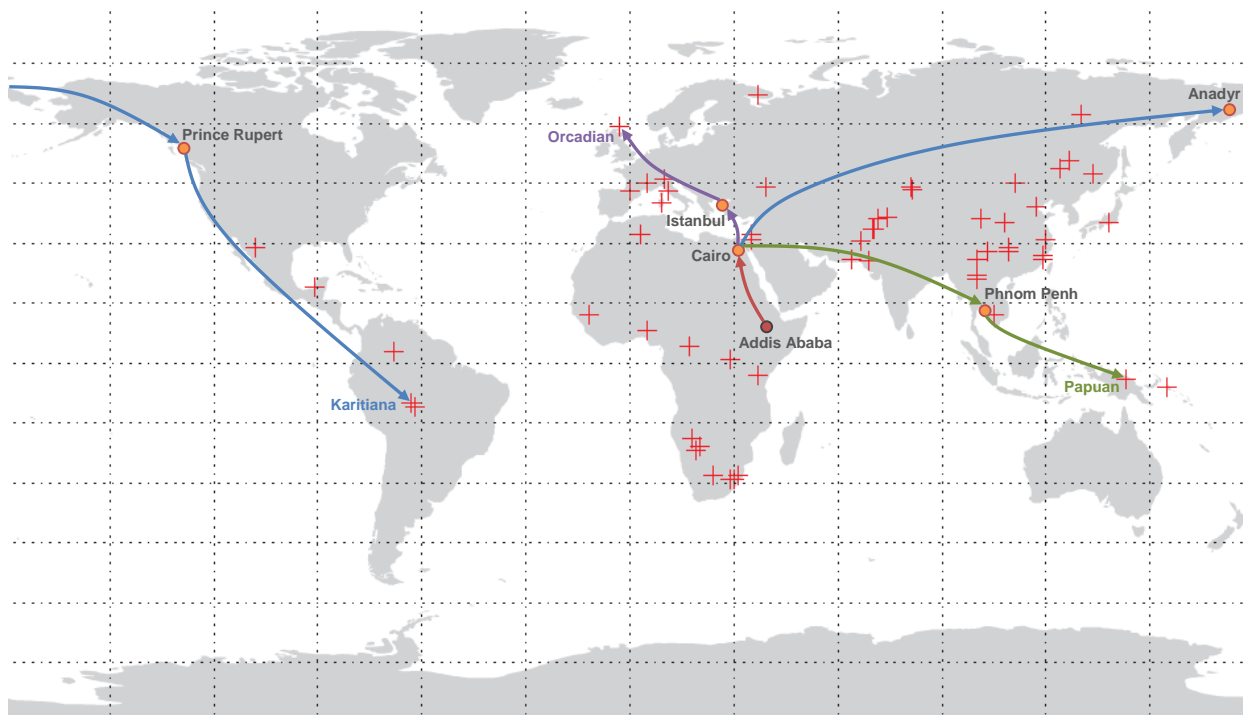


Figure 1: The “Out of Africa” Migration from the Cradle of Mankind

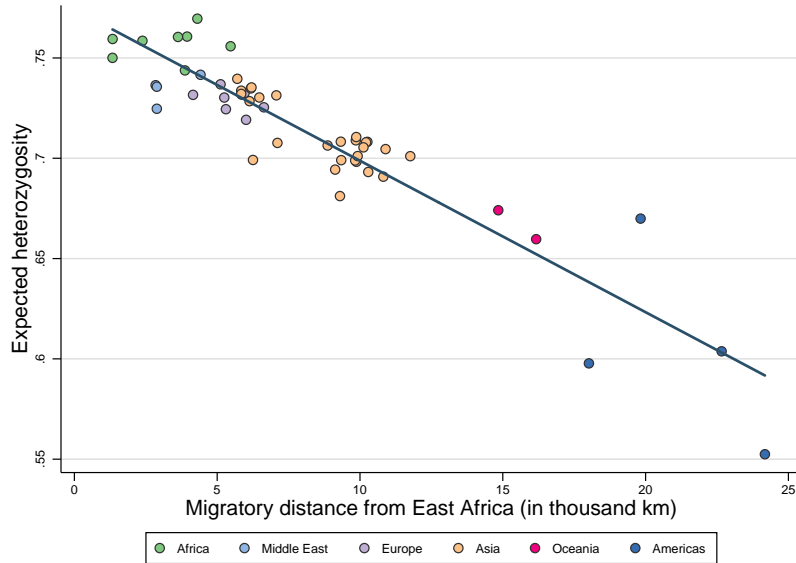
*Notes:* This figure depicts on a world map (i) the locations (denoted by crosses) of the 53 ethnic groups that constitute the HGDP-CEPH Human Genome Diversity Cell Line Panel; (ii) the locations (denoted by circles) of the intermediate waypoints used to construct migratory paths from Addis Ababa to these ethnic groups; and (iii) some migratory paths (denoted by solid lines) based on these waypoints.

*Sources:* Ashraf and Galor (2013a).

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 genetic diversity of their parental colony, the extent of genetic diversity observed *within* a geographically indigenous contemporary ethnic group decreases with increasing distance 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). The scatter plot in Figure 2 reflects this chain of ancient population bottlenecks originating in East Africa, illustrating the negative influence of migratory distance from the cradle of mankind on intrapopulation genetic diversity in a sample comprising 53 globally representative ethnic groups from the Human Genome Diversity Cell Line Panel, compiled by the Human Genome Diversity Project (HGDP) in collaboration with the Centre d’Etudes du Polymorphisme Humain (CEPH). According to population geneticists, these ethnic groups have not only been indigenous to their current geographical locations, but they have also been largely isolated from genetic flows from other ethnic groups.

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 called expected





*Figure 2: Expected Heterozygosity and Migratory Distance from East Africa*

*Notes:* This figure depicts the negative influence of migratory distance from East Africa on expected heterozygosity (genetic diversity) across the 53 ethnic groups that constitute the HGDP-CEPH Human Genome Diversity Cell Line Panel.

*Sources:* Ashraf and Galor (2013a).

heterozygosity, which can be interpreted simply as 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 traits. In particular, the construction of the measure starts with incorporating information on the allelic frequencies for a particular gene or DNA locus – i.e., the proportional representations of different alleles or variants of a given genetic trait in the population. This permits the computation of a gene-specific expected heterozygosity index (i.e., the probability that two randomly selected individuals differ with respect to the genetic trait in question), and upon measuring heterozygosity for a large number of genes or DNA loci, the information is averaged across loci to yield an overall expected heterozygosity for the relevant 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 selectively neutral. For the purposes of examining the influence of genetic diversity on socioeconomic outcomes, this measure possesses the 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 the 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 impact of diversity.



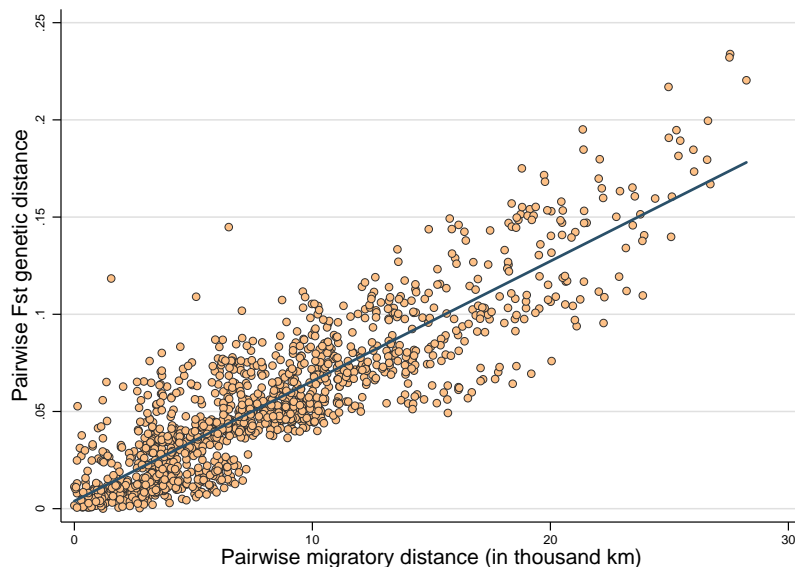


Figure 3: Pairwise  $F_{ST}$  Genetic Distance and Pairwise Migratory Distance

Notes: This figure depicts the positive influence 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.

Sources: Ashraf and Galor (2013a).

Nevertheless, to be conceptually meaningful for socioeconomic outcomes, the measure of genetic diversity needs to serve as a valid proxy for diversity in phenotypically expressed traits. Reassuringly, as argued and empirically established by Ashraf and Galor (2013a), the observed socioeconomic influence of expected heterozygosity in microsatellites reflects the positive relationship between diversity in microsatellites and intrapopulation heterogeneity in phenotypically and cognitively expressed genomic material. This latent relationship can be inferred from mounting evidence in the fields of physical and cognitive anthropology on 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), and pelvic traits (Betti et al., 2013), as well as intralingual phonemic diversity (Atkinson, 2011).<sup>2</sup>

In addition to giving rise to the worldwide variation in genetic 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

<sup>2</sup>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).

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. Following the splitting up of populations from one another during the “out of Africa” migration process, this residual genetic variation between populations arose from (i) random mutations (even in selectively neutral genes) 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, the scatter plot in Figure 3 depicts the aforementioned relationship arising from “isolation by distance” across all pairs of ethnic groups represented in the HGDP-CEPH Human Genome Diversity Cell Line Panel.

## 2.2 Evolutionary Processes in Human Societies since the Neolithic Revolution

Existing evidence suggests that the composition of genetic traits within a population can indeed evolve rather swiftly and that major evolutionary processes have transpired in human populations since the arrival of anatomically modern humans to their destinations following their exodus from Africa, particularly, since the onset of the Neolithic Revolution. For instance, 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). In addition, the genetic immunity to malaria provided by the sickle cell trait has been shown to be highly prevalent among the descendants of those African populations whose early engagement in agriculture provided fertile breeding grounds for mosquitoes and, thereby, elevated the historical incidence of malaria, whereas the trait is largely absent among the descendants of populations that did not practice early agriculture (Livingstone, 1958; Wiesenfeld, 1967; Tishkoff et al., 2001).

In a recent study, Mathieson et al. (2015) compare the genomes of ancient West Eurasians, dated to have lived between 6500 BCE and 300 BCE, with the genomes of present-day Europeans, reporting that the Neolithic transition from hunting and gathering to sedentary agriculture gave rise to selection at genetic loci associated with pigmentation, immunity, height, and diet. Specifically, 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. 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, and although early Neolithic migrants to southern Europe were under selection pressures that favored decreased height, the selection of increased height operated on the steppe populations that ultimately migrated to northern Europe.<sup>3</sup>

### 3 Academic Literature

#### 3.1 Genetic Diversity and Comparative Development

The importance of interpersonal genetic diversity *within* populations has been the focus of a recent but vibrant research program in the academic literature on the deep roots of comparative development, originating in [Ashraf and Galor \(2013a\)](#). This research has advanced the hypothesis and empirically established that migratory distances from the cradle of mankind in East Africa to indigenous settlements across the globe adversely affected their levels of genetic diversity and, thereby, generated a persistent hump-shaped influence on development outcomes, reflecting the trade-off between the beneficial and detrimental effects of diversity on productivity at the societal level. Diversity can positively influence economic development by widening a society's spectrum of individual skills, abilities, and cognitive approaches, which fosters innovative activity, stimulates specialization, and allows societies to adapt more rapidly to changing technological environments. Conversely, by also widening a society's spectrum of individual values, beliefs, preferences, and predispositions in social interactions, diversity can reduce the extent of social cohesion, generate inefficiencies in the provision of public goods, and hamper economic coordination, thus conferring a negative influence on economic performance. In light of a diminishing marginal effect of diversity associated with each of these two counteracting forces, the hypothesis predicts an inverted-U relationship between diversity and development, capturing the trade-off between the social costs and benefits of diversity.

The extent of ethnic fractionalization within national populations has been recognized as an important adverse correlate of development ([Easterly and Levine, 1997](#); [Alesina et al., 2003](#); [Alesina and La Ferrara, 2005](#)). This body of research has established that across countries, fractionalization tends to be negatively correlated with income per capita, economic growth, institutional quality, efficiency in provision of public goods, and the extent of social cohesion. The standard measure of ethnic diversity at the national level – namely, the index of ethnic fractionalization – reflects the probability that two randomly selected individuals from the national population will belong to different ethnic groups. This and other similar measures of ethnic diversity, however, predominantly

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<sup>3</sup>More generally, [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, the study by [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. Further, 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](#)). Additional evidence on recent human adaptive evolution is provided by [Sabeti et al. \(2006\)](#), [Hawks et al. \(2007\)](#), and [Nielsen et al. \(2007\)](#).

capture only one dimension of diversity in a society – the proportional representation of ethnic groups. Importantly, unlike genetic diversity at the national level, these measures do not incorporate the extent of interpersonal diversity within each ethnic group in the population, and they also generally ignore the degree of differentiation (or the “distance”) between constituent groups.

**Reduced-Form Evidence** Exploiting the data on expected heterozygosity discussed in Section 2.1, Ashraf and Galor (2013a) empirically examine their prediction regarding the trade-off between the beneficial and detrimental effects of the degree of interpersonal diversity on productivity at the societal level. Consistent with their hypothesis, they find that genetic diversity, as determined predominantly by the 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 establish 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. Demonstrating that the hump-shaped relationship between diversity and development can be observed even in historical periods is important for two reasons. First, since the mechanisms through which diversity can influence productivity at the societal level are conceptually independent of the stage of economic development (i.e., agricultural vs. industrial), the hump-shaped influence of diversity is expected to hold not only across modern economies but across preindustrial societies as well. Second, 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 from the cradle of mankind, and as such, the diversity of a precolonial society was overwhelmingly determined by the ancient serial founder effect originating in East Africa, as depicted in Figure 2. The great intercontinental migrations associated with the Columbian Exchange, however, drastically altered the ethnic composition of many regional populations, particularly in the New World, thereby introducing additional complexities to the measurement of diversity for contemporary national populations, as elaborated further below.

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 of the influence of genetic diversity on comparative development focuses on explaining the variation across preindustrial societies in population density in the year 1500.

To overcome sample limitations and potential concerns about reverse causality associated with the use of *observed* genetic diversity, the authors exploit the strong explanatory power of migratory distance from East Africa for the worldwide variation in observed genetic diversity across

ethnic groups in the HGDP-CEPH sample, as depicted in Figure 2, in order to generate a measure of *predicted* genetic diversity for all societies around the world, based on their respective geographical locations in the year 1500. As illustrated by scatter plot in Panel A of Figure 4, employing the measure of predicted genetic diversity, the authors establish a hump-shaped influence of diversity on population density in the year 1500, in a sample of observations spanning the entire globe. Notably, the depicted relationship already 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 cross-continental differences. This finding is robust to a large number of sensitivity checks, including “placebo” tests which show that a similar hump-shaped pattern does not exist when employing either aerial distance from East Africa or migratory distances from other geographical locations as the explanatory variable of interest in the analysis of historical comparative development.

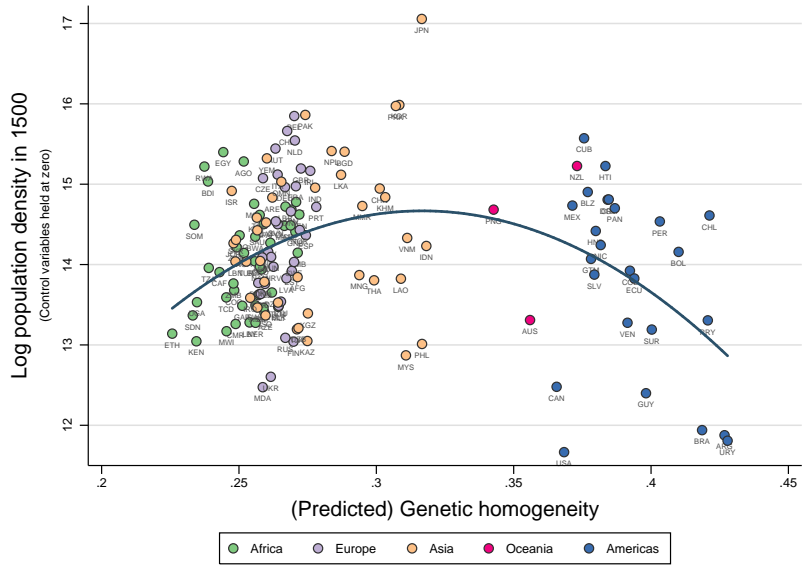
Ashraf and Galor’s analysis of contemporary comparative development exploits data on the ethnic compositions of modern national populations, which reflect the great intercontinental and interregional migrations over the past half millennium. Specifically, it incorporates this information to construct a country-level measure of contemporary genetic diversity that takes into account not only the expected heterozygosity of each ethnic group in a national population but also the pairwise genetic distances amongst these constituent ethnic groups.<sup>4</sup> Applying their measure of contemporary genetic diversity, the authors establish a significant hump-shaped influence of diversity on income per capita in the year 2000. This relationship, depicted by the scatter plot in Panel A of Figure 5, accounts for potentially confounding effects arising from cross-country heterogeneity in the timing of the Neolithic Revolution, various geographical, cultural, and institutional correlates of contemporary economic development, and unobserved continent-specific characteristics. The relationship is additionally robust to controlling for population density in the year 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 international population flows over the past five hundred years.

The main finding from Ashraf and Galor’s analysis of contemporary comparative development suggests that (i) increasing the diversity of the most homogenous country in the sample (Bolivia) by 1 percentage point would raise its income per capita in the year 2000 by 41 percent; (ii) decreasing the diversity of the most diverse country in the sample (Ethiopia) by 1 percentage point would raise its income per capita by 21 percent; (iii) a 1 percentage point change in genetic diversity (in either direction) at the “optimum” level of 0.721 (that most closely resembles the diversity level of the United States) would lower income per capita by 1.9 percent; (iv) increasing the diversity of Bolivia to the level prevalent in the United States would increase Bolivia’s per-capita income by a

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<sup>4</sup>Additional details regarding the construction of this measure of contemporary genetic diversity are provided in the online appendix of Ashraf and Galor (2013a).

Panel A



Panel B

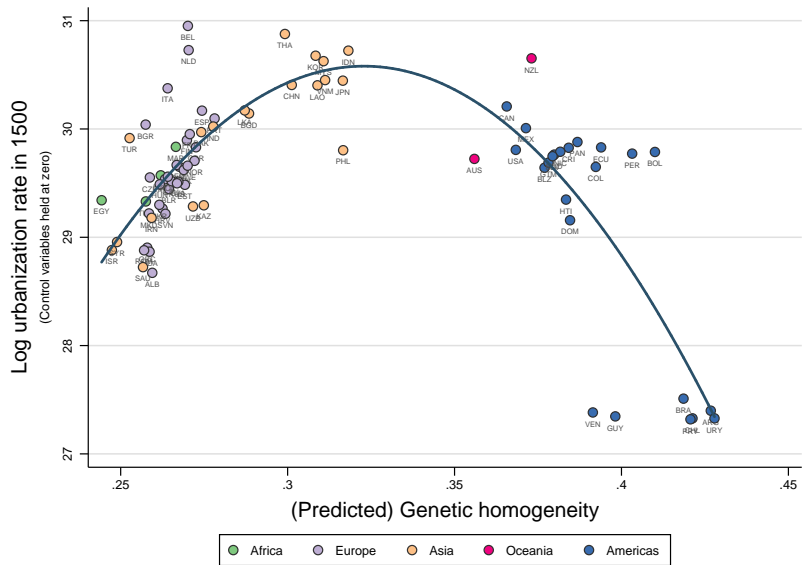


Figure 4: Genetic Diversity and Historical Comparative Development

Notes: This figure depicts the cross-country hump-shaped influence of predicted genetic homogeneity (i.e., 1 minus genetic diversity as predicted by migratory distance from East Africa) on economic development in the year 1500, as reflected by either log population density (Panel A) or log urbanization rate (Panel B), conditional on the timing of the Neolithic Revolution, land productivity, and continent/regional fixed effects. Please refer to Ashraf and Galor (2013a) for additional details.

Sources: Ashraf and Galor (2013a).

factor of 5.4, closing the income gap between the two countries from a ratio of 12:1 to 2.2:1; and (v) decreasing the diversity of Ethiopia to the level prevalent in the United States would increase Ethiopia's per-capita income by a factor of 1.7 and, thus, close the income gap between the two countries from a ratio of 47:1 to 27:1. Further, the level of diversity most conducive to economic development is found to be higher in the contemporary period, relative to the preindustrial era, consistently with the underlying premise that the beneficial effects of diversity are expected to be more pronounced in an increasingly demanding technological environment.

In light of the possibility, however, that income per capita in the modern world could be noisily measured, especially for less-developed economies, Ashraf, Galor and Klemp (2014) establish the hump-shaped influence of diversity on contemporary comparative development as reflected by the cross-country variation in per-capita adjusted nighttime luminosity, measured by satellites from outer space. The scatter plot presented in Panel B of Figure 5 illustrates this pattern, lending further credence to the hypothesis that diversity explains a significant portion of the worldwide variation in contemporary living standards.

More recently, Ashraf, Galor and Klemp (2015) have empirically examined the influence of 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 country-specific characteristics. This research establishes that observed genetic diversity in a worldwide sample of 230 ethnic groups (Pemberton, DeGiorgio and Rosenberg, 2013), as well as predicted genetic diversity (based on migratory distance from East Africa) in a global sample of 1,331 ethnic groups, confers a significant hump-shaped effect on economic prosperity, demonstrating that the variation in genetic diversity across ethnic homelands has contributed to variations in economic development across ethnic groups and regions at the subnational level.<sup>5</sup>

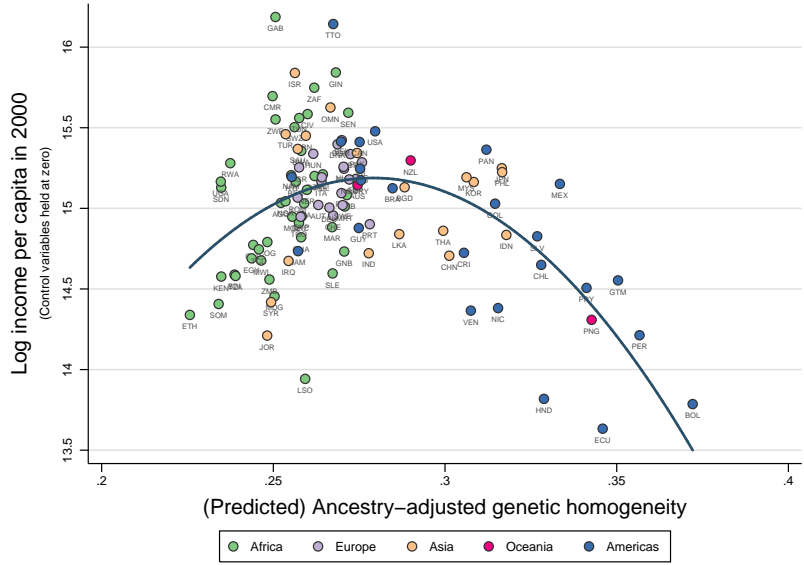
Interestingly, the salience of the trade-off associated with the influence of genetic diversity on productivity has been established even at the microeconomic level. Specifically, exploiting variations across high schools in the state of Wisconsin, Cook and Fletcher (2015) have empirically established that the heterozygosity of the student body of a high school in 1957 confers a significant hump-shaped influence on the average economic performance of the school's graduates later in life, as captured by average net worth in 1992 and in 2004, average income in 1974, average labor force participation between 1957 and 1975, and average job tenure in 1992. Importantly, because these findings are established by exploiting variations within a single state, they are unaffected by cross-country (and even cross-state) confounders. In addition, because the high-school student bodies

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<sup>5</sup>Although the aggregation of the observed genetic diversity of these 230 ethnic groups from the ethnicity level to the country level does not yield a systematic hump-shaped pattern between diversity and historical development in the resulting sample of 38 countries, this finding reflects sample selection bias at the country level. Indeed, in a *globally representative* sample of countries, employing genetic diversity *predicted* by prehistoric migratory distance from East Africa establishes the hump-shaped influence of diversity on either historical or contemporary comparative development. In addition, Ashraf, Galor and Klemp (2015) highlight the hump-shaped influence of observed genetic diversity on economic development *at the ethnicity level* (i.e., exploiting variations across these 230 ethnic groups), and they show that the pattern holds even after accounting for the confounding influence of unobserved time-invariant country-level characteristics.



Panel A



Panel B

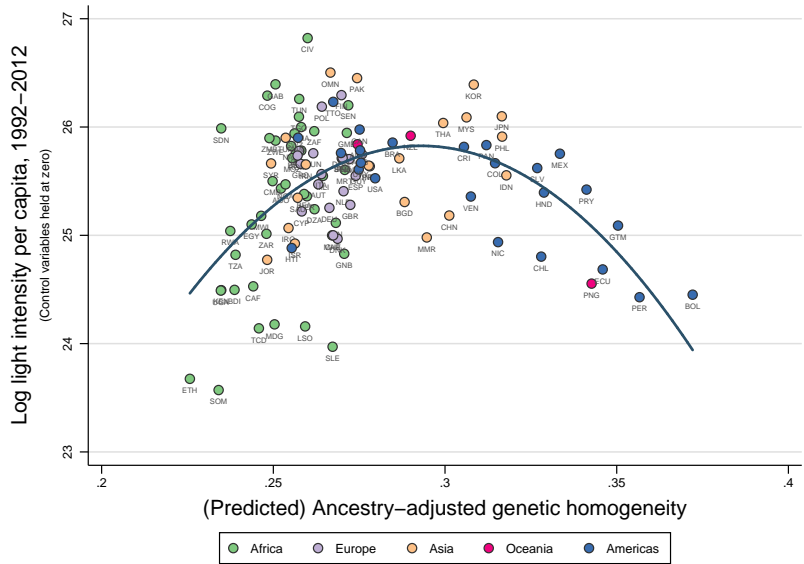


Figure 5: Genetic Diversity and Contemporary Comparative Development

*Notes:* This figure depicts the cross-country hump-shaped influence of ancestry-adjusted genetic homogeneity (i.e., 1 minus ancestry-adjusted genetic diversity) on contemporary economic development, as reflected by either log income per capita in the year 2000 (Panel A) or log light intensity per capita in the 1992–2012 time horizon (Panel B), conditional on the ancestry-adjusted timing of the Neolithic Revolution, land productivity, a vector of institutional, cultural, and geographical determinants of development, and continent/regional fixed effects. Please refer to Ashraf and Galor (2013a) and Ashraf, Galor and Klemp (2014) for additional details.

*Sources:* Ashraf and Galor (2013a) and Ashraf, Galor and Klemp (2014).

in the authors' data set were entirely comprised of individuals of European ancestry, the results are not afflicted by issues of population stratification that could otherwise conflate the influence of heterozygosity with those of ethnicity or ancestral origins on economic outcomes. These findings therefore provide evidence for the robustness of the hypothesized effect of diversity on productivity at a much lower level of aggregation than countries or ethnic groups.

Finally, it has also been shown that migratory distance from the cradle of mankind imparts a reduced-form hump-shaped influence on comparative economic development (Ashraf and Galor, 2013a). Although the reduced-form influence of migratory distance from East Africa appears to operate through its impact on genetic diversity as observed in the HGDP-CEPH sample, it is plausible that migratory distance per se has had a direct hump-shaped impact on economic development, independently of the influence of genetic diversity, potentially reflecting the self-selection of individuals into migration that may have taken place in the course of the demic expansion of anatomically modern humans from Africa.

**Mechanisms** The reduced-form hump-shaped influence of diversity on productivity suggests several potential mechanisms through which diversity can influence economic performance, reflecting various elements of the trade-off between the social costs and benefits of diversity. Ashraf and Galor (2013a) furnish cross-country empirical evidence for two such mechanisms. Specifically, they establish that contemporary genetic diversity imparts (i) a positive influence on innovative activity (as reflected by the average annual number of scientific articles per capita in the 1981–2000 time horizon); and (ii) a negative influence on the degree of social cohesion (as reflected by the prevalence of interpersonal trust in survey data on individual values, collected over the 1981–2008 time period).

Further evidence on some of the mechanisms through which diversity can affect economic prosperity is provided by four other papers in this research program. Bearing in mind that ethnic diversity has been shown to be associated with various dimensions of economic underperformance at the national level (as discussed earlier), the evidence uncovered by Ashraf and Galor (2013b) suggests that prehistorically determined genetic diversity could be an underlying cause of different manifestations of the ethnolinguistic fragmentation of national populations. Specifically, their hypothesis suggests that following the “out of Africa” migration, the initial endowment of genetic 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 of a 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 genetic diversity to the lack of cohesiveness of a group, a larger initial endowment of genetic 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 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, genetic 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 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 prehistoric migratory distance from East Africa as a plausibly exogenous source of variation in contemporary genetic diversity in a global sample of countries.

Civil and other forms of intrastate conflicts are another mechanism through which the genetic diversity of a national population can lead to its economic underperformance. Exploiting cross-country variations, [Arbath, Ashraf and Galor \(2015\)](#) establish that genetic diversity in the contemporary era has been a significant contributor to the emergence, prevalence, recurrence, and severity of civil conflicts over the last half century, conditional on the geographical and institutional correlates of conflict, outcomes of economic development, and unobserved continental characteristics. Importantly, because unlike standard measures of ethnic diversity, genetic diversity captures both intergroup and *intragroup* differences in interpersonal traits, the latter possesses explanatory power for not only interethnic conflicts but *intraethnic* factional conflicts as well. This research additionally demonstrates that genetic diversity can contribute to intergroup conflicts in society potentially through the channels of greater ethnic fragmentation, reduced interpersonal trust, and sharper divergence in preferences for public goods and redistributive policies.<sup>6</sup>

The emergence and persistence of autocratic forms of societal governance is yet another mechanism through which genetic diversity can give rise to contemporary economic underperformance. Specifically, [Galor and Klemp \(2015\)](#) advance the hypothesis and empirically establish that although prehistorically determined genetic diversity triggered the formation of institutions in early human societies that mitigated the adverse influence of diversity on social cohesion, the contribution of diversity to economic inequality and class stratification within societies ultimately reshaped early institutional development towards more extractive and autocratic forms of governance. Exploiting variations across precolonial ethnic homelands, the authors demonstrate that conditional on the potentially confounding effects of various geographical factors and unobserved continental characteristics, genetic diversity imparts a positive influence on the prevalence of precolonial autocratic institutions and that this relationship plausibly reflects the dual impact of diversity on the formation of institutions and the emergence of social stratification. Furthermore, the authors document that the spatial variation in genetic diversity across the globe has contributed to the cross-country

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<sup>6</sup>Relatedly, [Becker, Enke and Falk \(2015\)](#) provide evidence that links the ancient serial founder effect of the “out of Africa” migration with contemporary heterogeneity in risk-taking individual preferences at the national level. The authors additionally document that such heterogeneity in risk attitudes is associated with lower income per capita across countries.

variation in contemporary degrees of autocracy, partly reflecting the persistence of institutional, cultural, and compositional characteristics of populations over time.

Beyond the aforementioned three studies that highlight some of the mechanisms associated with the social costs of genetic diversity, Depetris-Chauvin and Özak (2015) present evidence in support of its social benefits.<sup>7</sup> Motivated by the initial hypothesis that genetic diversity can foster the division of labor in society by widening the spectrum of individual skills, abilities, and cognitive approaches, this research exploits variations across precolonial ethnic homelands to empirically establish that conditional on a wide range of geographical characteristics, prehistorically determined genetic diversity 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 trade. The authors additionally document that present-day populations residing in regions that were characterized by a higher degree of precolonial economic specialization tend to exhibit significantly greater occupational heterogeneity and a higher level of economic development.

**Criticism** Perhaps unsurprisingly, the academic literature on the influence of genetic diversity on comparative development has attracted the attention of the scholarly community beyond the discipline of economics and has generated some controversy. In particular, three criticisms have been raised: (a) the precolonial population data employed for the analysis of historical development are imperfectly measured, and in particular, the population sizes of precolonial Amerindian societies are underestimated; (b) expected heterozygosity in neutral genetic markers, employed to capture the degree of genetic diversity within a population, does not reflect diversity in functional (phenotypic) markers and, therefore, cannot influence behavioral and social interactions; and (c) the findings can be used to justify disturbing policy prescriptions, designed to “engineer” an “optimal” diversity level in a population. As discussed below, however, these criticisms are unfounded.

- (a) Ashraf and Galor’s historical analysis accounts for the possibility that the data on population density in the year 1500 could be afflicted by measurement errors, demonstrating that this issue has no bearing on the validity of their empirical findings. First, population density is the *dependent* variable in their historical analysis, and as such, classical measurement error in this variable does not introduce any bias to 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 their estimates would be even higher. Second, if there are indeed *systematic* differences across continents in the noisy measurement of historical population density (e.g., if

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<sup>7</sup>The beneficial effects of genetic diversity on economic development are also documented empirically by Ager and Brückner (2016). Exploiting variations across counties in the United States in the late nineteenth-century, these authors document that county-level populations that experienced a larger initial increase in their genetic 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. (Forthcoming), the authors exploit panel variations across firms listed in the stock markets of North America and the United Kingdom to demonstrate 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 other measured indices of diversity.

historical population density in the Americas is indeed consistently underestimated), any bias arising from these differences is accounted for by the continent fixed effects in their analysis. Specifically, the influence of diversity on historical development is identified by exploiting intersocietal variations within continents rather than across continents. Third, as illustrated by the scatter plot in Panel B of Figure 4, employing an alternative measure of historical development – namely, the extent of urbanization in the year 1500 (obtained from sources that are entirely independent of the source for historical population density data) – does not qualitatively alter the hump-shaped influence of genetic diversity on historical development. Lastly, and most importantly, issues related to the noisy measurement of historical population density are irrelevant for Ashraf and Galor’s main analysis of *contemporary* comparative development, in which the dependent variable is income per capita in the year 2000.

- (b) Admittedly, expected heterozygosity in neutral genetic markers, employed for the measurement of the degree of genetic diversity within a population, does not directly reflect diversity in functional (phenotypic) markers. Nevertheless, as elaborated in Section 2.1, the observed socioeconomic influence of expected heterozygosity in microsatellites reflects the positive relationship between diversity in microsatellites and intrapopulation heterogeneity in phenotypically and cognitively expressed genomic material. In particular, as is the case with expected heterozygosity in neutral genetic markers, evidence suggests that migratory distance from East Africa imparts a negative influence on and various forms of intragroup morphological and cognitive diversity (Henn, Cavalli-Sforza and Feldman, 2012), including intralingual phonemic diversity, as well as interpersonal diversity in skeletal features pertaining to cranial characteristics, dental attributes, and pelvic traits.
- (c) As elaborated in the following section on policy implications, the view that Ashraf and Galor’s research can be used to justify disturbing policy prescriptions is heavily distorted by the fact that it completely disregards the proximate mechanisms through which genetic diversity affects economic outcomes. Indeed, there exists a far more nuanced view of the possible broader implications for economic policy from this research.

**Policy Implications** Ashraf and Galor’s analysis establishes a fundamental trade-off associated with the influence of genetic diversity on economic performance: diversity can stimulate specialization and innovative activity, but it can also diminish social cohesion. The fact that genetic diversity has been a deep *determinant* of economic development, however, does not imply that the genetic composition of a population governs its economic *destiny*. The influence of diversity on productivity reflects both genetic and cultural components, implying 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.

The controversy over the implications of Ashraf and Galor’s findings has focused on their assertion that intermediate levels of genetic diversity tend to be most conducive to economic

development, thereby leading uninformed critics to suggest that their work could be used to justify the forcible movement or “engineering” of populations. This viewpoint, however, disregards Ashraf and Galor’s key argument that the influence of diversity on development operates through various proximate mechanisms, and as such, if there are indeed any reasonable implications for policymaking from their work, it is that policies should be aimed at conditioning these intervening channels. Specifically, 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 cultural values of tolerance needed in overly diverse societies, and it can also promote cultural receptiveness to different types of productivity-enhancing knowledge that may be lacking in overly homogenous societies.

### **3.2 Human Evolution and Long-Run Economic Growth**

The effect of the economic environment on the evolution of human traits and the contribution of this evolutionary process to long-run economic development has 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 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 traits in the population over time contributed to the process of development, the pace of the transition from stagnation to growth, and comparative economic development across societies.

In line with the evidence discussed in Section 2.2, regarding human evolutionary adaptations since the onset of the Neolithic Revolution, this research additionally suggests that due to the egalitarian nature of hunter-gatherer societies, the forces of evolutionary selection within a society were 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, subsequently reinforced the association between parental income and reproductive success and, thus, amplified the pace of these evolutionary processes (Galor and Moav, 2002).

Subjecting hypothetical evolutionary processes to the scrutiny of evolutionary growth models, 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 and economic development. In particular, these studies have highlighted the selection of innate preferences for quality rather than quantity of offspring (Galor and Moav, 2002), resistance to infectious diseases (Galor and Moav, 2007), human body size (Lagerlöf, 2007), predisposition towards entrepreneurial

spirit (Galor and Michalopoulos, 2012), time preference (Galor and Özak, 2014), lactase persistence (Cook, 2014), and conspicuous consumption (Collins, Baer and Weber, 2015).<sup>8</sup>

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 predispositions towards the quality rather than 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 that ultimately triggered the demographic transition and brought about a state of sustained economic growth. The quantitative analysis of Collins, Baer and Weber (2014) confirms this hypothesis.

An empirical test of the hypothesis advanced by Galor and Moav (2002) has recently been conducted by Galor and Klemp (2014). Using an extensive data set of genealogical records for nearly half a million individuals in Quebec between the 16th and 18th centuries, their study establishes that moderate fecundity, and thus predisposition towards investment in child quality, was conducive for long-run reproductive success, reflecting the negative influence of higher fecundity on the survivability, marital age, and education of each offspring. The finding lends credence to the hypothesis that during the Malthusian epoch, natural selection favored individuals with lower fecundity and greater predispositions towards child quality, thus contributing to human capital formation, the demographic transition, and the transition from stagnation to growth.

The evolutionary origins of worldwide variations in the resistance to infectious diseases, as well as their implications for comparative development, have been examined by Galor and Moav (2007). This research hypothesizes and empirically establishes that the socioeconomic transformations associated with the Neolithic Revolution triggered an evolutionary process that imparted positive selective pressures on the resistance to infectious diseases. 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, significantly shaped the contemporary global distribution of human longevity. In a related paper, Cook (2015) further links this evolutionary process to the degree of intrapopulation genetic diversity in the human leukocyte antigen (HLA) system.

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 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

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<sup>8</sup>It may be noted that the interaction between human evolution and the process of development, as emphasized by this literature, is applicable to either cultural or genetic propagation mechanism for the intergenerational transmission of individual traits (Weibull and Salomonsson, 2006; Bisin and Verdier, 2011; Bowles and Gintis, 2011; Robson and Samuelson, 2011; Doepke and Zilibotti, 2014).



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 coevolution of subsistence consumption, the ability to engage in efficient and diversified food procurement strategies, and the process of development has also been examined by this line of research. Specifically, Lagerlöf (2007) has argued that resource depletion associated with technological progress and rising population density during the Malthusian epoch generated 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. In addition, Cook (2014) has provided empirical evidence documenting that heterogeneity across regions in the contemporary prevalence of the lactase persistence trait is positively associated with differences in the level of precolonial economic development, presumably reflecting the reproductive success and the productivity-enhancing benefits associated with this post-Neolithic adaptation that confers the ability of digest milk into adulthood.<sup>9</sup> Furthermore, Collins, Baer and Weber (2015) have argued that female mating preferences increased the reproductive success of males predisposed to engage in conspicuous consumption in order to credibly signal their quality, and because conspicuous consumption is funded through increased participation in the labor force, the increase in the prevalence of signaling males in the population gave rise to an increase in economic activity that contributed to long-run economic growth.

Finally, Galor and Özak (2014) have explored the evolutionary origins of the contemporary distribution of time preference across regions. They advance the hypothesis and empirically establish that geographical variation in the natural return to agricultural investment has had a persistent effect on the distribution of time preference across societies. In particular, exploiting a natural experiment associated with the expansion of suitable crops for cultivation in the course of the Columbian Exchange, these authors establish that preindustrial agro-climatic characteristics that were conducive to higher returns from agricultural investment, triggered selection and learning processes that have had a persistent positive effect on the prevalence of long-term orientation.

## 4 Summary and Critique of Wade's Book

### 4.1 Overview

Wade hypothesizes that heterogeneity across regions in the duration of selective pressures on genetic traits, potentially associated with the social behaviors of nonviolence, cooperation, and thrift, gave rise to interregional variation in the nature of institutions and has therefore been a major driving force in comparative economic development. Specifically, he posits that European and East Asian societies are genetically predisposed for economic success, and it is the genetically determined unsuitability of African societies to adopt market-friendly Western institutions that

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<sup>9</sup>The long-run codetermination of human physiology and economic development is explored further by Dalgaard and Strulik (2015, Forthcoming).

drives comparative development across regions.<sup>10</sup> Despite being transparent about the speculative nature of his theory, Wade boldly makes some remarkable assertions: “When North Korea adopts market-friendly institutions, a safe prediction is that it would in time become as prosperous as South Korea. It would be far less safe to predict that Equatorial Guinea or Haiti needs only better institutions to attain a modern economy; their people may not have yet had the opportunity to develop ingrained behaviors of trust, nonviolence and thrift that a productive economy requires” (p. 188).<sup>11</sup>

Wade suggests that economic differences across racial categories, which he classifies along continental lines, ultimately arose from deeply rooted differences in genetically driven social behavior. He argues that his definition of race is “pragmatic,” reflecting his proposition that differences in genetic traits across continents are central to understanding the origins of comparative development: “history has little coherence when analyzed in terms of individuals or even nations. But when seen in terms of the institutions developed by different civilizations and races, the outline of a logical development emerges” (p. 134). Although it is conceivable that gene-culture coevolution has had a major influence on comparative development across societies, it is highly speculative that race in general, and Wade’s classification of race in particular, is the right unit of analysis for understanding the interrelationship between human evolutionary processes and comparative development.

There are several components in Wade’s theory of comparative development, many of which suffer from a lack of credible scientific foundations. First, as Wade acknowledges, there is currently no scientific consensus regarding the extent to which the key behavioral traits of nonviolence, cooperation, and thrift are genetically determined. Second, he provides no tangible evidence on how variations across societies in their geographical setting or historical experience could have given rise to differential selective pressures on these traits and, thus, generated variation in the growth-promoting genetic makeup of their populations.<sup>12</sup> Third, although plausible a priori, there is little evidence to support the claim that the variation in institutions across societies is driven by differences in their endowment of specific genetic traits that might govern key social behaviors (as opposed to differences in the interpersonal *diversity* of traits). Finally, Wade’s assertion that the variation in institutions across societies must be rooted in differences in their endowment of favorable genetic traits is simply based on the observation that a society’s institutions tend to be

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<sup>10</sup>For example, Wade states: “The fact that China, Japan and South Korea developed modern economies so easily, once the appropriate institutions were in place, is evidence that their populations, like those of Europe, had undergone equivalent behavioral changes to those documented in England” (p. 178). At times, however, Wade appears to make somewhat contradictory statements, emphasizing potential genetic differences between East Asians and Europeans that favor Europeans in comparative development. Specifically, he suggests that European societies are genetically more predisposed to “openness to new ideas,” whereas in parts of Asia, excessive conformity may be a genetic trait that was selected for through the civil service examination system (pp. 166, 218).

<sup>11</sup>All unattributed page references throughout the text are to Wade (2014).

<sup>12</sup>As discussed in Section 3.2, the academic literature on human evolution and economic growth provides a more nuanced perspective on the positive selection of long-run growth-promoting traits during the Malthusian era (e.g., Galor and Moav, 2002, 2007; Galor and Michalopoulos, 2012; Galor and Özak, 2014).

highly persistent over time, but this proposition disregards the role of cultural persistence and the well-documented role of economic incentives in generating institutional persistence.<sup>13</sup>

In an important deviation from the academic literature on human evolution and the process of development, Wade additionally assumes that the socioeconomic ramifications of cultural and genetic evolution are conceptually separable, an assumption that runs contrary to long-standing research from the fields of evolutionary anthropology and population genetics that has emphasized the notion of gene-culture coevolution (e.g., Cavalli-Sforza and Feldman, 1981; Boyd and Richerson, 1985; Durham, 1991; Henrich and McElreath, 2003). Unfortunately, Wade’s overarching emphasis on the role of genetic traits in comparative development leads him to make some unsubstantiated claims regarding gene-culture separability.

## 4.2 Evolutionary Processes during the Malthusian Epoch

A significant portion of Wade’s book is devoted to discussing the evidence on recent human adaptive evolution. Wade’s general narrative on human evolution and economic development echoes earlier economic research, surveyed in Section 3.2, which demonstrates the interaction between human evolution and the process of economic development.

Wade proposes an evolutionary theory of comparative economic development, highlighting regional variation in the intensity of positive selection of individual traits that are conducive to growth-enhancing institutions. In line with the insights established by Galor and Moav (2002), and consistent with evidence on evolutionary processes triggered by the Neolithic Revolution, Wade focuses on selection during the Malthusian stage of economic development and plausibly argues that natural selection favored growth-enhancing traits during this era when richer individuals enjoyed higher reproductive success than poorer ones, thereby increasing the representation of their traits in the population over time.<sup>14</sup> In addition, echoing earlier arguments by Galor and Moav (2002), Wade posits that due to the egalitarian nature of hunter-gatherer societies, the forces of evolutionary selection within a society were likely to have been muted prior to the onset of the Neolithic Revolution.

In contrast to the existing literature on human evolution and economic growth, however, Wade’s narrative relies on unsubstantiated selection mechanisms.<sup>15</sup> Rather than subjecting his hypothesized mechanism to the scrutiny of evolutionary growth theory, Wade follows the speculative supposition of Clark (2007), merely positing that in historically densely populated regions of the world that were characterized by early statehood, there existed a class of rich elites, endowed with genetic traits conducive to growth-enhancing institutions, whose evolutionary advantage increased

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<sup>13</sup>In addition, although institutions are indeed widely considered to be a fundamental determinant of development, their sole primacy over other fundamental determinants has not been established in the academic literature on comparative development.

<sup>14</sup>It is important to note, however, that in contrast to Wade’s theory, the intergenerational transmission of behavioral traits in evolutionary growth theory could be the result of cultural rather than purely genetic propagation mechanisms.

<sup>15</sup>Unfortunately, Wade’s theory appears unaware of most of the literature on the topic, and his approach not only remains atheoretical but also leaves key elements of the selection process unspecified.

the prevalence of these traits in the populations of those regions over time. Importantly, unlike traits associated with entrepreneurial spirit and preferences toward offspring quality that have been shown to be subject to positive selection during the Malthusian era, the traits that are central in Wade’s argument (e.g., nonviolence, cooperation, and thrift) need not necessarily generate higher incomes in a Malthusian environment and, thus, may not necessarily lead to higher reproductive success. In particular, in the violent society of medieval England (p. 167), it is quite possible that pacifism and trust would have hindered rather than promoted individual wealth accumulation and, thus, would not have been favored by the forces of natural selection. In addition, although thrift is generally considered to be a virtue that leads to economic gains via the return to capital accumulation, in a Malthusian world, refraining from having more children is an important aspect of thrift, and it may therefore undermine the strength of the selection process. It is also far from evident why the rich elites in a society would have initially possessed the traits of cooperation and nonviolence in higher degrees than the rest of the population.

Subjecting hypothetical evolutionary processes to the scrutiny of evolutionary growth theory, which could detect why certain traits made individuals richer and, therefore, why these traits generated higher reproductive success, is essential to identifying the traits that could have been positively selected (genetically or culturally) during the Malthusian stage of economic development. Proper theoretical foundations can also illuminate what one should expect to occur once Malthusian constraints are relaxed in the transition from the epoch of stagnation in income per capita to the modern regime of sustained economic growth. In particular, the rigorous models of evolutionary growth theory have suggested that traits associated with higher evolutionary fitness during the Malthusian era may place individuals at a disadvantage once societies emerge into the modern growth regime (Galor and Moav, 2002, 2007; Galor and Michalopoulos, 2012).

### 4.3 The Biological Basis of Race

Wade argues that there exists a biological underpinning to his “five-race, continent-based” classification of populations (p. 98). Citing evidence from the field of population genetics that genetic traits tend to be clustered at the continent level to a greater degree than would be predicted purely by the “out of Africa” migration process (and the associated serial founder effect), Wade asserts that “[a]t least at the level of continental populations, races can be distinguished genetically, and this is sufficient to establish that they exist” (p. 122).<sup>16</sup> Even if one were to accept Wade’s interpretation of the genetic evidence, the spatial analysis of the potential clustering of genetic traits across different regions of the world is not sufficiently refined to support Wade’s crude five-race model. Nevertheless, the fragility of the evidence does not inhibit him from arguing that “the five-race, continent-based scheme seems the most practical for most purposes” (p. 98).

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<sup>16</sup>It is beyond the scope of this review to discuss and evaluate the specifics of the genetic evidence that Wade purportedly exploits, although it may be noted that population geneticists have argued that this evidence has been misrepresented (see, e.g., Coop et al., 2014; Balter, 2014).

Wade’s argument, however, raises an important concern. Specifically, it appears that Wade’s definition of race is implicitly based on differences in socioeconomic *outcomes* rather than on purely biological underpinnings. Wade believes that human history and comparative development are best understood in the context of five major races, and he therefore simply appeals to the “practicality” of this division – along with potentially fragile evidence – to justify his classification scheme. Thus, the unit of analysis itself (i.e., race) in Wade’s conceptual framework is nonrandom, as it is *chosen* based on the ex post realization of outcomes (i.e., contemporary institutions and economic prosperity) that his theory is attempting to explain. The methodology of Wade’s classification of race therefore implies that his theory of comparative development – speculative as it may be – is marred by endogeneity bias and is unable to conceptually disentangle cause from effect.

#### 4.4 The Causes of Institutional Variation

Wade’s modified evolutionary theory of comparative economic development suggests that variation in the selection of genetic traits across regions forms the basis of differences in social behaviors across racial groups, thereby shaping the variation in the nature of institutions and, thus, in long-run development outcomes across the globe. There is little evidence, however, to support the claim that the variation in institutions across societies is driven by differences in their endowment of specific genetic traits that might govern social behaviors. Further, Wade’s assertion that institutional variation across societies must be rooted in differences in their endowment of favorable genetic traits, based on the observation that a society’s institutions tend to be highly persistent over time, disregards the role of cultural persistence and the well-documented role of economic incentives in shaping institutional persistence. Moreover, in contrast to Wade’s theory, existing findings in the economics literature support the contribution of the interpersonal *diversity* of traits (rather than the *prevalence* of any *specific* traits) within a society to the emergence and persistence of institutions (Galor and Klemp, 2015).

**Incentives** In his narrative on the causes and consequences of institutional variations, Wade refers to the view of Acemoglu and Robinson (2012) that institutions are central amongst the deep determinants of comparative development. Acemoglu and Robinson have argued that a society’s political elites harbor the incentive to propagate extractive institutions over time, in order to sustain and benefit from existing structures of economic and political inequality. Thus, as long as the socioeconomic environment does not alter the incentives of the elites, institutions may persist over a long period of time, and variations in institutions across societies and over time can only arise from “critical junctures,” when an exogenous event alters this path. Although Wade acknowledges the fundamental importance of institutions for economic development, he disregards the role of economic incentives in generating institutional persistence, arguing that Acemoglu and Robinson’s framework is largely unsatisfactory because it relies on the “luck” associated with historical accidents to explain differential institutional dynamics and, thus, comparative development across societies.

Wade’s rejection of Acemoglu and Robinson’s emphasis on historical contingencies, however, is not a credible justification for disregarding the role of economic incentives in shaping differential paths of institutional evolution across societies. Specifically, as highlighted by research in the area of unified growth theory (Galor, 2011), institutional change in a society may emerge as a natural by-product of the process of industrialization, even without appealing to the incidence of “critical junctures.” In particular, Galor and Moav (2006) have argued that physical capital accumulation in the process of industrialization enhanced the importance of human capital in the production process and, thereby, generated incentives for capitalists to support the provision of public education for the masses, triggering the emergence of human capital promoting institutions. Further, Galor, Moav and Vollrath (2009) have suggested that inequality in the distribution of landownership adversely affected the advent of human capital promoting institutions and, thus, the pace of the transition from an agricultural to an industrial economy. Wade’s unjustified dismissal of other plausible determinants of institutional variation across societies, leaving the arena open to only genetic underpinnings, undermines a crucial building block of his proposed theory of comparative development.

**Culture** The “dual inheritance theory” of gene-culture coevolution suggests that it is inherently challenging, if not impossible, to disentangle the influence of genes and culture on institutions.<sup>17</sup> As Wade himself notes, the concern regarding gene-culture separability is further complicated by the lack of scientific evidence directly linking genes to specific social behaviors: “[w]ithout knowing the nature of genes involved in social behavior, it’s impossible at present to disentangle the respective roles of culture and genetics in shaping social institutions” (p. 124).<sup>18</sup>

Wade nevertheless diminishes the potential for culture to impart a major influence on institutions, independently of genetic traits. In particular, Wade states that “[i]f running a productive, Western-style economy were simply a matter of culture, it should be possible for African and Middle-Eastern countries to import Western institutions and business methods, just as East Asian countries have done. But this is evidently not a straightforward task” (p. 177). Wade’s dismissal of the importance of the cultural channel in institutional development is based on two assertions: first, institutional persistence is much too protracted to be explained by culture, and second, the transfer of institutions across societies would have been more prevalent if they were indeed based solely on culture.

Although Wade acknowledges that cultural traits can influence a society’s institutions, he maintains that given the persistence of both institutions and genetic traits, the foundation of institutions can be traced primarily to genetics. For instance, he states that “when a civilization produces a distinctive set of institutions that endures for many generations, that is the sign of a

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<sup>17</sup>For the purposes of the present discussion, culture is viewed as the particular set of society’s norms, values, beliefs, and preferences that arise from repeated social interactions amongst individuals and that can persist over time through purely “memetic” as opposed to genetic propagation, although the two transmission mechanisms are clearly highly correlated.

<sup>18</sup>Although conclusive evidence on the extent to which social behaviors are determined by genes is largely elusive, Wade appeals to studies that have linked the oxytocin hormone and the MAO-A inhibitor gene to cooperative and aggressive individual behavior, respectively (e.g., De Dreu, 2012; Beaver et al., 2013).



supporting suite of variations in the genes that influence human social behavior” (p. 150). This argument implicitly assumes that cultural traits cannot exhibit long-term persistence, in contrast to the views of prominent scholars in the social sciences. For instance, Weber (1930) argued that Protestantism and its emphasis on material rewards contributed to the emergence of modern capitalism in Western societies, and Putnam (1993) suggests that idiosyncratic differences between the medieval histories of Northern vs. Southern Italy led to a divergence in the degree of social capital that persists to the modern era.

Wade further suggests that in light of existing barriers to the transfer of institutions across societies, culture cannot be a fundamental cause of institutions. He states: “[o]ne indication of such a genetic effect is that, if institutions were purely cultural, it should be easy to transfer an institution from one society to another” (p. 126). This view, however, underestimates the substantial coordination problem associated with cultural change – namely, the possibility that the set of norms, values, beliefs, and preferences in a given society may prevent the *de facto* adoption of culture and institutions from other societies in the first place.<sup>19</sup>

#### 4.5 Comparative Development

Wade’s theory of comparative development suggests that regional variation in the length of exposure to the forces of evolutionary selection gave rise to variation across societies in their endowment of genetically determined behavioral traits that are conducive to growth-enhancing institutions. Since the forces of natural selection were largely muted in egalitarian hunter-gatherer societies, this selection process became fortified only after the transition to sedentary agriculture, and as such, the time elapsed since a society (or region) experienced the Neolithic Revolution governs the length of its exposure to evolutionary processes associated with the positive selection of favorable behavioral traits. In particular, since Europe and Asia are both characterized by a long history of settled societies, Wade hypothesizes that societies in these regions have come to harbor the genetic makeup conducive to the development or adoption of growth-enhancing institutions, in contrast to societies in Sub-Saharan Africa.

Rather than proposing that variation across societies in their endowment of genetic traits is the *singular* cause of comparative development, Wade offers a multilayered approach in which development occurs only when societies with the “proper” genetic predisposition actually implement growth-promoting institutions. In particular, Wade argues that unlike Africa, East Asia experienced economic growth and development since the mid-twentieth century because of their genetically determined ability to adopt market-friendly institutions from the West. This argument, however, is based on the *existing* distribution of institutions across societies rather than underlying forces that brought about this realization. Specifically, Wade hypothesizes that African societies are unable to adopt growth-enhancing institutions based on the observation that they have not adopted them,

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<sup>19</sup>In contrast to the dominant view in the social and economic sciences regarding the (non)transferability of culture and institutions across societies, when discussing the causes of income disparities across the globe, Wade states that “in situations where culture and political institutions can flow freely across borders, long enduring disparities are harder to explain” (p. 13).



but this flawed reasoning implies that any society that has not yet adopted virtuous institutions is necessarily unable to adopt them. In addition, Wade’s conjectures are based on the supposition that societies are generally willing to unilaterally adopt virtuous institutions (but are often unable to do so because of inappropriate genetic predispositions), disregarding the incentives of those with economic and political power in society to block institutional reform.

Finally, although Wade’s main argument focuses on the shared genetic predisposition of Europeans and East Asians to develop or adopt market-friendly institutions (due to a higher prevalence of traits associated with nonviolence, cooperation, and thrift), he highlights a secondary level of differentiation between European and East Asian societies. In particular, Wade argues that East Asian societies have not been genetically predisposed towards “openness to new ideas,” which led to differential paths of historical development between Europe and East Asia (pp. 217–218). For instance, he suggests that China’s long history of civil service examinations exerted positive selection pressures on traits like “excellent memory, high intelligence and unwavering conformity” (p. 166). Of course, commonality between European and East Asian societies in their length of exposure to evolutionary pressures does not necessarily imply commonality in their set of selected traits, but this differentiation appears to run counter to Wade’s argument that East Asians are genetically predisposed towards adopting growth-enhancing institutions, especially because he stresses “openness to new ideas” as a key characteristic of such institutions.

Regardless of the speculative nature of Wade’s overall theory of comparative development, or the fragility of its individual building blocks, the credibility of his thesis as a scientific proposition boils down to whether it is empirically falsifiable. In this respect, the fact that Wade’s theory emphasizes intercontinental differences (based on his classification of race) implies that the theory does not lend itself well to falsification. Setting aside the endogeneity of his classification scheme, the existence of only five data points (one for each continent), does not provide the necessary statistical degrees of freedom to properly account for the confounding influence of cross-continental heterogeneity in various geographical and historical forces that could have affected both the genetic makeup of societies and their economic development.

Nevertheless, Wade’s narrative that economic disparities across societies may emerge from slight variations in social behaviors that result from differential selective pressures and location-specific genetic adaptations permits a falsification test of his theory based on cross-*national* variations (possibly within continents) in economic development and the genetic makeup of populations. Such a setup would possess the key advantage of exploiting a much larger sample size, providing the statistical degrees of freedom necessary to account for the potentially confounding influence of heterogeneity in a wide variety of geographical and historical factors, and perhaps most importantly, in other aspects of the macrogenetic structure of human populations – like the degree of genetic diversity *within* populations – that were partly codetermined with the extent of genetic differentiation *between* populations during the prehistoric “out of Africa” diffusion of anatomically modern humans.

## 5 The Impact of Genetic Diversity vs. Genetic Distance to the Frontier: A Falsification Test

Wade’s theory of comparative development suggests that economically more advanced contemporary societies possess a larger endowment of genetic traits associated with social behaviors that are conducive to economic development. To the extent that the measure of  $F_{ST}$  genetic distance between any pair of contemporary populations (as discussed in Section 2.1) can serve as a reasonable metric of the difference in their endowment of such traits, an empirically falsifiable prediction of Wade’s theory is that poorer contemporary societies should be characterized by a greater  $F_{ST}$  genetic distance to the societies that happen to occupy the frontier of economic development in the modern world, reflecting the smaller endowment of favorable traits in less-developed societies. Moreover, insofar as genetically determined individual predispositions are empirically separable from the influence of culture on associated social behaviors, any credible falsification test of Wade’s theory of economic development would need to account for the confounding influence of cultural distance (as proxied by linguistic and religious distances) to the economic frontier.

Accounting for the influence of cultural distance is particularly important in light of the fact that the  $F_{ST}$  genetic distance between any pair of populations partly reflects the time elapsed since they diverged from a common ancestral population during the prehistoric spatial expansion of humans “out of Africa,” and as such, it is expected to be highly correlated with the extent of cultural divergence that arises from the forces of “cultural drift” and “isolation by distance” between the two populations (Cavalli-Sforza, Menozzi and Piazza, 1994). Critically, however, because the worldwide variations in intrapopulation genetic diversity and interpopulation genetic distance were partly *codetermined* by the prehistoric “out of Africa” migration process, a credible empirical assessment of Wade’s theory cannot be made independently of the hump-shaped influence of genetic diversity on development, as established by Ashraf and Galor (2013a). Needless to say, such an assessment also ought to account for the potentially confounding influence of various geographical characteristics and historical forces that could have shaped both the process of economic development and the macrogenetic structure of societies since the completion of the “out of Africa” expansion.

This section presents the results from a regression analysis of Wade’s theory of comparative development. The analysis exploits contemporary variations across national populations in income per capita, genetic diversity, genetic distance to the economic frontier, and various geographical, historical, and cultural correlates of economic development (including cultural confounders of genetic diversity and of genetic distance to the frontier) to test whether patterns consistent with Wade’s theory exist in the cross-country data, while accounting for the hump-shaped influence of genetic diversity on economic development.

Before proceeding to the results from this analysis, it is worth mentioning that there exists precedence in the literature on long-run economic development of applying data on interpopulation  $F_{ST}$  genetic distances, in the form of contributions by Spolaore and Wacziarg (2009, 2013). These authors have employed  $F_{ST}$  genetic distance as a proxy measure of the extent of divergence between two populations in intergenerationally transmitted (cultural and/or biological) traits to emphasize

a *barrier effect*. In this view, societies that have experienced greater divergence from one another over time are less likely to have adopted or implemented institutions and technologies that share common features, thus generating *persistence* in their comparative development, without necessarily determining the *origins* of this comparative performance. This notion is conceptually distinct from a *direct effect* imparted by the difference in genetic traits between populations on their comparative economic performance, which is the interpretation espoused by Wade’s theory and, thus, by the current strategy of exploiting genetic distance to the economic frontier to test Wade’s conjecture regarding the origins of comparative development.<sup>20</sup>

Table 1 reports the results from examining the influence of genetic distance to the economic frontier versus the hump-shaped influence of genetic diversity on contemporary comparative development, while accounting for the potentially confounding effects of various geographical, historical, and cultural forces.<sup>21</sup> The analysis considers four variations on the definition of the world economic frontier, including the population of (i) the United States (Columns 1–2); (ii) the United Kingdom (Columns 3–4); (iii) the representative Western European or Western “offshoot” nation (Columns 5–6); and (iv) the representative member nation of the OECD, including member nations from East Asia and Latin America. For each of these variants, two separate regression models are estimated to assess the explanatory power of genetic diversity vs. genetic distance to the frontier for the cross-country variation in the standard of living. The first model accounts for the potentially confounding effects of cultural distance (proxied by linguistic and religious distances) to the frontier; unobserved factors associated with being a previous European colony or possessing a particular legal origin (e.g., British common law vs. French civil law); and geographical characteristics (i.e., absolute latitude, agricultural suitability, terrain ruggedness, distance to the coast, temperature, precipitation, shares of land in tropical and temperate climatic zones, disease prevalence, and unobserved factors associated with being landlocked or being a small island). The second model is conditioned to additionally account for the potentially confounding effects of various forms of cultural diversity, including measures of fractionalization across groups in the national population, differentiated by ethnic, linguistic, and religious markers. All models are estimated using the ordinary least squares estimator, and they additionally account for unobserved heterogeneity at the regional level, implying that the analysis only exploits cross-country variations *within* world regions.

As is apparent from the results reported in Table 1, regardless of the definition of the world economic frontier or the set of covariates included in the specification, genetic diversity confers a highly significant and quantitatively robust hump-shaped influence on income per capita, whereas

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<sup>20</sup>The ex post absence of a direct effect of genetic distance to the economic frontier on comparative development across countries in the current analysis does not contradict the presence of a barrier effect of pairwise genetic distance on pairwise differences in economic outcomes across population pairs, as demonstrated empirically by the work of Spolaore and Wacziarg.

<sup>21</sup>The data on income per capita for the 2000–2009 time period is from version 8.1 of the Penn World Table (Feenstra, Inklaar and Timmer, 2015), whereas the data on genetic, linguistic, and religious distances are sourced from Spolaore and Wacziarg (2016). The data for all other variables in the analysis in Table 1 are based on the data sets constructed by Ashraf and Galor (2013a,b). The size of the cross-country sample is conditioned by the availability of data on all the variables considered by the analysis in Table 1.

TABLE 1: The Impact of Genetic Diversity vs. Genetic Distance to the Frontier on Comparative Development

	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)
	Log of the average annual real GDP per capita, 2000–2009							
	United States as the global frontier		United Kingdom as the global frontier		Mean “Western” nation as the global frontier		Mean OECD nation as the global frontier	
Genetic diversity	284.779*** (80.508)	299.374*** (82.710)	289.081*** (81.120)	296.325*** (82.002)	281.941*** (82.822)	307.484*** (84.966)	259.092*** (85.361)	285.992*** (88.979)
Genetic diversity squared	-200.594*** (58.289)	-213.209*** (59.678)	-203.329*** (58.652)	-211.081*** (59.100)	-199.153*** (59.895)	-219.301*** (61.257)	-183.194*** (61.618)	-204.178*** (64.041)
Genetic distance to the global frontier	2.543 (2.256)	1.368 (2.177)	1.974 (1.882)	0.919 (1.798)	2.857 (2.274)	1.621 (2.200)	3.532 (2.408)	2.410 (2.343)
Linguistic distance to the global frontier	0.134 (0.592)	0.869 (0.636)	0.751 (0.743)	1.372* (0.722)	-1.595 (1.649)	0.344 (1.800)	-3.313* (1.982)	-1.475 (2.160)
Religious distance to the global frontier	-1.440** (0.717)	-1.391* (0.720)	-1.386 (0.946)	-1.406 (0.937)	-1.732** (0.821)	-1.712** (0.845)	-1.721** (0.838)	-1.720* (0.876)
Absolute latitude	-0.007 (0.014)	-0.007 (0.014)	-0.010 (0.015)	-0.008 (0.014)	-0.005 (0.015)	-0.007 (0.014)	-0.002 (0.016)	-0.004 (0.015)
Agricultural suitability	-0.742** (0.345)	-0.878** (0.363)	-0.788** (0.355)	-0.933** (0.372)	-0.672* (0.350)	-0.819** (0.363)	-0.676* (0.342)	-0.794** (0.353)
Terrain ruggedness	-0.001* (0.001)	-0.001* (0.001)	-0.001* (0.001)	-0.001* (0.001)	-0.001* (0.001)	-0.001* (0.001)	-0.001* (0.001)	-0.001* (0.001)
Distance to coast	-0.438* (0.233)	-0.383 (0.231)	-0.486** (0.229)	-0.412* (0.224)	-0.443* (0.232)	-0.386* (0.231)	-0.413* (0.230)	-0.365 (0.232)
Mean monthly temperature	-0.498 (2.069)	0.725 (2.153)	-0.619 (2.070)	0.716 (2.166)	-0.101 (2.108)	0.938 (2.166)	0.338 (2.153)	1.313 (2.219)
Mean monthly precipitation	-0.184 (0.206)	-0.242 (0.209)	-0.222 (0.207)	-0.263 (0.207)	-0.162 (0.208)	-0.226 (0.210)	-0.147 (0.209)	-0.197 (0.210)
Percent land in tropical and subtropical climates	-0.495* (0.253)	-0.497* (0.253)	-0.508** (0.253)	-0.488* (0.254)	-0.533** (0.255)	-0.512** (0.253)	-0.524** (0.261)	-0.525** (0.255)
Percent land in temperate climates	0.478* (0.261)	0.423 (0.271)	0.514* (0.267)	0.438 (0.278)	0.450* (0.260)	0.413 (0.269)	0.402 (0.257)	0.378 (0.264)
Disease richness	-0.000 (0.006)	-0.003 (0.006)	0.000 (0.006)	-0.003 (0.006)	0.002 (0.006)	-0.001 (0.006)	0.002 (0.005)	-0.000 (0.006)
Ethnic fractionalization		-0.192 (0.392)		-0.244 (0.399)		-0.187 (0.379)		-0.201 (0.373)
Linguistic fractionalization		-0.106 (0.320)		-0.098 (0.326)		-0.090 (0.303)		-0.044 (0.296)
Religious fractionalization		1.013*** (0.322)		1.068*** (0.323)		0.964*** (0.320)		0.912*** (0.315)
Regional fixed effects	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes
Landlocked and small island fixed effects	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes
Colonial history and legal origin fixed effects	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes
Observations	127	127	127	127	127	127	127	127
Partial $R^2$ of genetic diversity	0.136	0.159	0.135	0.152	0.129	0.157	0.107	0.133
Partial $R^2$ of genetic distance	0.011	0.003	0.009	0.002	0.014	0.005	0.019	0.009
Partial $R^2$ sum of all distance measures	0.045	0.049	0.037	0.051	0.063	0.051	0.073	0.056
Adjusted $R^2$	0.795	0.809	0.791	0.807	0.797	0.810	0.801	0.813

*Notes:* The analysis in this table exploits cross-country variations to establish that although genetic diversity confers a hump-shaped influence on economic development, the influence of genetic distance to the global economic frontier is statistically indistinguishable from zero, conditional on the potentially confounding effects of cultural distance (as proxied by linguistic and religious distances) to the frontier; various geographical, topographical, and climatological characteristics; institutional factors associated with historical colonial experience; regional fixed effects; and measures of ethnic, linguistic, and religious fractionalization. The various measures of genetic, linguistic, and religious distances considered by the analysis include (i) distances to the contemporary population of the United States (columns 1–2); (ii) distances to the contemporary population of the United Kingdom (columns 3–4); (iii) mean distances to the contemporary populations of Western European and Western “offshoot” nations (columns 5–6); and (iv) mean distances to the contemporary populations of the OECD member nations, including nations from Asia and Latin America (columns 7–8). The set of legal origin fixed effects include dummies for British, French, Socialist, and Scandinavian legal origins. The set of regional fixed effects include dummies for the Sub-Saharan Africa, Middle East and North Africa, Europe and Central Asia, South Asia, East Asia and Pacific, North America, and Latin America and Caribbean regions. Heteroskedasticity robust standard errors are reported in parentheses. \*\*\* denotes statistical significant at the 1 percent level, \*\* at the 5 percent level, and \* at the 10 percent level.

the effect of genetic distance to the frontier is statistically indistinguishable from zero. In addition, based on the partial  $R^2$  statistics reported towards the bottom of the table, while genetic diversity explains between 11 percent and 16 percent of the cross-country variation in the standard of living, the explanatory power of genetic distance to the frontier for comparative development is at best an order of magnitude smaller.

Interestingly, the influence of cultural distance to the frontier, while marginally significant in some specifications (particularly, in the case of the religious distance measure), does not appear to be quantitatively very important for comparative development either. Indeed, the three measures that capture genetic and cultural distances to the frontier together only account for between 4 percent and 7 percent of the cross-country variation in income per capita. Moreover, for each variant of the world economic frontier, a comparison of the estimates from the two regression models suggests that additionally accounting for the potentially confounding influence of cultural diversity hardly alters the main findings, and if anything, the hump-shaped influence of genetic diversity becomes marginally stronger.

Taken collectively, these results confirm earlier findings in the literature regarding the hump-shaped influence of genetic diversity on cross-country comparative development, but they fail to uncover any systematic patterns in the data that are consistent with Wade's theory. Importantly, the findings here reveal that as far as the influence of macrogenetic factors on economic performance is concerned, the role of interpersonal diversity *within* societies (as captured by genetic diversity) is quantitatively far more important for understanding the origins of comparative development than are differences *between* societies in their endowment of individual traits (as captured by genetic distance), regardless of whether these traits are conducive to economic development.

## 6 Concluding Remarks

The past decade has witnessed the emergence of a large and influential body of academic research that has focused on the evolutionary roots of comparative economic development across regions, countries, and ethnic groups. This line of inquiry has been exploring the influences of human evolution and the genetic composition of populations on comparative economic performance across societies, emphasizing the roles played by the Neolithic Revolution and the prehistoric "out of Africa" migration of anatomically modern humans in generating variations in the composition of genetic traits across populations around the globe.

Nicholas Wade's *A Troublesome Inheritance: Genes, Race and Human History* attempts to expose the biological origins of comparative economic development to a wider audience. He advances a modified evolutionary theory of long-run economic development, conjecturing regional variation in the selection of traits that are conducive to growth-enhancing institutions. His theory suggests that regional variation in the duration of selective pressures has formed the basis of differences in social behaviors across racial groups, thereby shaping variations in the nature of institutions and, thus, the level of economic development across the globe. Although at the outset, the broad outline of this argument may appear plausible and largely consistent with existing evolutionary theories of

comparative development, there is no compelling evidence for supporting the actual mechanisms proposed by Wade. Furthermore, Wade's focus on genetic differentiation *between* societies and its hypothesized ramifications for comparative development omits the more dominant role that interpersonal genetic diversity *within* populations has played in generating differential processes of economic development across societies.

Wade's theory of comparative development relies on unsubstantiated selection mechanisms and on empirically unsupported conjectures regarding the determinants of institutional variation across societies. His proposed selection mechanism merely posits that in historically densely populated regions of the world that were characterized by early statehood, there existed a class of rich elites whose evolutionary advantage increased the prevalence of favorable genetic traits (e.g., nonviolence, cooperation, and thrift) in the populations of those regions over time. Setting aside the issue of the extent to which these behavioral traits may be genetically determined, it is far from evident whether these traits necessarily conferred reproductive success in a Malthusian environment and were, thus, necessarily favored by natural selection. In addition, Wade's assertion that the variation in institutions across societies must be rooted in differences in their endowment of favorable genetic traits is simply based on the observation that a society's institutions tend to be highly persistent over time, but this proposition disregards the important roles played by cultural persistence and persistence in economic incentives.

An empirically falsifiable prediction of Wade's theory is that poorer contemporary societies would be characterized by a greater genetic distance to societies that occupy the frontier of economic development. Exploiting worldwide variations across contemporary national populations, genetic distance to the global economic frontier is employed to conduct a simple falsification test of Wade's hypothesis, conditional on the role of genetic diversity in shaping economic development. Although the results confirm earlier findings in the literature regarding the influence of genetic diversity on cross-country comparative development, they fail to uncover any systematic patterns that are consistent with Wade's theory.

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