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**Genetic Diversity and Economic Development:
Assessing the Key Findings in
Ashraf and Galor (2013)**

by

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Genetic Diversity and Economic Development:
Assessing the Key Findings in Ashraf and Galor (2013)*

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Abstract

We replicate Ashraf and Galor (2013) and find that its conclusions concerning the association between human genetic diversity and economic development depend substantially on inconsistent coding and data selection. We correct the coding inconsistencies and add or update data on genetic diversity and population density from high-quality sources. We find little support for the hypothesis that variation in genetic diversity among subpopulations has a systematic relationship with economic development.

JEL classification: N10, N30, N50, O10, O50, Z10.

Keywords: genetics, development.

1   Introduction

Ashraf and Galor (2013) proposes to uncover in population genetics the "deep roots" of comparative development, the forces associated with the spread of *Homo sapiens* from our origin point in Africa to the rest of the globe, and the bearing of these forces on subsequent economic development through the present.

A wide-ranging critique by Guedes et al. (2013), published in an anthropology journal, and a pair of unpublished responses (Ashraf and Galor, 2012; Ashraf and Galor, 2014) show how provocative and contested are the claims of Ashraf and Galor concerning genetic determinism in economic development.

Our replication and extensions of Ashraf and Galor identify substantive problems and demonstrate that Ashraf and Galor is sensitive to specification and method and fragile with respect to data selection. The Ashraf and Galor results largely disappear when more current higher-quality data are used in lieu of the data selected for the original paper.

Three propositions underpin the Ashraf and Galor argument. First, the population genetics of serial founding, or the repeated extensions of human migration via pioneer groups from the human origin point in Africa to increasingly distant destinations, generates a gradient of genetic diversity from its zenith at the origin point in Africa, decreasing through Europe and Asia, over the Bering Strait, south across North America and the Central American Isthmus, to its nadir at the extremum of prehistoric human migration in the Andes or Amazonia. Second, genetic diversity is positively associated with creativity, innovation, and diffusion. Third, genetic diversity is negatively associated with trust and cooperation.

Ashraf and Galor proposes that development requires creativity, innovation, and diffusion as well as trust and cooperation. Ashraf and Galor asserts an association between genetic diversity and these social constituents of development. Trust and cooperation increase with the decreasing genetic diversity associated with distance from the origin point in Africa. Creativity, innovation, and diffusion decrease with the decreasing genetic diversity associated with distance from the origin point in Africa. Because of its position at the high end of the diversity gradient, Africa is too diverse and hence hobbled by distrust and conflict. South America is not diverse enough and hence lacking sufficient creativity and innovation to support development. There is a sweet spot where the overlay of the two opposed gradients provide optimal support for development — in Europe. With these three propositions, Ashraf and Galor professes to explain the basic facts of global development.

The operationalized measure of population genetic diversity is expected heterozygosity, the probability that for a random pairing of two individuals in a population, the haplotypes at a set

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of micro-satellite regions of DNA do not match.[1] A wider variety and broader distribution of haplotypes at each micro-satellite constitute higher heterozygosity. As a probability, heterozygosity is measured on a $0-1$ scale. For human sub-populations in the data we examine (the union of the Ashraf and Galor data and the Wang et al. (2007) data discussed below), 0.5 is an extremely low heterozygosity (2.5th percentile) and 0.77 is the maximum heterozygosity. Mean heterozygosity is 0.69, median heterozygosity is 0.70, and the standard deviation is around 0.06. As these summary values suggest, there is substantial left skew in the distribution of heterozygosity.

Ashraf and Galor first tests the hypothesis with contemporary measured biological data on genetic diversity from 53 ethnic groups, which they collapse to the 21 countries that are home to the 53 ethnic groups. From the 53 ethnic groups and an estimated relationship between location and heterozygosity, Ashraf and Galor generate predictions of genetic diversity for 208 countries, including 197 for which Ashraf and Galor has no observed biological data.

Ashraf and Galor use three alternative measures of genetic diversity: (1) measured contemporary heterozygosity for the 53 ethnic groups for whom genetic testing was done, collapsed to the 21 countries associated with those ethnic groups; (2) predicted pre-colonial heterozygosity for 208 countries predicted from the relationship between migratory distance and heterozygosity in the measured modern data; and (3) contemporary heterozygosity for 208 countries derived from the distance-predicted pre-colonial heterozygosity and then "ancestry-adjusted" to account for migration and mixing of genes in the colonial and post-colonial eras.

The key outcome variables, the measures of economic development, are population density in 1500 CE — a Malthusian marker of societal success in the absence of wealth or income data suitable for cross-societal comparison — and GDP per capita in 2000 CE. Ashraf and Galor also explore the proposed channels from genetic diversity to the final outcomes, with trust measured by contemporary survey data, and creativity measured by contemporary scientific publications per capita.

Before we turn to the quantitative empirical critique, we note three broad problems with the Ashraf and Galor approach. Ashraf and Galor steers clear of crude first-degree genetic determinism that proposes that some genes are better than others. Instead, Ashraf and Galor proposes that some mixes of genes in the population deliver better population outcomes (second-degree genetic determinism).

The escape from first-order genetic determinism is not altogether clean. First, the heterozygosity used by Ashraf and Galor is computed from micro-satellites in non-coding regions of DNA, sometimes referred to as "junk DNA," rather than protein-coding portions of DNA. The logic of limiting attention to non-coding regions is that Ashraf and Galor wants to designate a pure marker of heritage

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[1] Homozygosity, the probability that the haplotypes at a set of micro-satellite regions of DNA do match, is one less the heterozygosity, $1 - heterozygosity$.

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and to avoid analyzing DNA portions selected for survival by their association with advantageous traits. The focus on the impact of non-coding regions indicates a paradox. If the portions of DNA do not code, then their effects cannot manifest. If micro-satellites are closely associated with coding regions that do have manifest effects, then the micro-satellite measurement simply rolls back the selection problem, which means that the analysis really does rely on genes associated with advantageous traits, i.e., "good genes," which is supposedly not the argument.

Second, the proposition that there is population-level selection for advantageous population mixes of genes is controversial. Claims of group-level or higher-level selection are often controversial and difficult to establish. Classical selection occurs at the level of the individual organism. A population with a diverse array of genes may survive, for example, an environmental change because some members of the population are better suited — more fit — for the new context, but it is the better-suited individuals that survive. Selection at the population level does not maintain the population diversity (Okasha, 2009).

Finally and critically, the genetic diversity data to explain the course of development in the Ashraf and Galor analysis is entirely post-treatment. The Human Genomic Diversity Project-Centre Etude Polymorphism Humain (HGDP-CEPH) sampled people between planning in 1991 and publication in 2002 (Cann et al., 2002). The only measured genetic data in the study come from modern populations. The authors seek to explain world outcomes with genetic distributions that are themselves the product of that world, in particular of the construction, migration, destruction, and reconstruction of human groups. The boundaries of the groups that constitute the units of analysis are weakly and endogenously defined.

As an adjunct to this endogeneity problem, distance from Africa can work as an excluded exogenous instrument only if distance from Africa does not otherwise correlate with any of the unobserved factors determining development. The exclusion restriction is unlikely to hold; distance is widely used as a determinant of many factors in development. Other uses of distance in explaining differential development have included, for example, gravity models of trade.

1.1 Summary of empirical results

Ashraf and Galor (2013) follows four lines of empirical argument. First it examines association between measured genetic data and pre-1500 population data. Second, it analyzes the association between predicted diversity and pre-1500 population density with diversity predicted on the basis of distance from Addis Ababa, Ethiopia, according to a serial-founder model of population genetics. Third, it analyzes the association between predicted diversity adjusted for post-1500 migration and contemporary GDP per capita. Finally, it examines proposed pathways of trust and creativity that are channels between diversity and final outcomes.

Our critical replication operationalizes criticisms presented in Guedes et al. In addition to an underlying critique of the monocausal explanation of the global pattern of development based on genetic fitness, Guedes et al. makes three important criticisms of the Ashraf and Galor empirical analysis. Our reassessment incorporates expanded and updated data, with particular attention to the Americas. We outline concerns about genetic diversity data and use an expanded sample that includes ethnic groups omitted from the Ashraf and Galor sample. In addition to concerns about the data on genetic diversity, the population estimates for the 1500 CE estimates of population density are problematic as well. We use more recent and reliable data on pre-colonial population.

With actual measured haplotype data on ethnicities collapsed to the country level, the Ashraf and Galor data include only four (4) ethnic groups for the entire Western hemisphere. The paucity of data for the Americas represents a significant selection process underlying the entire project that goes unremarked in Ashraf and Galor. Reardon (2009) recounts the struggle over the collection of the HGDP data. The original project proposed to collect data from hundreds of ethnic groups worldwide, including a substantial sample from the Americas. The conflict over the HGDP plan included an organized boycott of participation in providing biological data by groups representing indigenous communities worldwide and especially in the Americas. The HGDP-CEPH data are thus the product of a contested and geographically-biased selection process. That the sample used included only a fraction of the potential responders and that the process of sample selection was politically fraught generate significant concerns about representativeness. For example, more socially cohesive and intact indigenous groups may have been more strongly positioned to decline participation, with unknowable implications for the heterozygosity of the sample and potential for bias in estimating the relationship between location and heterozygosity.

Ashraf and Galor cites but does not employ publicly available data from Wang et al. that extends sampling of genetic diversity to additional populations in the Western Hemisphere. We introduce the Wang et al. data on genetic diversity and explore the effect on the core results between observed genetic diversity and population density in 1500 CE. The addition of the Wang et al. data substantial revises the core findings of Ashraf and Galor with regard to the relationship between genetic diversity and economic development.

Ashraf and Galor use early historical population estimates from McEvedy and Jones (1978). An important reason for using these data is convenience; McEvedy and Jones reports ancient populations based on the borders of modern countries. After we replicate the Ashraf and Galor results, we incorporate alternative pre-Columbian population data on the Western Hemisphere.

We use Denevan (1992) population estimates to empirically assess the criticisms in Guedes et al. regarding McEvedy and Jones's systematic underestimates of Native American populations in 1500 CE. Scatterplots reveal that the addition of these data seems to flatten out the marginal effects

of an increase in genetic diversity for the least diverse regions, and slopes computed from relevant regression models confirm this observation in most cases, as we discuss in more detail in Section 3.2.

We then examine the analysis associating genetic diversity induced by preshistoric migration with modern economic development. We find that the core results, an inverted-u relationship between GDP per capita in 2000 CE and genetic diversity, depends critically on "ancestry adjustment," which assigns to each country the weighted average of the genetic diversities of the regions of origin of the people who have settled in the country since 1500 CE. We find that this adjustment for migration and mixing of genes in the colonial and post-colonial eras is utterly essential for the Ashraf and Galor result. There is little indication of a relationship in the data for countries that did not have substantial colonial and post-colonial migration. These results are, thus, dependent on historical contingency rather than genetic diversity resulting from out-of-Africa migration of early humans.

We additionally test the relationship between modern economic development and genetic diversity by using GDP per capita in 1900 CE using the Maddison data from Bolt et al. (2018). While the inverted-u relationship appears in the ancestry-adjusted data using GDP per capita data for 1900 CE, the sample that excludes the cases of substantial ancestry adjustment does not show the inverted-u relationship that is the main result in Ashraf and Galor.

Lastly, coding and sample inconsistencies in the portion of Ashraf and Galor that investigates the channels of trust and creativity through which genetic diversity ostensibly affects development outcomes. Both the trust and creativity models have coding inconsistencies in the statistical-software implementation and the samples vary based on the availability of data. In both cases, the variable legal origins, a categorical variable at the national level that takes on one of five possible values (French, English, German, Scandinavian, and Socialist) is miscoded. In each case only some of the possible values are included. The strength and significance of the relationship between genetic diversity and the proxies for trust and creativity varies by sample and specification suggesting substantial fragility in the estimated relationships.

2   Background

Ashraf and Galor advances a bold hypothesis that genetic diversity within a society has a substantial effect on development, with the results visible in both historical and contemporary indicators. A summary in *Nature* (Callaway et al., 2012) records the controversy associated with the assertion of this "uneasy union" between genetics and development.

Guedes et al. proposes a wide-ranging critique of the paper identifying an array of confusions and misinterpretations that imply, but does not test or implement corrections for significant shortcomings

in the empirical approach. Guedes et al. highlights misunderstandings in Ashraf and Galor related to the "Out of Africa" hypothesis, weak empirical support for proposed mechanisms, and concerns with the quality of the genetic and population data.

First, Guedes et al. suggest that the use of migratory distance in Ashraf and Galor is based on a misunderstanding of serial-founder effects, for which Ashraf and Galor use geographic distance as a proxy. Guedes et al. observes that while geographic distance is suitable for predicting genetic diversity trends on a continental level, it is not adequate for predicting within-continent variation. The concern threatens the validity of the linear model that Ashraf and Galor applies to predict genetic diversity in the wider sample of countries for which measures of genetic diversity are not available.

Guedes et al. notes shortcomings in the population data used by Ashraf and Galor. A key dependent variable in Ashraf and Galor's analysis — population density in 1500 CE — is taken from an unreliable source, McEvedy and Jones (1978), which fails to cite sources and relies heavily on records that more recent analysis shows to be faulty.

Guedes et al. notes that current estimates for the population of the Americas in 1500 CE are much larger than those reported in McEvedy and Jones. For example, McEvedy and Jones estimates the total population of Mexico in 1500 CE as less than 5 million. In contrast, Denevan (1992) suggests an estimate of over 21 million. Similarly, McEvedy and Jones estimates that the population of Peru in 1500 CE was about 2 million, while more current research suggests a population between 4 and 9.4 million (Guedes et al., 2013). Guedes et al. also comments on the problematic nature of assigning 1500 CE population estimates to the boundaries of modern nations as opposed to contemporaneous political or cultural boundaries.

Guedes et al. discusses problems related to the genetic diversity data used by Ashraf and Galor. Guedes et al. notes that the Ashraf and Galor genetic data contain only 4 observations of ethnic groups in the Americas, and that Wang et al., which is cited by Ashraf and Galor, provides additional heterozygosity data on the Americas. Reflecting their comments regarding Ashraf and Galor's misunderstanding of the serial founder effect, Guedes et al. suggests that heterozygosity in the Americas varies on a local level with few trends observable on a transcontinental gradient. For example, Guedes et al. notes that one of the countries included in that Ashraf and Galor dataset for observed genetic diversity — Brazil — is derived from a single, non-representative ethnic group located in the rainforest.[2]

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[2]Other concerns of Guedes et al., which we do not operationalize, include Ashraf and Galor's analysis regarding inaccurate data with respect to Neolithic transition timing and land suitability. Guedes et al. criticizes the Ashraf and Galor model and evidence with respect to the channels by which genetic diversity might affect development. In empirical and game-theoretic analyses of cooperation within and between societies, genetic homogeneity does not predict cooperation in the form of food-sharing. Guedes et al. critique Ashraf and Galor's use of a single question from the World Values Survey for their trust variable and inadequate attention to intra-country and temporal variation in

In an unpublished response, Ashraf and Galor (2012) addresses some of the issues of interpretation. The response introduces some ambiguity about whether their proxy for genetic diversity acts is in fact a proxy for a more general diversity, whether it be genetic, cultural, or otherwise socially-constructed. After discussing the lack of data on variation in cooperation across hunter-gatherer societies, Ashraf and Galor conclude the response by emphasizing that the difficulties inherent in interdisciplinary work.

A more recent critique, Tang (2016) investigates the dependence of the Ashraf and Galor results on two key interrelated issues. The Neolithic transition timing is an important control variable in Ashraf and Galor. Tang critiques the operationalization of the Neolithic transition timing. While Ashraf and Galor uses individual continent fixed effects, Tang notes that the inclusion of a single Eurasia indicator better captures the Diamond (1998) hypothesis of a Eurasian advantage in easily transported innovations in agriculture due to shared latitude and climate.

The Tang specification indicates weakness in the case for a genetic diversity channel. The impact of genetic diversity on development disappears, and the newly added Eurasia indicator shows a high significance level. We note some problems with Tang as a critique of Ashraf and Galor. First, Tang does not explain why including Eurasia specifically as an indicator — as opposed to Asia and Europe separately — captures the Eurasian Advantage more effectively, as the single indicator model is nested in the more complete model. Furthermore, Tang does not empirically test the same model as specified by Ashraf and Galor. Besides using alternative measures, Tang does not test the "baseline model" of Ashraf and Galor against the alternative operationalization of Diamond's Eurasian Advantage hypothesis. Our analysis subsumes the Tang critique.

The Ashraf and Galor (2012) response does not address data issues raised by Guedes et al., and Guedes et al. raises but does not implement or test these potentially important empirical critiques. We undertake a full replication guided by the econometric and data concerns raised in Guedes et al. We follow the methods of Ashraf and Galor closely, we use improved data on heterozygosity and population, and we identify several methodological flaws in Ashraf and Galor (2013).

measured "trust." Guedes et al. also assess the basis for the assertion that diversity enhances innovation. Ashraf and Galor invoke animal studies of diversity to model technological innovation in human societies. There is little reason to expect cross-species comparisons to model the relationship between variation in genetic diversity and the particular construct of innovation — contemporary scientific publications. Guedes et al. suggests that insect studies cannot demonstrate a relationship between heterozygosity and innovation, and that the number of scientific articles published per year is largely a result of national education policy and scholarly practices. Guedes et al. remarks on the ahistorical nature of innovations as conceptualized by Ashraf and Galor, noting inconsistencies and an ahistorical representation of the flows of innovation.

3 Replications, criticisms, and extensions

3.1 Additional heterozygosity data for the Western Hemisphere

Guedes et al. notes the paucity of measured heterozygosity data on the Americas in Ashraf and Galor. The shortfall is visible in Figure 1, which maps the ethnic groups used by Ashraf and Galor. Ashraf and Galor represents the entire Western Hemisphere using genetic diversity data from only 4 ethnic groups collapsed to 3 countries: Pima and Maya (Mexico), Colombian[3] (Colombia), and Karitiana (Brazil). The remaining 49 ethnic groups and 18 countries comprise: 9 ethnicities collapsed to 8 countries in Africa; 38 ethnicities collapsed to 9 countries in Eurasia; and 2 ethnicities collapsed to 1 country in Oceania.

A necessary condition to take seriously the relationship between genetic diversity and development that Ashraf and Galor posit, is that the relationship appear robustly in actual measured heterozygosity data throughout the world.

Wang et al. (2007) gathered data from 422 individuals representing 24 Native Americans populations in North, South, and Central America.[4] Ashraf and Galor cites Wang et al. in their discussion of the "Out of Africa" hypothesis in a footnote but does not incorporate the Wang et al. data. The Wang et al. heterozygosity data can be appropriately appended to the Ashraf and Galor sample. The Wang et al. sample was collected to be compatible with the HGDP-CEPH data of Ramachandran et al. (2005) used by Ashraf and Galor and is in fact analyzed in conjunction with the HGDP-CEPH data in Wang et al.[5]

Ashraf and Galor and Wang et al. disagree substantially in their interpretation of the Wang et al. findings. In comparison to their own R-squared of 0.85 Ashraf and Galor, p. 14 note, "Wang et al. (2007) find that migratory distance explains a more modest 74 percent of the variation in genetic diversity based on allelic frequencies for 678 loci. The authors attribute their somewhat weaker results to the fact that the additional Native American ethnic groups in their augmented sample were historically subjected to a high degree of gene flow from foreign populations (i.e., European colonizers), which obscured the genetic legacy of a serial founder effect in these groups."

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[3]Referred to as Piapoco in Wang et al. (2007).

[4]In "Genetic Variation and Population Structure in Native Americas," Wang et al. (2007) address a variety of questions related to genetic variation in Native Americans; especially, they seek to investigate the original colonization patterns that are retained in genetic records, examine the geographic routes taken by original colonizers, and analyze the extent to which genetic differentiation parallels linguistic differentiation. More generally, this study is concerned with the gradients of diversity implied by the "Out of Africa" hypothesis. Wang et al. finds that while genetic variation seems to decrease as a function of geographic distance from the Bering Strait, the relationship is uneven. The Wang et al. results suggest greater diversity among Andean populations in western South America than in eastern South America and imply that these Andean populations lack differentiation with Mesoamerican groups.

[5]The same framework of haplotypes were used. We replicated the heterozygosity computations in Ashraf and Galor (2013) and Wang et al. (2007) using data from Wang et al. (2007) and Ramachandran et al. (2005) following the method of Nei (1987).

But Wang et al. concludes that there is little "admixture" — or genetic influence — of European ancestry among the Native American ethnic groups, and argue that their contemporary sample is historically representative of the indigenous populations studied.[6] Additionally and critically, Wang et al. finds that while average heterozygosity declines continent-by-continent from East Africa towards the Americas, the "out of Africa" hypothesis does not imply a linear relationship within continents, a relationship critical to Ashraf and Galor's identification strategy. Wang et al. notes that its findings are consistent either with more recent genetic divergence or with a coastal migration route involving "early southward migration among the western side of the Andes" during the early stages of colonizing the continent (Wang et al., 2007, p. 2060).

We appended the additional heterozygosity data calculated by Wang et al. (2007). Figure 2 presents a map of the newly added ethnic groups. Wang et al., p. 2053 reports average heterozygosity for 29 Western Hemisphere ethnicities. Of these, 24 represent newly sampled haplotype data and 5 are from previously sampled populations. Four of the 5 previously sampled ethnic groups, the Pima, Maya, Colombian (Piapoco), and Karitiana, were present in the Ashraf and Galor data from HGDP-CEPH. The heterozygosity for these four ethnicities reported by Wang et al. agrees substantively but not precisely with the Ashraf and Galor HGDP-CEPH data. One population (the Surui) in the original HGDP-CEPH data was not present in the Ashraf and Galor data. We combine all 29 new populations with the Ashraf and Galor ethnicity data. In instances where both Wang et al. and Ashraf and Galor report heterozygosity data for the same ethnic groups, we rely on the Ashraf and Galor values.[7]

In the next sections we re-examine the core Ashraf and Galor results, on the relationship between heterozygosity and distance in Section 3.2, and between population density and heterozygosity in Section 3.3.

3.2   Migratory Distance and Heterozygosity

A key component of the Ashraf and Galor method is the prediction of heterozygosity using migratory distance from Addis Ababa, the origin point of humanity and the serial founder theory of human expansion and settlement around the world. Ashraf and Galor use of the serial founder concept enables them to expand their sample from the 53 ethnicities from 21 countries for which genetic data are observed to 208 countries on the basis of the countries distance from Addis Ababa and the coefficient of the linear model of heterozygosity on distance for the observed populations. The

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[6] "Almost no genetic membership from the cluster containing Africans and a relatively small amount of membership from the cluster containing Europeans were detected in the Native Americans, indicating that with relatively few exceptions, the samples examined here represent populations that have experienced little recent European and African admixture" (Wang et al., 2007, p. 2051)

[7] The alternative is not consequential.

credibility of this relationship is central to the Ashraf and Galor argument. In this section we discuss the estimation of this relationship with a focus on two related provisions: the addition of the Wang et al. data on heterozygosity in the Americas; and the distinction between the heterozygosity-distance relationship between and within continents.

Figure 3 shows the scatterplot of heterozygosity against migratory distance from Addis Ababa in thousands of kilometers. The 53 filled dots show the Ashraf and Galor ethnicity data with only four Western Hemisphere ethnicities, and the 26 unfilled dots show the additional ethnicity data for the Western Hemisphere from Wang et al. The slope of the heterozygosity-distance relationship for the original Ashraf and Galor data and the original data enhanced with the Wang et al. data are quite similar, although the fanning out of the data for the Americas at the right end of the figure is evident. The R-squared for the Ashraf and Galor ethnicity data is 0.86 and the R-squared for the full dataset falls to 0.75.

Consistent deviations from the predicted diversity model used by Ashraf and Galor are observed in Figure 3, which plots observed heterozygosity from Ashraf and Galor (filled dots and a dashed line and from Wang et al. (empty dots and a dotted line) against migratory distance from East Africa. The Wang et al. data introduces substantial heteroskedasticity, with the ethnic groups furthest from East Africa (i.e., the South American groups) exhibiting the largest error from the estimated linear model. The Ashraf and Galor model generally underestimates the heterozygosity of the South American countries, with the exceptions of Paraguay and Brazil. This underestimation of heterozygosity is consistent with Wang et al. findings of higher diversity along western South America, and further corroborates the Guedes et al. critique that within-continent variation in heterozygosity is more complex than a simple linear model can predict. This linearity is the basis for Ashraf and Galor's predicted diversity measure and their ancestry-adjusted predicted diversity measure. By using this predicted measure, Ashraf and Galor is collapsing substantial variation in heterozygosity. The overall effect is that distance from East Africa rather than genetic diversity is the key explanatory variable.

The relationship between migratory distance and heterozygosity depends critically on the definition of regions. In Figure 4 and Table 1 we explore the sensitivity of the relationship. Using the extended data from Wang et al., Figure 4 first illustrates the global relationship between migratory distance and observed heterozygosity as in Figure 3. The coefficient for the slope of the heterozygosity-distance regression for the pooled global data is $-0.007(0.00)$.

For some parts of the analysis Ashraf and Galor use continental indicator variables, and Ashraf and Galor (2014) states that the entire analysis depends exclusively on within-continent variation. But the distance-heterozygosity relationship, a key underpinning of the analysis, depends on a pooled estimate that combines variation between and within continents. We observe that Ashraf and Galor

code the Americas as a single continent, thereby constructing a single large region with substantial variation in both heterozygosity and migratory distance. We consider both the Ashraf and Galor definition of five continents or continent groups: (1) Africa; (2) Europe; (3) Asia; (4) Oceania; and (5) the Americas. We also construct an alternative set of seven regions: (1) Sub-Saharan Africa; (2) North Africa Europe, and Central Asia; (3) East Asia; (4) Oceania; (5) North America; (6) Central America; and (7) South America, which correspond to clusters of the actual genomic data.

In addition to the global pooled relationship, Figure 4 also plots the relationship between migratory distance and observed heterozygosity for each of the five continents (dotted lines) and seven regions (dashed lines). If there is indeed a uniform global relationship between heterozygosity and distance from Addis Ababa, then linear fits for the regional or continental subsamples should lie along the same linear fit as the pooled sample. While the linear fit for the continental subsamples generally lie rather close to the pooled linear fit, the linear fits for the regions do not. With the exception of two small-sample cases, the three datapoints for North America and the two datapoints for Oceania, the linear fits for the regions have substantially lower slope than does the pooled global fit. Table 1 reports the accompanying regression results.

The first three columns of Table 1 report the coefficient on migratory distance for the pooled model, the model with five continents, and the model with seven regions. For the pooled model and the model with five continents, the coefficient on distance is stable, at roughly -0.006 heterozygosity points per 1000 km. For the model with seven regions, the coefficient drops sharply to -0.002 and loses statistical significance.

In columns 4 and 5 of Table 1, we report within-continent and within-region regressions of observed heterozygosity on migratory distance from Addis Ababa, i.e., each coefficient is from a separate bivariate regression. For the within-continent gradients reported in column 4, the Americas and to a lesser extent Asia show a coefficient on migratory distance similar to that at the global scale (in column 1). The gradient within Africa and within Europe is smaller. (Oceania has only two datapoints.)

Among the seven within-region regressions reported in column 5, the coefficient on distance is typically about half as large as for the pooled data and is significantly different from zero only for one of the seven regions (East Asia, with a coefficient of -0.004 and a standard error of 0.002). In most cases, the within-region estimates are sufficiently small and sufficiently precise that the slope estimate from the pooled data in column 1 does not fall in the 95-percent confidence interval of the within-region estimates in column 5.

The implication of the pooled, fixed-effect, and by-region results is that observed heterozygosity has a significant between-region gradient but not an especially strong within-region gradient. This result consistent with the finding of Wang et al. for the Americas and the critique of Guedes

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et al. The result is at odds with the assertions of Ashraf and Galor (2013) and Ashraf and Galor (2012) that the key results based on heterozygosity predicted from migratory distance are not based exclusively on continent-scale variation.

Although Ashraf and Galor uses continent dummies in much of the second-stage analysis, i.e., in the regressions of proxies for development on predicted heterozygosity, heterozygosity itself is predicted from the single global gradient rather than from the substantially smaller within-region gradients. The method of predicting heterozygosity from continent-scale variation in migratory-distance calls into question the parts of Ashraf and Galor that rely on predicted heterozygosity.

3.3 Population Density Results with Expanded Heterozygosity Data

Employing the augmented heterozygosity data to examine the proposed relationship between genetic diversity and societal success measured by population density, Figure 5 presents a scatterplot of log population density in 1500 CE against genetic diversity with both the original Ashraf and Galor heterozygosity data, with gray lines and filled points representing the original data, and black lines and open points representing the additional data from Wang et al. The dotted lines represent quadratic fit, and the dashed lines are non-parametric fits.

The quadratics estimated in Ashraf and Galor flatten out substantially when the Wang et al. data are added, largely because of the lower heterozygosities yet moderate population densities found within the Southern Cone of South America from countries such as Paraguay.

Computed from the estimated linear and quadratic terms, "optimal diversity" expresses the homozygosity that maximizes the quadratic function. The site of optimal diversity, which Ashraf and Galor locates in Eurasia, shifts towards the highest heterozygosities, i.e., in Africa, as the hump-shaped quadratic shifts towards a downward-sloping linear fit. The non-parametric analysis (dashed line) presents a similar story; though there is a distinct hump with the peak located among the Eurasian countries, the rest of the curve has uneven behavior, even increasing again slightly in Mesoamerica.

The regression results presented in the first two columns of Table 2 correspond to the scatterplot in Figure 5. Column 1 exactly replicates the Ashraf and Galor Table 1, column 1 regression, and column 2 presents the results from the identical model but with the incorporation of the new genetic diversity data.

The linear and quadratic coefficients on genetic diversity change from 413.5 to 57.6, and from -302.6 to -38.2. Because the coefficients of a quadratic must be interpreted jointly, we follow Ashraf and Galor in characterizing the shape of the quadratic by reporting the peak ("optimal diversity" according to Ashraf and Galor) and by reporting the slope, the implied effect of diversity on outcomes, at relevant points.

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The results in column 1, replicating those of Ashraf and Galor, imply that for Brazil, the country with the lowest heterozygosity in the original dataset, a 1 percentage-point increase in genetic diversity would result in a 79.1 log point increase in 1500 CE population density, the Ashraf and Galor proxy for pre-colonial economic development. At South Africa, with the largest observed heterozygosity in the sample, a 1 percentage-point decrease in genetic diversity would result in an increase in pre-Columbian economic development (population density) of 52.3 log points. Optimal diversity occurs at a heterozygosity of 0.68, which applies to typical countries in the core of Eurasia. We additionally compute standard errors for the optimum and for the slope estimates, and all three estimates are statistically significant.

When we add the data from Wang et al., the flattening of the quadratic is reflected in the point-slope estimates based on the coefficients in column 2. At Brazil, the impact of a 1-percentage-point increase in heterozygosity according to column 2 would result in a 15.4 log-point increase in economic development, substantially lower than the Ashraf and Galor estimate of 79.1. The collapse in magnitude is equally striking for South Africa, with a 1 percentage-point decrease in heterozygosity resulting in a mere 1.2 log-point increase in economic development. Neither slope estimate is statistically significant.

As seen in the accompanying Figure 5, the optimal diversity shifts substantially: from the ethnic groups of Eurasia, to the highest levels of those in East Africa, at a heterozygosity of 0.75. Neither the linear nor the quadratic term remains statistically significant, and the shift in the estimated peak is accompanied by a drop in its statistical significance, with the standard error of the peak estimate increasing from 0.01 to 0.23. The implied 95-percent confidence interval for the location of the peak would encompass the entire world range of heterozygosity. The drop in the R-squared, from 0.35 to 0.05, indicates a substantial decrease in the ability of the model to explain population density in 1500 CE, especially in the Americas.

The disappearance of the quadratic that Ashraf and Galor hypothesizes is further corroborated when we re-estimate the baseline historical model, which includes the full set of covariates and continent fixed effects, with the expanded genetic data. This is reflected in Figure 6, which presents the partial relationship between genetic diversity and log population density in 1500 CE with both the original data (top panel) and the additional heterozygosity data (bottom panel).

In order to illustrate the partial relationship between outcome variables and predicted haplotype diversity (in their Figures 4, 5, A1, and A2), Ashraf and Galor relies on an "augmented component-plus-residual plot rather than the typical added-variable plot of residuals against residuals." We employ instead the consistent estimator of Yatchew (2003) to capture the partial, quadratic effect in the multivariate context.

The "augmented component-plus-residual" method proposed by Ashraf and Galor misses the

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essential element of multivariate regression, i.e., controlling for extraneous variables and expressing the partial relationship between the outcome and the explanatory variable of interest. The importance of this issue is illustrated in Figure 7, which presents the bivariate fit utilizing the original data with a solid line, the Ashraf and Galor method of depicting partial relationships via "augmented component-plus-residual" with a dashed line, and the partial linear model (Yatchew, 2003). The "augmented-component plus residual" method yields a slightly more downward slope. While the impact of adding the additional data is not as visually dramatic with the full set of covariates, the quadratic still substantially appears to flatten, especially for the Americas.[8]

Columns 3 and 4 of Table 2 present the results for these regressions, with column 3 of Table 2 replicating column 5 of Ashraf and Galor Table 1 and column 4 of Table 2 presenting the results for the equivalent model but incorporating the additional Wang et al. heterozygosity data. Again, the linear and quadratic terms drop substantially in magnitude and statistical significance. In column 3 linear term is statistically significant at 5 percent and the quadratic term at 10 percent; in column 4, neither term is statistically significant.

When the Wang et al. data are added in column 4, the slope of the heterozygosity-population density curve at Brazil drops by a factor of 3.5, with a 1 percentage-point increase in heterozygosity implying an increase in density of 12 log points to an increase of 43 log points with the original data. Statistical significance of the slope at Brazil was already borderline in column 3, and the t-statistic falls well below 1 with the addition of the Wang et al. data.

The slope at South Africa drops as well, indicating a marginal decrease in diversity would result in an increase in development of 12 log points rather than 21. The optimal diversity shifts closer to the Americas in this quadratic: from 0.699 in the original data, to 0.658. The R-squared drops by 3 percentage points, with the results in column 4 explaining 80% of variation in pre-Columbian population density — indicating in comparison to column 2 that the additional covariates such as log Neolithic transition timing and land suitability explain substantial variation in development outcomes. The evidence from these regressions indicate that the "limited historical analysis" presented in Ashraf and Galor is not robust to the addition of data on the Americas. Because establishing the development–diversity hypothesis with actual biological data is a key component without which the instrumented results based on distance cannot be justified, these results undermine the hypothesis.

In the last set of columns, we build upon the analysis conducted in Tang (2016) concerning continent effects. Columns 5 and 6 present the results — with the original and then the Wang

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[8]The figures in Ashraf and Galor based on the "augmented component-plus-residual" method suffer from large errors in scale. In Figure 4 of Ashraf and Galor, population density in 1500 CE ranges from 121,000 persons per square kilometer (in the region that is now the USA) to 24,155,000 persons per square kilometer (in the region that is now Japan). In Figure 5 of Ashraf and Galor, annual income per capita in 2000 CE (in constant 2000 international dollars) ranges from $890,900 in Ecuador to $10,853,500 (in Gabon, followed closely by Trinidad and Tobago). Figure 5 shows per capita income for the United States at $5,389,700.

et al.-augmented data — of a model in which the only additional controls are continent fixed effects. While Tang is concerned specifically with the "Eurasian advantage," we obtain similar results with the standard set of continent fixed effects rather than a single Eurasia dummy. We find that the results of Ashraf and Galor are not robust when the continent effects are the only additional controls. The coefficients are smaller than the original Ashraf and Galor results in column 1 and are statistically insignificant.

In column 5, the slope at Brazil continues to suggest that a 1 percentage-point increase in genetic diversity is associated with an increase of population density of approximately 42 log points (with a standard error of 18 log points), the slope at South Africa now implies a *positive* effect of an increase in genetic diversity (with a t-statistic of 1). The implied optimal genetic diversity level is greater than 1, i.e., the function is increasing at the boundary, while the standard error is enormous.

With the Wang et al. data, the signs on the genetic diversity term have switched, with the linear term taking a negative sign and the quadratic term positive, implying a convex rather than concave relationship. Neither term is close to statistical significance. The slopes at both Brazil and South Africa are positive although close to zero. The lack of robustness of the effect of genetic diversity to the inclusion of exactly continent fixed effects undermines the hypothesis.

Columns 5 and 6 of Table 2 are important because Ashraf and Galor emphasize, both in the 2013 paper and in Ashraf and Galor (2014), the key role of within-continent variation in the identification strategy. In fact, the Ashraf and Galor results depend essentially on the other explanatory variables. The hump-shaped relationship that appears in the bivariate data disappears entirely when continent fixed effects are added. It is only the further addition of the explanatory variables that reestablishes the hump-shaped hypothesis. Evidence for a relationship between development and genetic diversity does not appear in within-continent bivariate relationships.

Ashraf and Galor acknowledge potential reverse causality between heterozygosity measured around the year 2000 and population density measured in 1500 CE and present 2SLS results to address the problem. Two excluded exogenous variables are needed to instrument for the potentially endogenous linear and quadratic terms in heterozygosity. Using the observed heterozygosity data aggregated from 53 ethnic groups to 21 countries, Ashraf and Galor presents the results of two-stage least squares regressions in which heterozygosity and its square are instrumented with heterozygosity predicted with migratory distance from Addis Ababa and with the square of the distance from Addis Ababa. Ashraf and Galor emphasize the support that 2SLS strategy gives to the baseline results. In Table 3, we replicate results from Columns 5 and 6 of Table 2 in Ashraf and Galor and re-examine the results with the extended data from Wang et al.

Column 1 of Table 3 replicates the Ashraf and Galor, and the Column 2 presents the identical specification using the Wang et al.-extended data. With the addition of the Wang et al. data, the

point estimate of the slope at Brazil falls by almost 75 percent, from 0.569 (0.175) to a statistically insignificant 0.158 (0.105). The slope of the quadratic remains upward sloping even at the higher heterozygosity in South Africa, and the implied peak has migrated to 0.891, out of the range of observed values. Columns 3 and 4 repeat the 2SLS analysis with the addition of three continent fixed effects to the list of covariates. Again, while the initial dataset generates a statistically significant positive slope of population density versus heterozygosity, 0.447 (0.106) at the heterozygosity of Brazil, the more complete Wang et al. data shows slope falling to a statistically insignificant 0.114 (0.118).

In Columns 5 and 6, we extend the 2SLS analysis by presenting a specification with the covariates limited to three continent fixed effects. Column 5 uses the original Ashraf and Galor data. The quadratic of population density in response to heterozygosity is substantially upward-sloping both at Brazil with a slope of 0.428 (0.153) and at South Africa with a slope of 0.209 (0.355), with the peak population density at a very imprecisely estimated heterozygosity of 0.977 (0.817). There is little sign of an inverted-U relationship in the original Ashraf and Galor data. When we re-estimated with the extended data from Wang et al., the quadratic is convex rather than concave, although very imprecisely estimated. The slope at the heterozygosity of Brazil is zero, again imprecisely estimated.

Considering the paired columns in Tables 2 and 3, the addition of the Wang et al. data for the Americas significantly reduces support for the overall hypothesis. The addition of the new data for the Americas has a sufficiently strong effect on the estimated quadratic that significance for the effect of diversity at South Africa is substantially reduced. The implied development premium for increased diversity at Brazil drops by a factor of between 5 and 20 and is never statistically significant when locally relevant data for the Americas are added.

3.4 Updated population data for the Americas

The debate over the size of pre-Columbian American populations is intense and ongoing. The full range of estimates of pre-contact population have increased sharply over the past half century with the lowest estimates today at the level of what were considered implausibly high estimates a generation ago (Mann, 2005). Guedes et al. observe that the estimates of McEvedy and Jones are particularly low.

We re-estimate Ashraf and Galor with higher-quality estimates of the pre-colonial population of the Americas from Denevan (1992), which provides estimates for a cross-section of countries or regions of the Western Hemisphere.[9] Because Denevan provides these estimates for countries or

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[9]More up-to-date estimates would need to survey and assess a large and contentious archaeological literature. Some of this literature provides detailed analysis of single sites to produce regional population estimates. See, for example, Ortman (2016) and Kohler and Reese (2014). Other parts of the literature, for example, Russell Thornton and Marsh-Thornton (1981), estimate the precolonial population by estimating the rate of indigenous population

regions not necessarily mapped to contemporary national boundaries, we conduct the re-analysis by constructing clusters of one or more countries to operationalize Denevan's estimates in the context of the Ashraf and Galor analysis.

As needed we aggregated countries, the unit of analysis in Ashraf and Galor, to Denevan country-clusters: Denevan's Amazonia comprises Brazil, Guyana, and Suriname; Andes comprises Ecuador, Peru, and Bolivia; North America comprises Canada and the United States; Hispaniola comprises Haiti and the Dominican Republic; Honduras-Belize comprises Honduras and Belize; and Lowland South America comprise Paraguay and Uruguay. For country-clusters that include more than one country, population and area were totaled for entire set of constituent countries; and heterozygosity was computed as the area-weighted average of the heterozygosities of the constituent countries. Area-weighted averages were applied for the additional covariates.

To give a sense of the importance of the population updates, Figure 8 summarizes the results of updating the population density data in 1500 CE to reflect the current state of knowledge. In every case of difference, estimated population density based on Denevan population estimates exceeds those based on the McEvedy and Jones data used by Ashraf and Galor. (Countries on the solid 45-degree line indicating no change in the population density estimate are not shown.)

The increase in the estimated population density in 1500 CE is especially striking in Mesoamerica. Ashraf and Galor, fn14 discuss the possibility of random measurement error in the dependent variable in a footnote regarding statistical significance and expand on this possibility in Ashraf and Galor (2014). Figure 8 suggests that even within the Americas, errors in measured population density are neither random nor a single systematic underestimate but systematically biased.

We first establish that the aggregation to country-clusters, when we retain the underlying original Ashraf and Galor population data, has minimal effect on the results. We then update from McEvedy and Jones to Denevan population values with the country-cluster as the unit of observation.

3.5 Empirical results with updated population data

Figure 9 presents the bivariate relationship between log population density in 1500 CE and observed heterozygosity with both the original population data (the dashed line) and updated Denevan data, both with quadratic fits. Figure 10 reports the same results but with a non-parametric fit (dotted line). In both instances, the updated population data generates a noticeable increase in the height of the curve through the Americas.

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decline following colonial contact. Based on these methods, estimates for the population of North America on the eve of contact range from 1.1 million to 18 million (R. Thornton, 1987). Denevan (1992) has the advantage of compiling estimates from the literature. While estimates for the Americas continue to change, typically upwards, Denevan remains respected in the archaelogical literature, while McEvedy and Jones (1978), despite many citations in economics, is not. See Guedes et al. (2013) for a discussion.

The dotted lines in Figure 9 and Figure 10 represent best estimates with actually observed heterozygosity data and up-to-date population data. In both cases, the Ashraf and Galor estimates are substantially modified, yielding curves that for the most part do not fall within the 95-confidence interval for the original curves. In the quadratic, Figure 9, the peak, or optimal diversity, has migrated substantially into the Americas. In the non-parametric estimate, there is no longer a single peak.

The remainder of this section uses 145 countries analyzed by Ashraf and Galor or the 137 country-clusters in the data based on Denevan. Unlike in Section 3.1 in which the heterozygosity measure is based on observed genetic data, the heterozygosity measure is predicted from the distance of the country or country-clusters from Addis Ababa, Ethiopia, using the regression model described in Ashraf and Galor.

Table 4, columns 1 through 3 present the results based on the bivariate model in Ashraf and Galor Table 3, column 1. Column 1 replicates the point estimates in column 1 of Table 3 in Ashraf and Galor. As the standard errors are bootstrapped following the algorithm described in Ashraf and Galor but with a different random-number generator, the estimated standard errors vary slightly from the original but are substantively unchanged.

We continue to report estimates for the instantaneous slope of the development-diversity curve at Brazil and South Africa. In this model, the estimated slope for Brazil implies that a 1 percentage point increase in predicted heterozygosity for Brazil would lead to a 45 log-point increase in pre-Columbian population density. The equivalent decrease in predicted genetic diversity for South Africa would result in a 12 log-point decrease in population density. Optimal diversity occurs at a heterozygosity of 0.707.

The second column of Table 4 presents the same model with the observations aggregated into the country-clusters described above to confirm the neutrality of the aggregation. The results are effectively similar, with the estimated terms of the quadratic, the implied slopes and optimum, and the standard errors largely unchanged. The R-squared falls somewhat, from 0.21 to 0.16. The alternative aggregation, i.e., the use of country clusters, thus has limited effect on any of the coefficients in the bivariate model or in the models that add covariates and continent fixed effects (columns 4 and 6), largely reprising the originals in Ashraf and Galor.[10]

Figure 11 plots the bivariate relationship, with the dashed quadratic representing the coefficients estimates from column 2. The dotted line represents the quadratic using the updated population data from Denevan. As expected, the quadratic-based estimate is essentially the same for populations with high heterozygosity (i.e., low homozygosity). However, the quadratic with updated population data appears to substantially flatten out towards the upper end of the homozygosity spectrum, with

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[10]The pure replication models with covariates and with continent fixed effects are available from the authors.

the higher population estimates from Denevan reducing the slope of the key relationship for Central and South America.

Figure 12, which estimates the non-parametric bivariate relationship, produces similar results, again with estimated slopes for the Americas substantially smaller. This result is confirmed in Table 4, column 3, which presents the regression results for the quadratic specification. While both terms of the quadratic remain statistically significant at the 1% level, the magnitude of the effect drops substantially, most notably in the Americas. At Brazil, the estimated slope suggests an increase in predicted heterozygosity of 1 percentage point would increase population density by only 26 log points, not 45. The magnitude of the slope at South Africa is roughly stable with the point estimates not distinguishable. The site of optimal diversity declines to a heterozygosity of 0.678 from 0.704, reflecting the higher Mesoamerican population density estimates, and the R-squared declines sharply, to 0.03 indicating that genetic diversity explains little variation in population density in 1500 CE.

Table 4, columns 4 and 5 compare the results with the original and updated data including the additional explanatory variables outlined in Ashraf and Galor: Neolithic transition timing; arable land percentage; absolute latitude; and land suitability for agriculture. Column 4 corresponds to column 5 of Ashraf and Galor Table 3, but with the data re-aggregated into country-clusters (with no substantive impact on any of the results).

In the results reported in column 5 with updated population data, the statistical significance for both linear and quadratic terms drops substantially, from the 1 percent to the 10 percent level. In comparison with the results in column 4, the results with the updated population data imply a substantial decrease in the slope at Brazil: from a slope of 0.333 with the McEvedy and Jones data to a slope of 0.141. With a standard error of 0.096, the estimated slope at Brazil is statistically indistinguishable from zero. The magnitude of the negative slope for South Africa again increases slightly. The site of optimal diversity shifts again towards the Americas, decreasing from 0.706 to 0.665.

Figures 13 and 14 illustrate the relationship between population density and predicted homozygosity with controls for the covariates. The partial relationship is similar to the bivariate relationship shown in Figures 11 and 12. The increase in the estimated population density in 1500 CE substantially raises the curve in the Americas which largely flattens the relationship between population density and heterozygosity. The peak or optimum heterozygosity has shifted definitively to Mesoamerica.

The last two columns of Table 4 include all explanatory variables and add indicators for Africa, Europe, Asia, Oceania, and the Americas. Column 6 presents the replication of Ashraf and Galor with the data re-aggregated into country-clusters, which makes essentially no difference to the

results reported in column 6 of Ashraf and Galor Table 3. The numerical results presented in column 7 of Table 4, which includes both covariates and continent fixed effects, present a different picture relative to column 5. In this specification with covariates and continent fixed effects, the linear and quadratic terms are at roughly the same values as in the bivariate relationship with the original data. Relative to both model with updated data but lacking continent fixed effects (columns 3 and 5) and even relative to the original data in this specification, the model in column 7 shows a substantial increase in the magnitude of the slope at Brazil at 0.435. The dashed line in Figure 15 plots this quadratic relationship with full covariates including continent indicators using the consistent estimator of the partial linear model method (Yatchew, 2003) to estimate the quadratic relationship. The dotted line in Figure 15 presents the quadratic from the updated population data including continent fixed effects.

Further investigation with non-parametric methods in Figure 16 shows that this increased gradient at Brazil is due to a substantial intra-hemisphere gradient in the Americas.[11] The specific location of the effect in the Americas can be seen in the fit of quadratics, which presents the non-parametric portion of a partial linear model that includes continent fixed effects for both the original data (dashed line) and the updated population data (dotted line). The shape generated by the original data presented with the dashed line contrasts with the steep drop in the updated population data. The increased estimates of population density in the countries of Mesoamerica create a sizable drop to the less dense populations of the lower-heterozygosity Southern Cone and Amazonia as distance from East Africa, and hence predicted heterozygosity, increases.

While the slope increases, the standard error of the slope at Brazil increases sharply with the addition of continent fixed effects. Columns 6 and 7 have a standard error for the slope at Brazil that is substantially larger than in all the preceding columns. This indicates that while the model with continent fixed effects shows a substantial downward slope within the Americas, there is significant variability associated with the estimate because of the effect coming from a relatively small number of cases in the Americas with wide spreads in estimated population densities between countries.

We emphasize again that the estimated relationship in all of Table 4 and the accompanying Figures 11 through 16 is based on the updated population estimates from Denevan, but the heterozygosity is not measured. The heterozygosity is predicted from the distance-to-Addis model, which guarantees that locations in South America will have lower values of heterozygosity than will locations in Mesoamerica, which largely accounts for any indication of a downward-sloping relationship in this region of the plot.

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[11]North America is a clear outlier in Figures 11 through 16. We note that there is enormous variation in population density across the large area of North America. The aggregation to Canada and the United States yields an average population density that does not usefully characterize the high local densities of the region that reflect the large and complex societies that inhabited the region (Guedes et al., 2013, p. 74).

3.6 Genetic Diversity, Ancestry Adjustment, and Modern Economic Development

For the analysis of contemporary income, Ashraf and Galor argues that contemporary heterozygosity data must be adjusted for ancestry to account for the migration of peoples in the colonial and post-colonial eras. The ancestry adjustment of heterozygosity assigns to each location the weighted average of the heterozygosities of the subpopulations that currently inhabit the location based on the distance-predicted heterozygosity of the source location where that subpopulation lived in 1500 CE.

As we discuss in Section 3.2, the genetic composition of the 79 ethnic groups for which heterozygosity was actually observed is already a post-treatment characteristic, reflecting differences in extermination, transfer, and assimilation of indigenous populations following contact at the dawn of the colonial era. Voluntary and involuntary migration in one epoch undoubtedly responded to differential development in the preceding period. The Ashraf and Galor ancestry adjustment proceeds as if the diversity of the source population was encoded in the genes of people from the source location, i.e., the measure does not describe population-level heterozygosity but proposes to characterize the diversity of the population by the population diversity of the source subpopulations.

Figure 17 illustrates the ancestry adjustment applied by Ashraf and Galor. Countries that lie on the 45-degree solid line in Figure 17 had no ancestry adjustment applied. We also illustrate with the parallel dotted lines the set of countries for which ancestry adjustment accounted for a change of no more than 0.01 units of predicted heterozygosity. The highly adjusted cases are largely in the Western Hemisphere, although New Zealand, Fiji, and Australia are also high-adjustment cases.

We undertake several investigations of ancestry adjustment on the results by estimating semiparametric relationships between ancestry-adjusted predicted heterozygosity and modern income per capita using samples with and without the cases for which ancestry adjustment involves large changes in predicted heterozygosity.

The left panel of Figure 19, which is equivalent to Figure 5 in Ashraf and Galor, shows the scatterplot and semiparametric estimate for the ancestry-adjusted data. The inverted-u relationship between GDP per capita in 2000 CE and ancestry-adjusted predicted heterozygosity is pronounced. The right panel of Figure 19 show the relationship between GDP per capita in 2000 CE and predicted heterozygosity. It is immediately clear that the results depend entirely on ancestry adjustment. The settler countries in the Western Hemisphere and Oceania were both high homozygosity (low diversity) on the eve of colonization and are high income today. Ancestry adjustment moves many of the data points in the cloud in the upper right of the right panel (at homozygosity of 0.38–0.40) to a lower homozygosity of 0.26–0.27 in the left panel, entirely reshaping the semiparametric estimated relationship.

The left panel of Figure 19, which is equivalent to Figure 5 in Ashraf and Galor, shows the scatterplot and semiparametric estimate for the full sample. The inverted-u relationship between GDP per capita in 2000 CE and ancestry-adjusted predicted heterozygosity is pronounced. The right panel of Figure 19 excludes the cases for which ancestry adjustment altered predicted heterozygosity by more than 0.01 units. The estimated semiparametric regression curves differ substantially. The peak in the right panel is around 30 log points below the peak in the left panel. Moreover in the right panel the regression curve flattens to the right of the peak and the standard error fans out, eliminating the inverted-u relationship.

Figure 20 repeats the analysis with log GDP per capita in 1900 (using Maddison data from Bolt et al. (2018)) as the dependent variable. The semiparametric estimate has multiple troughs and is noticeably rising at the right edge of the plot.

Figure 21 returns to log income per capita in 2000 CE as the dependent variable and, following the specification in column 8 of Table 7 in Ashraf and Galor, include average years of schooling as an explanatory variable. While the inverted-u relationship appears in the left panel which uses ancestry-adjusted data, there is an entirely different shape in the right panel, which limits the sample to cases where ancestry adjustment was small. There is a local peak at the same location on the homozygosity axis as in the left panel but the global peak GDP occurs at a much higher homozygosity.

Taken together, Figures 19 to 21 indicate substantial dependence on the method of ancestry adjustment that Ashraf and Galor use to account for migration and mixing of genes in the colonial and post-colonial eras. For much of the Western Hemisphere the ancestry-adjusted data have little to do with the pattern of genetic diversity attributable to early human migration and settlement. The inverted-u association of modern economic development with genetic diversity obtains only in data that have been ancestry adjusted to locate high-development locations in the Western Hemisphere and Oceania within the mid-range of homozygosity.

3.7 Omitted legal origin dummy variables

For the final component of the analysis, Ashraf and Galor (2013) examines the proposed channels of trust and creativity through which genetic diversity is supposed to affect economic development. Ashraf and Galor use a variant of the regression specified in their analysis of contemporary per capita income with two alternative dependent variables representing the channels from diversity to development: interpersonal trust, the percent of the population who agreed with the statement that "most people can be trusted" on the World Values Survey; and the average number of scientific articles published between 1981 and 2000. The mean across countries in the percent agreeing with the statement that most people can be trusted was 29 percent with a standard deviation of 16

percentage points and a modest right skew. The mean across countries of scientific articles per 1,000 capita was 0.2 with a standard deviation of 0.3, a strong right skew, and a substantial mass near 0 articles per capita.[12]

According to the Ashraf and Galor hypothesis, increasing genetic diversity should decrease interpersonal trust, a precursor of the types of conflict that can inhibit development. Genetic diversity should have a positive effect on the number of scientific articles published, reflecting the mechanism of increased diversity leading to superior creativity, innovation, and technological achievement. Because the analysis of the trust and creativity channels uses contemporary outcome data, the genetic diversity measure is ancestry-adjusted distance-predicted heterozygosity.

The specification of the analysis presented in Table 9 of Ashraf and Galor does not correspond to the implementation in the statistical software. Ashraf and Galor specify the inclusion of continent fixed effects, indicators for sub-Saharan Africa and OPEC membership, and legal origin fixed effects. The legal origin variables were originally devised to capture the effect of state-building and the provisioning of public goods, the strong effect of these controls may reflect the role of investment in education (LaPorta et al., 1999). Because of the undocumented coding inconsistency, the implemented regressions include only two out of five legal origin dummy variables: German and Scandinavian when the dependent variable is trust; and British and French legal origins when the dependent variable is average annual scientific articles per capita, the proxy for national creativity. In the baseline model of output per capita in 2000 CE as a function of genetic diversity, the full set of legal-origin fixed effects are included.

Table 5 explores the sensitivity of the Ashraf and Galor results to the inclusion of the legal origins indicators and to the samples on which the development-channel specifications are run. The Full Sample columns refers to the full set of countries for which data on the particular development channel are available (58 countries for trust, 93 countries for scientific articles). Common sample refers to the set of countries for which data on both development channels are available (56 countries).

In row 1, we replicate the models as implemented by Ashraf and Galor, i.e., with the truncated sets of legal origin fixed effects: in the trust equation, indicator variables are included for German and Scandinavian legal origins, grouping British, French, and socialist legal origins as the omitted category; in the articles equation, indicator variables are included for British and French legal origins, grouping German, Scandinavian, and socialist as the omitted category. The coefficient on ancestry-adjusted predicted heterozygosity is of the expected sign (negative for trust, positive for articles) and statistically significant in all specifications. For example, in the trust equation for the full sample, the coefficient on genetic diversity is statistically significant at the 5% level,

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[12]Ashraf and Galor (2013) report the variable as articles per capita, but the values of the variable, ranging from 0 to 0.97 are consistent with articles per 1,000 capita

and implies that a 1 percentage-point increase in genetic diversity is associated with a decrease of approximately 1.92 percentage points of interpersonal trust. The results suggest that a percentage point increase in ancestry-adjusted predicted genetic diversity implies an increase in annual scientific articles per capita by about 0.02, and the coefficient is statistically significant at the 5% level. The results presented in Table 9 of Ashraf and Galor are taken to corroborate the genetic diversity channels, bolstering "the theoretical assertion that diversity confers conflicting effects on productivity, generating inefficiencies in the production process while, at the same time, fostering the expansion of a society's production possibilities frontier" (p. 43).

In row 2, we include the full set of legal origin fixed effects, i.e., British, French, German, and Scandinavian, with socialist as the omitted category. For trust in the complete 58-country sample with the full set of legal origins, the coefficient remains statistically significant at −2.2. For article publication in the complete 93-country sample with the full set of legal origins, the coefficent drops by one third from the value in the first row with the published truncated set of legal origins.

In the common sample of 56 countries, the coefficient on ancestry-adjusted predicted heterozygosity is significant for neither trust nor articles. For trust, the coefficient declines slightly while the standard error increases so that statistical significance disappears. The point estimates of the coefficient on ancestry-adjusted predicted genetic diversity increases slightly in magnitude, with an 1 percentage-point increase in diversity now implying a 2-percentage point decrease in trust. However, the significance of the coefficient drops to below the 10% level, with a standard error slightly too large to reject the null hypothesis of zero at the conventional significance threshold.[13] For articles, the coefficient on ancestery-adjusted predicted heterozygosity declines by an order of magnitude. The estimated effect of a 1 percentage-point increase in genetic diversity results in only 0.004 additional annual scientific articles per capita, not 0.03. The standard error increases modestly.[14]

Row 3 omits the legal-origin indicators altogether. For trust with the full 58-country sample, the coefficient on ancestry-adjusted predicted heterozygosity drops by about one quarter and is significant at only the 10% level. When two countries are dropped to create the common sample, the coefficient (−1.27) is almost forty percent smaller than the published value for the full sample

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[13]Most of the covariates remain similar both in magnitude and statistical significance, as seen in Table 5, column 2, with the most substantial change occurring with the coefficient on social infrastructure, which drops both in magnitude and statistical significance. Full model results are available from the authors.

[14]The coefficients on other covariates change moderately with the inclusion of the full set of legal origins fixed effects. The coefficient on French legal origin is significant at the 10% level, and the coefficient on Scandinavian legal origins is statistically significant at the 1% level. Additionally, the coefficient value of ancestry-adjusted Neolithic transition timing drops and is no longer statistically significant. Similarly as between columns 1 and 2, the coefficient on social infrastructure decreases by over 50%, and drops substantially in statistical significance. The coefficient on distance from waterways increases both in magnitude and statistical significance, as does the coefficient on schooling. Full model results are available from the authors.

(-2.23) and is not statistically significant. For articles the omission of legal-indicator dummies in the full sample reduces the coefficient by about one standard error. In the common sample, the omission of legal indicator dummies raise the coefficient to 2.30, between the published values for the full article sample and the common sample.

Overall there is substantial instability in the channel results. Neither the full samples for trust and articles nor the common sample are selected on the basis of anything other than data availability, yet the results vary significantly based on which sample is used. The exclusion of only 2 countries out of 58 alters the coefficients by as much as one quarter.

The results are sensitive to specification and to sample. The inconsistent coding in the inclusion of an incomplete set of legal-origins indicators and the sample dictated by data availability result in coefficient values and standard errors that conform to the hypothesis that genetic diversity affects development through the proposed mechanisms. When the coding is standardized to include the full set of legal-origin inidicators and the common sample is used, neither the trust nor the creativity channel for genetic diversity remains statistically significant; in the case of creativity proxied by the number of scientific articles published, the corrected specification shows essentially no effect of genetic diversity.

The assignment of countries by the origin of their legal systems, while undoubtedly an important control for cultural and institutional factors (per Equation 9 in Ashraf and Galor) should not wholly mediate a robust relationship between genetic diversity and the proposed channels to development. The variable results call into question the validity of the proposed channels by which genetic diversity affects development. The hypothesis of Ashraf and Galor depends on simultaneous offsetting mechanisms from increasing diversity — the beneficial effect of increased creativity and innovation with the detrimental effect on trust cooperation. Without evidence for the mechanisms, the hump-shaped relationship between genetic diversity and some measures of development probably represents historical contingency. The case for "deep roots" appears weak.

4   Conclusion

Ashraf and Galor proposes the existence of a non-monotonic effect of genetic diversity on economic development: at high levels of diversity, a society has a larger number of traits, and can thus innovate, adapt, and spread technologies better. But at high levels of diversity, a society is afflicted with mistrust and a lack of cooperation, inhibiting productivity and economic development. Ashraf and Galor empirically tests this relationship for both the pre-colonial and contemporary eras to examine the stability of the relationship throughout history. They also examine the mechanisms or channels through which this relationship supposedly affects economic development. We operationalize several

critiques presented in Guedes et al.

Ashraf and Galor makes strong genetic determinist claims about the trajectory of economic development from prehistory to the present. Claims about the genetic basis for social and economic outcomes should face an especially high standard. By using contemporary genetic data to explain past outcomes, Ashraf and Galor *a priori* invert their proposed cause and effect. The study has chosen outdated and incomplete data for key independent and dependent variables. The data for a key dependent variables, population density in 1500 CE, the only dependent variable analyzed in relation to the directly measured independent variable, are from a source not considered credible in archaelology, the discipline with actual expertise in measurement.

The finding on the proposed causal mechanisms result from faulty coding. Our empirical analysis casts significant doubt on both points in the proposed causal pathways.

We incorporate additional genetic diversity data on the Americas from Wang et al. The empirical results presented in the only portion of Ashraf and Galor that uses actual observed genetic diversity data largely disappear. The addition of the Wang et al. data in Columns 2, 4, and 6 of Tables 2 and 3 show essentially no relationship between heterozygosity and population density in 1500 CE, the only result in Ashraf and Galor that associates observed heterozygosity data with development outcomes.

Genetic diversity, controlling for a variety of covariates, has no statistically significant effect on economic development in 1500 CE. We find substantial sensitivity to the selection of covariates in the additional specifications we present in which continent fixed effects are the only covariates in Tables 2 and 3 using the original Ashraf and Galor data, let alone the addition of the Wang et al. data.

We also incorporate an updated population dataset based on more recent, higher-quality research on the pre-colonial population of the Americas. We find that the size of the relationship between genetic diversity and population density, especially in the Americas, drops substantially, resulting in estimated effects much lower than those presented in Ashraf and Galor.

The last component of our analysis uncovers inconsistent coding present in the original paper. Ashraf and Galor fail to include the appropriate number of fixed effects. When corrected, the conclusions of their analysis regarding the mechanisms through which genetic diversity affects economic development no longer hold; according to their specifications, there seems to be no evidence that the two competing mechanisms of the genetic diversity channel are operating simultaneously in the same set of countries.

Our analysis casts the results presented in Ashraf and Galor into significant doubt. The results that depend on the most direct measurement of genetic diversity do not persist when improved data are used. The continent-level case is unpersuasive. Everyone knows that Africa and South America

are poorer than Europe and the much of Asia today. The Ashraf and Galor "deep roots" hypothesis depends on a combination of details, such as pre-colonial population size and the representativeness of HGDP-CEPH sampling, that do not hold up on closer inspection, and of continent-scale comparisons that express but fail to explain the central questions of development.

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Table 1: *Pooled and Within-Region Heterozygosity-Migratory Distance Regressions*

	Region fixed effect			Region-specific slope	
	(1)	(2)	(3)	(4)	(5)
Distance	−0.007*** (0.001)	−0.006*** (0.002)	−0.002 (0.003)		
Ashraf and Galor Regions					
Africa				−0.0001 (0.002)	
America		−0.014 (0.033)		−0.008** (0.004)	
Asia		−0.013 (0.011)		−0.005*** (0.001)	
Europe		−0.013** (0.006)		−0.003* (0.002)	
Oceania		−0.010 (0.025)		−0.011	
Alternative Regions					
Africa					0.001 (0.002)
N. Africa, Europe, and Central Asia			−0.023*** (0.008)		−0.002* (0.001)
East Asia			−0.040* (0.023)		−0.004 (0.002)
Oceania			−0.062 (0.043)		−0.011
North America			−0.043 (0.048)		0.007 (0.005)
Central America			−0.083 (0.059)		−0.003 (0.018)
South America			−0.105 (0.064)		−0.003 (0.009)
Constant	0.770*** (0.005)	0.778*** (0.008)	0.765*** (0.012)		
Observations	79	79	79	79	79
Adjusted R^2	0.746	0.736	0.749	0.998	0.998

Notes. Each column reports the regression of measured heterozygosity on migratory distance from Addis Ababa and, in columns 2 and 3, regional indicator variables. Columns 4 and 5 report the coefficient on migratory distance in within-region regressions of heterozygosity on migratory distance for each region. Heteroskedasticity-robust standard errors reported in parentheses. *p<0.1; **p<0.05; ***p<0.01.

Table 2: *Population Density in 1500 CE vs. Measured Diversity*

| | AG Table 1 Column 1 | | AG Table 1 Column 5 | | Continent Fixed Effects | |
| | Replication | Wang | Replication | Wang | Continent FEs only | Wang |
	(1)	(2)	(3)	(4)	(5)	(6)
Observed heterozygosity	413.504***	57.648	203.815**	72.138	67.979	−13.130
	(97.319)	(58.102)	(97.637)	(53.227)	(88.494)	(82.380)
Observed heterozygosity squared	−302.646***	−38.216	−145.718*	−54.842	−23.300	13.755
	(73.344)	(44.784)	(80.414)	(47.103)	(73.059)	(73.995)
log Neolithic transition timing			1.135*	1.733***		
			(0.658)	(0.518)		
log percentage of arable land			0.545**	0.391		
			(0.262)	(0.256)		
log absolute latitude			−0.129	−0.051		
			(0.174)	(0.165)		
log land suitability for agriculture			0.587*	0.798**		
			(0.328)	(0.328)		
Americas			−0.448	−1.317	1.292	−2.456
			(1.258)	(0.855)	(0.928)	(1.793)
Europe			−0.498	−0.414	−0.777	−0.227
			(0.666)	(0.600)	(1.003)	(1.011)
Africa			−0.251	0.413	−3.936***	−2.596**
			(1.140)	(1.024)	(0.930)	(1.236)
Constant	−138.889***	−20.631	−78.845***	−36.107**	−33.936	4.861
	(31.850)	(18.558)	(28.011)	(15.248)	(25.994)	(21.190)
Optimal heterozygosity	0.683	0.754	0.699	0.658	1.459	0.477
	(0.008)	(0.133)	(0.055)	(0.086)	(2.677)	(0.462)
Slope at Brazil	0.791	0.154	0.428	0.115	0.422	0.021
	(0.166)	(0.092)	(0.102)	(0.036)	(0.083)	(0.053)
Slope at South Africa	−0.523	−0.012	−0.205	−0.123	0.321	0.08
	(0.16)	(0.115)	(0.269)	(0.197)	(0.242)	(0.321)
Observations	21	28	21	28	21	28
Adjusted R^2	0.352	0.046	0.824	0.803	0.533	0.379

Notes. Each column reports the regression of log population density in 1500 CE on measured heterozygosity. Heterozygosity is the average expected heterozygosity of all ethnic groups located in the country. 21 countries comprising 53 ethnic groups in Ashraf and Galor (2013) data based on the HGDP-CEPH data of Ramachandran et al. (2005) and 28 countries comprising 79 ethnic groups in the Wang et al. (2007)-augmented data. Heteroskedasticity-robust standard errors reported in parentheses. Standard error for the optimum computed using the Delta method. *p<0.1; **p<0.05; ***p<0.01.

Table 3: *Population Density in 1500 CE vs. Measured Diversity, 2SLS*

| | AG Table 2 Column 5 | | AG Table 2 Column 6 | | Continent Fixed Effects | |
| | Replication | Wang | Replication | Wang | Continent FEs only | Wang |
	(1)	(2)	(3)	(4)	(5)	(6)
Observed heterozygosity	285.190***	41.705	243.107***	84.481	98.549	−79.277
	(88.063)	(58.198)	(63.880)	(93.388)	(118.514)	(124.521)
Observed heterozygosity squared	−206.576***	−23.402	−179.578***	−66.152	−50.445	71.874
	(66.852)	(44.732)	(52.038)	(79.266)	(96.200)	(96.896)
log Neolithic transition timing	1.014***	1.917***	1.119**	1.735***		
	(0.361)	(0.397)	(0.487)	(0.417)		
log percentage of arable land	0.608***	0.252	0.634***	0.420		
	(0.188)	(0.211)	(0.211)	(0.257)		
log absolute latitude	−0.209*	−0.118	−0.133	−0.040		
	(0.121)	(0.141)	(0.127)	(0.150)		
log land suitability for agriculture	0.494**	0.881***	0.549**	0.776***		
	(0.233)	(0.280)	(0.253)	(0.292)		
Americas			−0.935	−1.499	0.781	−1.663
			(0.880)	(1.082)	(1.081)	(1.811)
Europe			−0.396	−0.374	−0.631	−0.526
			(0.441)	(0.466)	(0.787)	(0.783)
Africa			0.238	0.626	−3.497***	−3.502***
			(0.789)	(1.272)	(1.162)	(1.131)
Constant	−105.033***	−31.596*	−89.772***	−39.321	−41.970	22.553
	(26.786)	(17.897)	(18.826)	(28.424)	(35.639)	(40.166)
Optimal heterozygosity	0.69	0.891	0.677	0.639	0.977	0.551
	(0.013)	(0.536)	(0.031)	(0.106)	(0.817)	(0.174)
Slope at Brazil	0.569	0.158	0.447	0.114	0.428	0.001
	(0.175)	(0.105)	(0.106)	(0.118)	(0.153)	(0.248)
Slope at South Africa	−0.328	0.057	−0.333	−0.173	0.209	0.313
	(0.183)	(0.127)	(0.235)	(0.374)	(0.355)	(0.33)
Observations	21	28	21	28	21	28
Adjusted R^2	0.843	0.792	0.821	0.802	0.528	0.357

Notes. Each column reports the 2SLS regression of log population density in 1500 CE on measured heterozygosity and its square, instrumented with distance-predicted heterozygosity and the square of distance from Addis Ababa. Heterozygosity is the average expected heterozygosity of all ethnic groups located in the country. 21 countries comprising 53 ethnic groups in Ashraf and Galor (2013) data based on the HGDP-CEPH data of Ramachandran et al. (2005) and 28 countries comprising 79 ethnic groups in the Wang et al. (2007)-augmented data. Heteroskedasticity-robust standard errors reported in parentheses. Standard error for the optimum computed using the Delta method. *p<0.1; **p<0.05; ***p<0.01.

Table 4: *Population Density in 1500 CE vs. Distance-Predicted Diversity*

	Replication	Country-Clusters	Denevan	Country-Clusters	Denevan	Country-Clusters	Denevan
	(1)	(2)	(3)	(4)	(5)	(6)	(7)
Predicted Heterozygosity	250.985***	262.525***	182.676***	188.132***	112.332*	199.964**	265.149***
	(69.828)	(69.768)	(63.372)	(56.915)	(62.933)	(89.861)	(92.135)
Predicted Heterozygosity (square)	−177.399***	−186.415***	−134.664***	−133.183***	−84.508*	−146.604**	−190.584***
	(51.478)	(51.125)	(47.054)	(41.344)	(46.060)	(62.530)	(64.059)
log Neolithic transition timing				1.159***	1.072***	1.286***	1.151***
				(0.149)	(0.206)	(0.224)	(0.265)
log percentage of arable land				0.404***	0.502***	0.383***	0.434***
				(0.096)	(0.112)	(0.108)	(0.114)
log absolute latitude				−0.329***	−0.366***	−0.403***	−0.421***
				(0.097)	(0.108)	(0.133)	(0.134)
log land suitability for agriculture				0.292***	0.248**	0.254***	0.238**
				(0.094)	(0.106)	(0.096)	(0.104)
Americas						−0.374	1.893
						(1.040)	(1.168)
Oceania						−0.216	−0.004
						(0.885)	(0.976)
Europe						0.662***	0.585**
						(0.228)	(0.246)
Africa						0.485	0.329
						(0.333)	(0.373)
Constant	−87.402***	−91.002***	−60.268***	−74.338***	−44.366**	−77.002**	−100.006***
	(23.506)	(23.658)	(21.160)	(19.293)	(21.060)	(32.442)	(33.266)
Optimal heterozygosity	0.707	0.704	0.678	0.706	0.665	0.682	0.696
	(0.029)	(0.015)	(0.179)	(0.018)	(0.487)	(0.932)	(1.488)
Slope at Brazil	0.447	0.458	0.261	0.333	0.141	0.295	0.435
	(0.103)	(0.107)	(0.09)	(0.091)	(0.096)	(0.178)	(0.183)
Slope at South Africa	−0.119	−0.138	−0.169	−0.093	−0.129	−0.173	−0.173
	(0.071)	(0.067)	(0.07)	(0.049)	(0.058)	(0.06)	(0.062)
Observations	145	137	137	137	137	137	137
Adjusted R^2	0.208	0.160	0.027	0.646	0.565	0.657	0.604

Notes. Each column reports the regression of log population density in 1500 CE on predicted heterozygosity. Heterozygosity for 145 countries or 137 country-clusters is predicted with migratory distance from Addis Ababa. Bootstrapped standard errors accounting for the use of predicted regressors in parentheses. *p<0.1; **p<0.05; ***p<0.01.

Table 5: *Trust and Creativity Channels: Replicated and Corrected Legal-Origins Specifications*

	Trust		Articles	
	Full sample	Common sample	Full sample	Common sample
Partial legal origins	−2.23**	−1.92**	1.86***	3.02**
	(0.86)	(0.94)	(0.55)	(1.22)
Full legal origins	−2.22**	−2.01	1.20**	0.42
	(1.01)	(1.25)	(0.50)	(1.52)
No legal origins	−1.68*	−1.27	1.42***	2.30**
	(0.90)	(1.01)	(0.48)	(0.96)
N	58	56	93	56

Notes. Each entry reports the coefficient on ancestry-adjusted predicted heterozygosity from the regression of a development channel — trust or creativity — on ancestry-adjusted distance-predicted heterozygosity and other variables. Trust is measured by the World Values Survey. Creativity is measured by the average number of scientific articles per capita from the World Bank. Ancestry-adjusted distance-predicted heterozygosity is explained in Ashraf and Galor (2013). Partial legal origins refers to inclusion of the subset of legal-origin indicator variables selected by Ashraf and Galor (2013) for the trust specifications (distinguishing only Scandinavian and German legal origins) and for the creativity specifications (distinguishing only British and French legal origins) in Table 9. Full legal origins refers to inclusion of the full set of legal-origin indicator variables (Scandinavian, German, British, and French). No legal origins refers to specifications excluding the legal-origin indicator variables. Full sample refers to the full set of countries for which data on the particular development channel are available (58 countries for trust, 93 countries for scientific articles). Common sample refers to the set of countries for which data on both development channels are available (56 countries). Heteroskedasticity-robust standard errors reported in parentheses. *p<0.1; **p<0.05; ***p<0.01.

Figure 1: *HGDP-CEPH Sample Map*

Map of 53 Ethnic Groups from Ashraf and Galor

Source: Authors' calculations with data from Ashraf and Galor (2013). See text for details.

Map of 28 Ethnic Groups from Wang et al.

Observed Heterozygosity   ● 0.50   ● 0.55   ● 0.60   ● 0.65

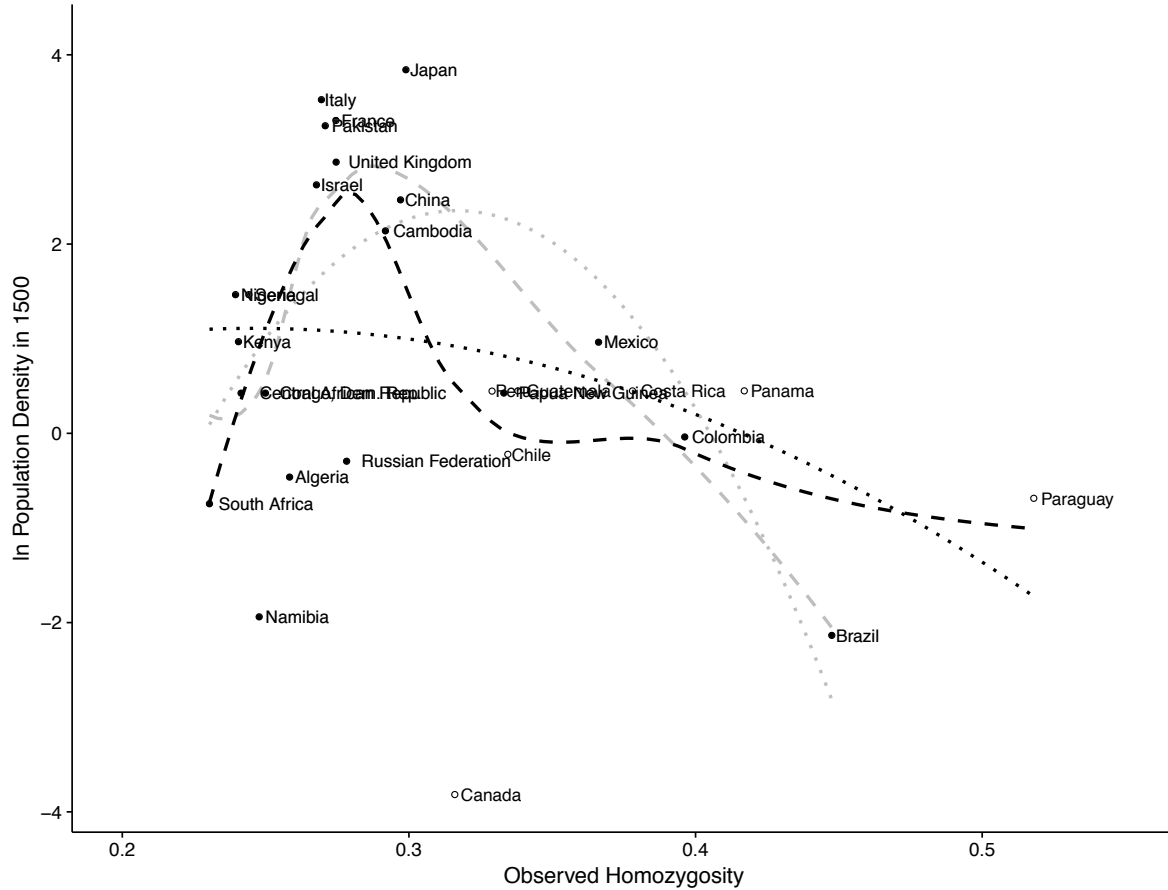Source: Authors' calculations with data from Ashraf and Galor (2013) and Wang et al. (2007). See text for details.

**Figure 3:** *Observed Heterozygosity vs. Migratory Distance: Original and Wang et al. (2007) Additions*
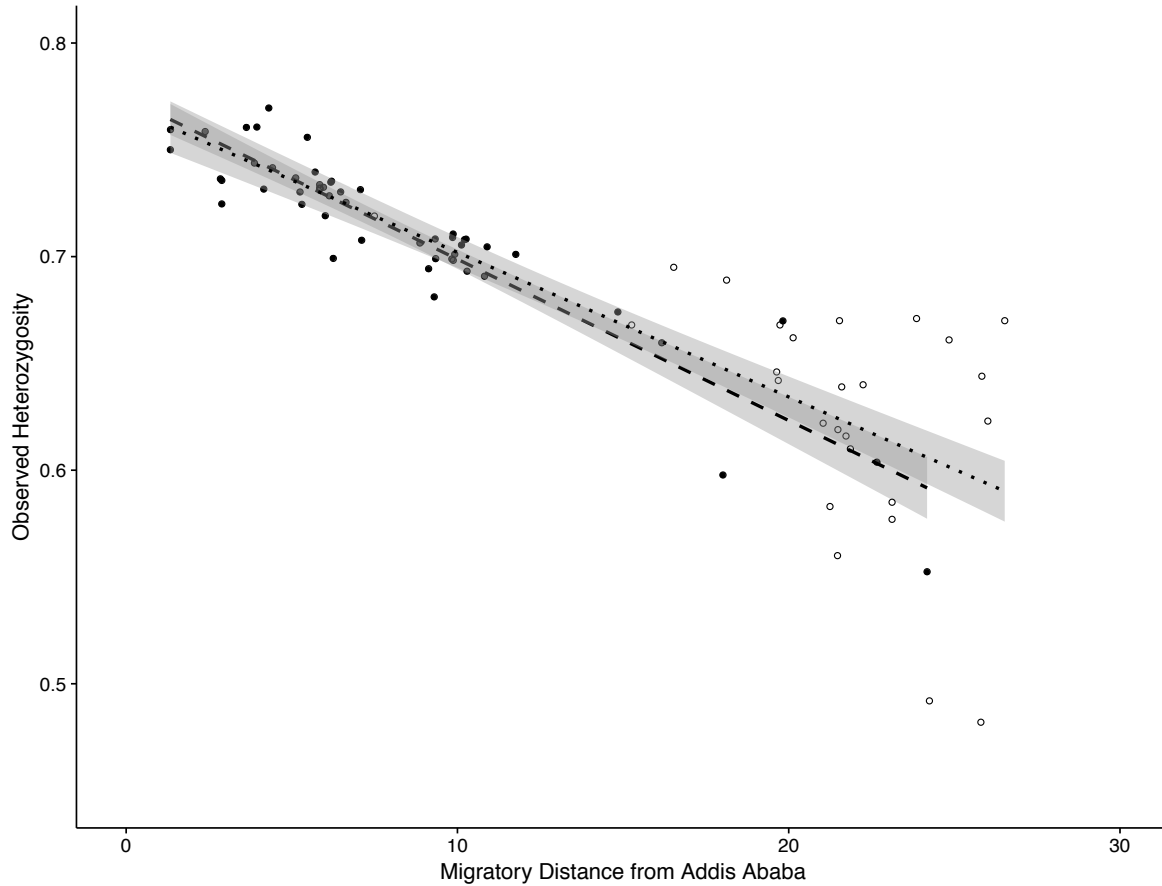
Notes. The plot shows the relationship between Observed Genetic Diversity (Heterozygosity) and Migratory Distance from Addis Ababa for 79 contemporary ethnic groups. The 53 filled dots show data from Ashraf and Galor (2013) and the dashed regression line shows the linear fit for this subset of the data. The 26 empty dots show additional data from Wang et al. (2007). The solid line regression line shows the linear fit for all of the data. The dotted line shows the fit for each of five continents. The dashed line shows the fit for each of seven regions. See text for details.

Source: Authors' calculations with data from Ashraf and Galor (2013) and Wang et al. (2007). See text for details.

Figure 4: *Observed Heterozygosity vs. Migratory Distance: Between and within regions*
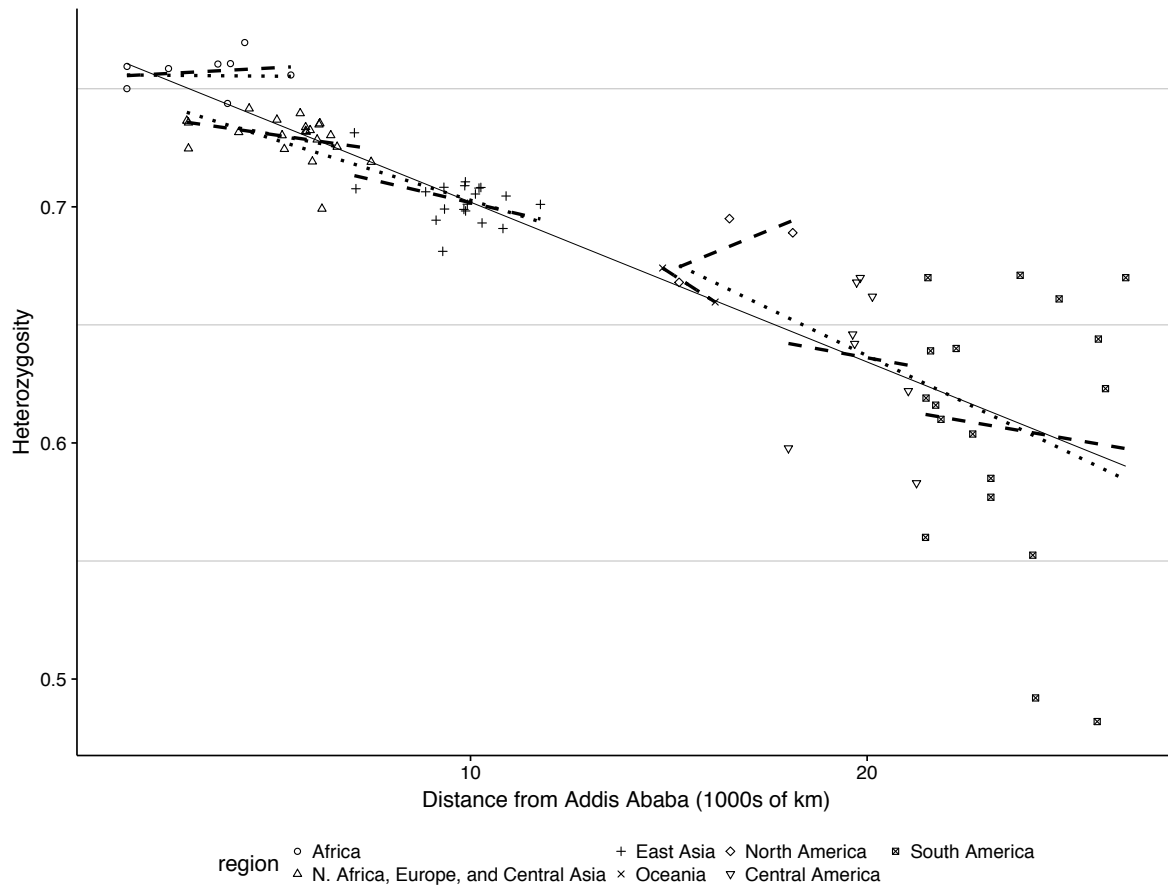
Notes. The plot shows the relationship between Observed Genetic Diversity (Heterozygosity) and Migratory Distance from Addis Ababa for 79 contemporary ethnic groups. The extended solid regression line uses the entire sample. The shorter regression lines show the relationship between Heterozygosity and Migratory Distance from Addis Ababa within each of seven regions: sub-Saharan Africa; North Africa, Europe, and Central Asia; East Asia; Oceania; North America; Central America; and South America.

Source: Authors' calculations with data from Ashraf and Galor (2013) and Wang et al. (2007). See text for details.

Figure 5: *AG Figure 3 with Wang et al. (2007) Western Hemisphere Data*

Notes. The plot shows the bivariate relationship between log population density in 1500 CE and Observed Genetic Homogeneity for 21 countries based on genetic data from 53 contemporary ethnic groups. The gray curves and filled points replicate Figure 3 in Ashraf and Galor (2013). The open points show the data for 7 additional countries based on 26 additional ethnic groups of the Western Hemisphere from Wang et al. (2007), and the black curves show the fit through the full data. Dotted lines are a quadratic fit; dashed lines are a non-parametric fit.

Source: Authors' calculations with data from Ashraf and Galor (2013) and Wang et al. (2007). See text for details.

Figure 6: *AG Figure 3 with Wang et al. (2007) Western Hemisphere Data and Covariates*
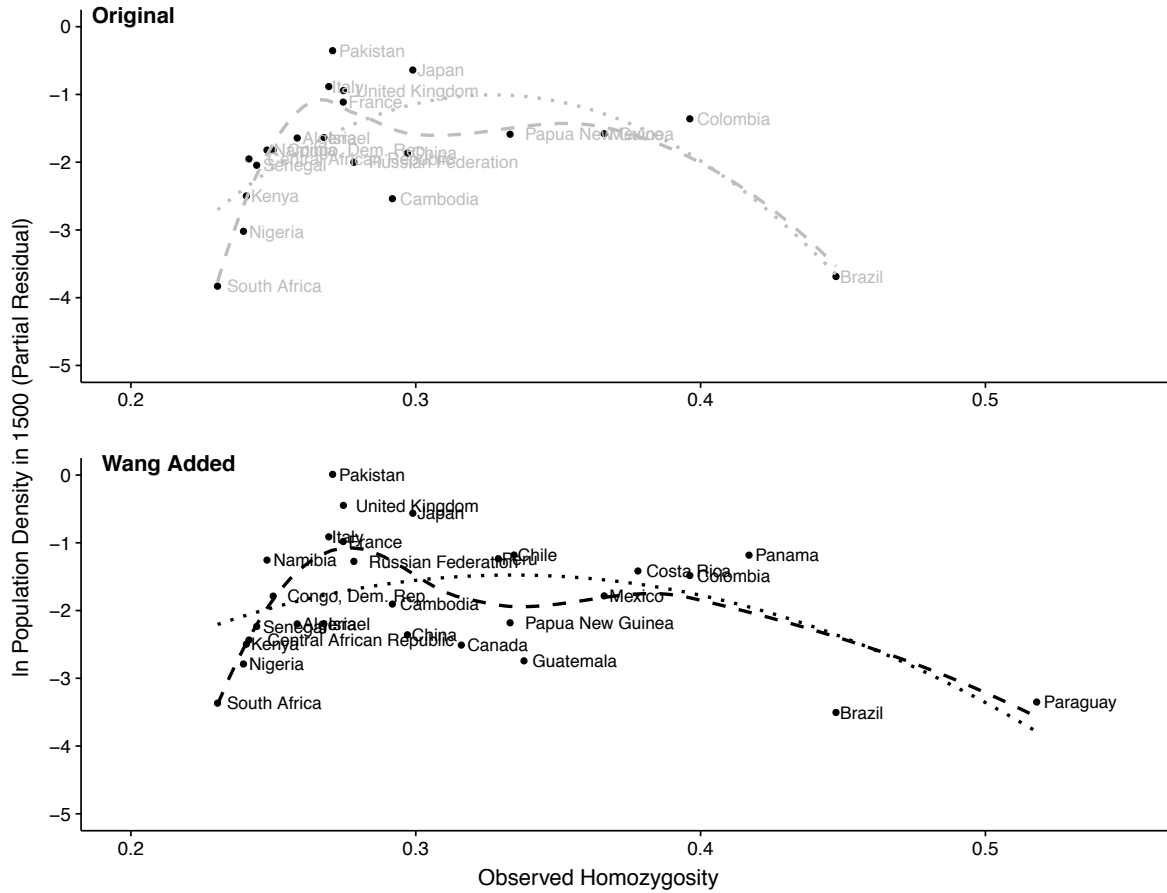
Notes. The plot shows the relationship between log population density in 1500 CE (from the McEvedy and Jones (1978) population data used by Ashraf and Galor (2013)) and Observed Genetic Homogeneity for 79 contemporary ethnic groups, with a partial linear model to control for covariates (four continent indicators and, all in natural log, years since the neolithic transition, arable share of land area, absolute value of latitude, land area suitable for agriculture). The upper panel uses data for the 21 countries for which homozygosity data are reported in Ashraf and Galor (2013). The lower panel additionally shows data for the 23 additional ethnic groups of the Western Hemisphere from Wang et al. (2007). Dotted lines are a quadratic fit; dashed lines are a non-parametric fit.

Source: Authors' calculations with data from Ashraf and Galor (2013) and Wang et al. (2007). See text for details.

Figure 7: *AG Figure 4 with Consistent Estimator*
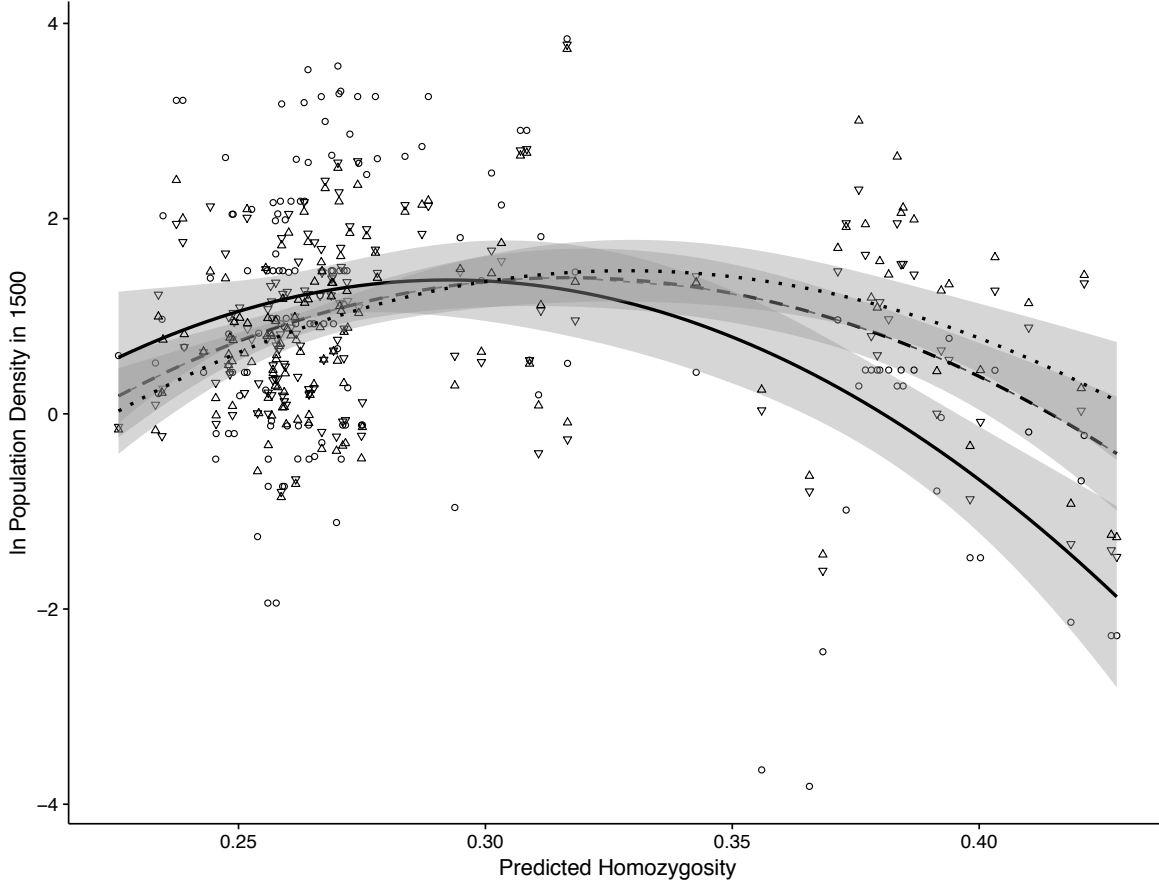
Notes. The vertical axis shows log of Population Density in 1500 CE from the Ashraf and Galor (2013) McEvedy and Jones (1978) population estimates. The horizontal axis shows homozygosity (1−heterozygosity) predicted from migratory distance from Addis Ababa. Three datasets and relationships are shown: (1) the bivariate data is shown with open circles, and the bivariate quadratic regression is indicated with the solid line; (2) replicating Figure 4 in Ashraf and Galor (2013), the "augmented component-plus-residual" plot is shown with triangles vertex down, and a quadratic regression through these points is indicated with the dashed line; and (3) the consistent residuals from a partial linear model using the method of Yatchew (2003) is shown with triangles vertex up, and a quadratic regression through these points is indicated with the dotted line.

Source: Authors' calculations with data from Ashraf and Galor (2013). See text for details.

Figure 8: *Denevan (1992) vs. McEvedy and Jones (1978) Population Density Estimates*
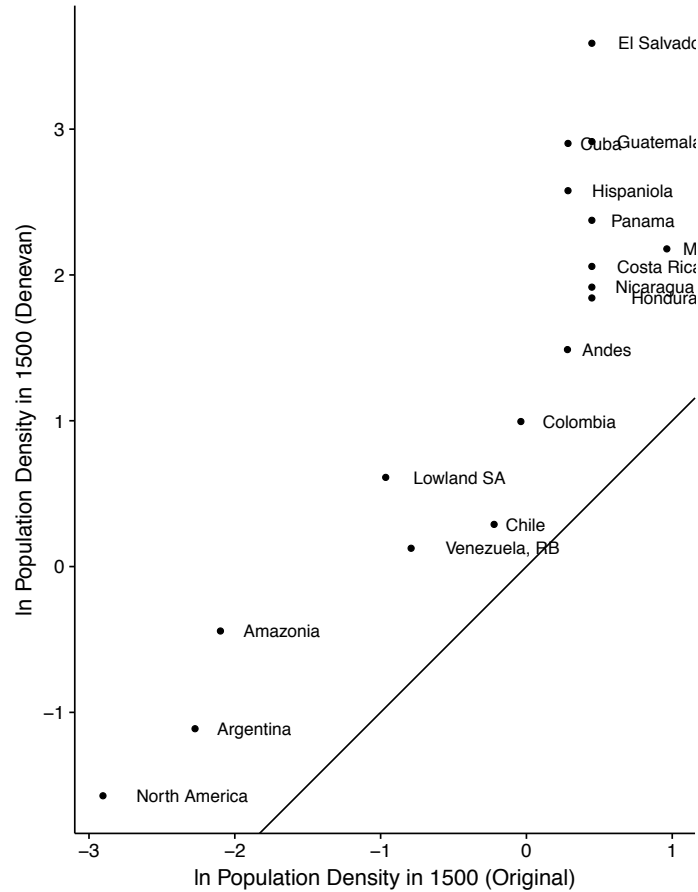
Notes. The horizontal axis shows country or country-cluster population density based on data from Ashraf and Galor (2013) computed from population estimates in McEvedy and Jones (1978). The vertical axis shows country or country-cluster population density based on data from Denevan (1992). The 45-degree line indicates countries for which the Denevan (1992). population and population-density estimates do not indicate a change from those of McEvedy and Jones (1978). Country clusters are based on Denevan (1992) and describe areas comprising one or several countries: Amazonia comprises Brazil, Guyana, and Suriname; Andes comprises Ecuador, Peru, and Bolivia; North America comprises Canada and the United States; Hispaniola comprises Haiti and the Dominican Republic; Honduras-Belize comprises Honduras and Belize; and Lowland South America comprise Paraguay and Uruguay. For the country clusters, population and area were totaled for entire set of constituent countries.

Source: Authors' calculations with data from Ashraf and Galor (2013) and Denevan (1992). See text for details.

Figure 9: *AG Figure 3 with Updated Population Estimates (Quadratic)*
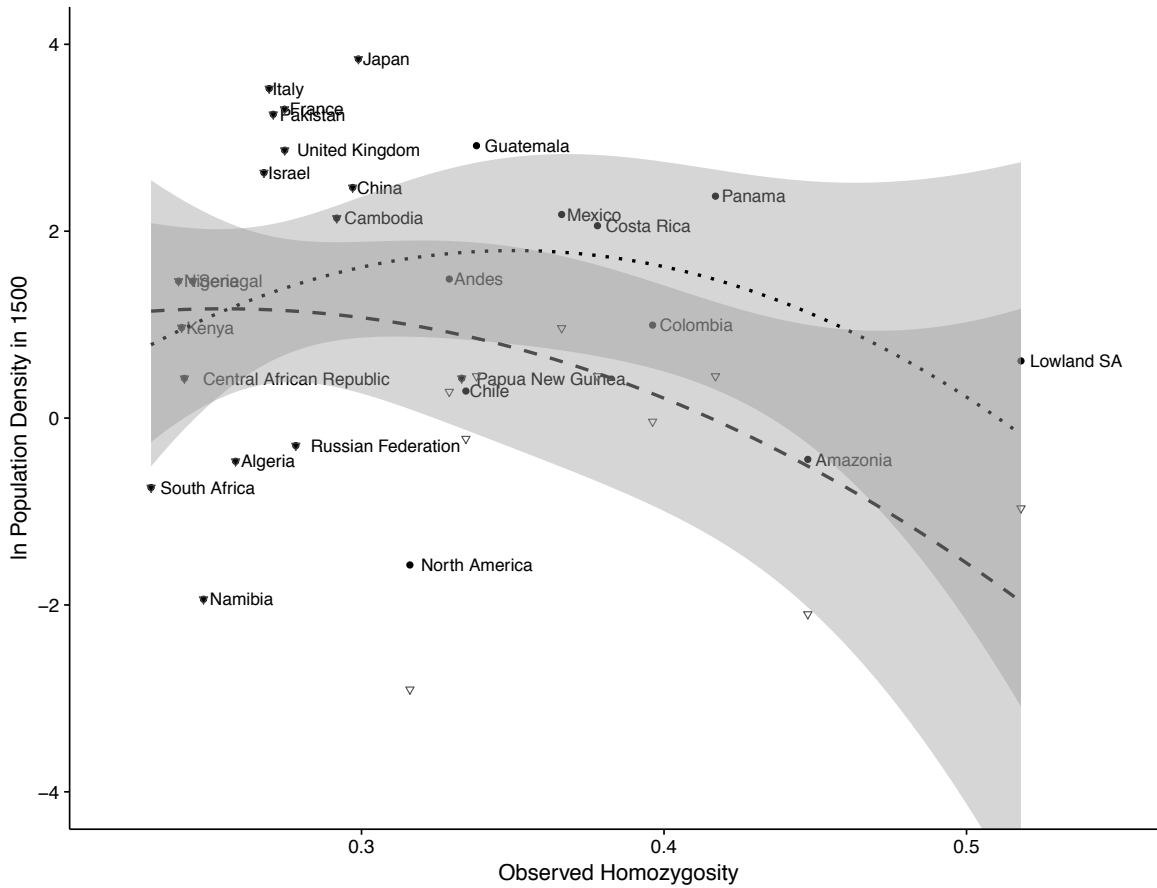
Notes. The plot shows the bivariate relationship between log population density in 1500 CE and Observed Genetic Homogeneity for 28 countries or country clusters based on genetic data from 79 contemporary ethnic groups. The analysis is identical to that of Figure 5 except Western Hemisphere population updates from Denevan (1992) are shown. The unchanged data or updated Denevan (1992) data are labeled points. The original data points from Ashraf and Galor (2013) using McEvedy and Jones (1978) population data are shown as vertex-down triangles, which are directly above or below the updated points for the same countries or country clusters. The dashed line shows the estimated quadratic relationship for the McEvedy and Jones (1978) population data; the dotted line shows the estimated quadratic relationship for the Denevan population data.

Country-clusters are based on Denevan (1992) and describe areas comprising one or several countries: Amazonia comprises Brazil, Guyana, and Suriname; Andes comprises Ecuador, Peru, and Bolivia; North America comprises Canada and the United States; Hispaniola comprises Haiti and the Dominican Republic; Honduras-Belize comprises Honduras and Belize; and Lowland South America comprise Paraguay and Uruguay. For the country clusters, population and area were totaled for entire set of constituent countries; homozygosity was computed as the area-weighted average of the homozygosity of the constituent countries. Source: Authors' calculations with data from Ashraf and Galor (2013) and Denevan (1992). See text for details.
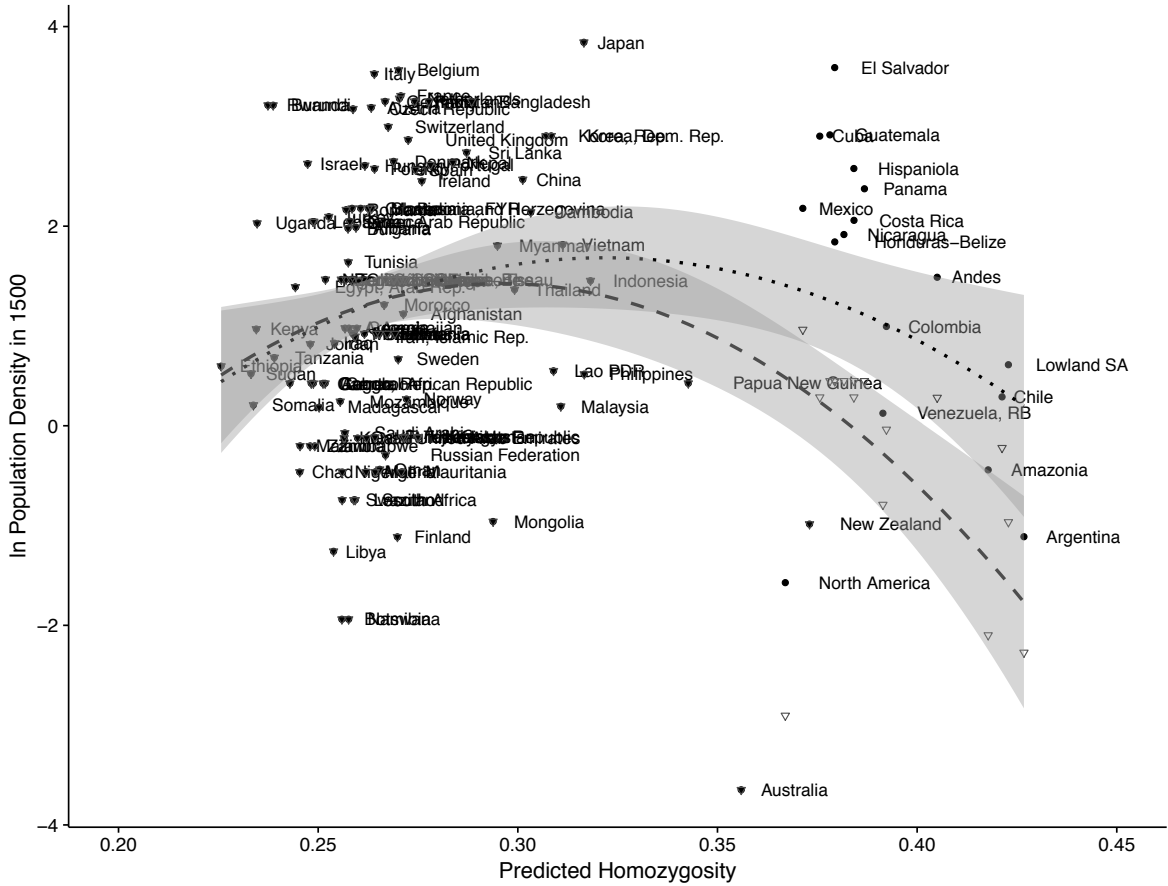
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Figure 10: *AG Figure 3 with Updated Population Estimates (Nonparametric)*
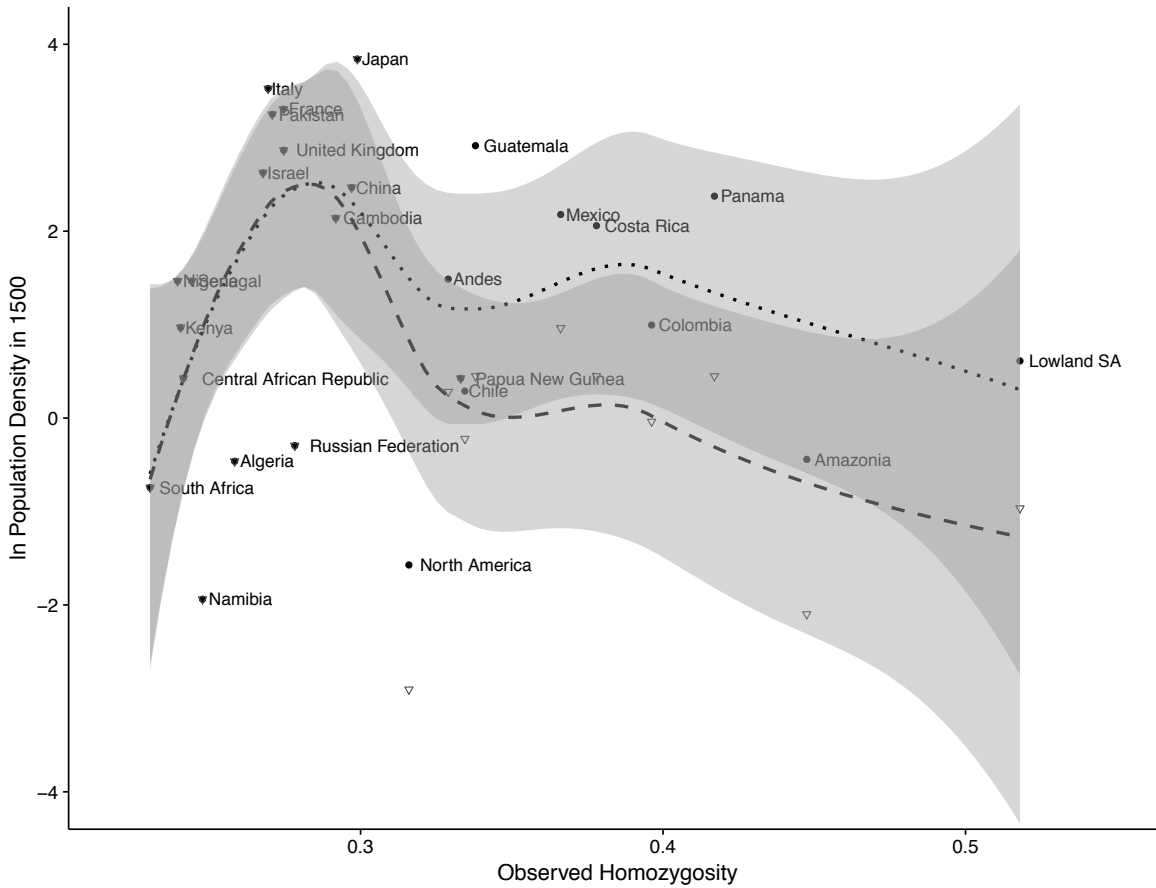
Notes. The plot shows the bivariate relationship between log population density in 1500 CE and Observed Genetic Homogeneity for 27 countries or country clusters based on genetic data from 53 contemporary ethnic groups. The analysis is identical to that of Figure 5 except Western Hemisphere population updates from Denevan (1992) are shown. The unchanged data or updated Denevan (1992) data are labeled points. The original data points from Ashraf and Galor (2013) using McEvedy and Jones (1978) population data are shown as vertex-down triangles, which are directly above or below the updated points for the same countries or country clusters. The dashed line shows the estimated non-parametric (loess) relationship for the McEvedy and Jones (1978) population data. The dotted line shows the estimated loess relationship for the Denevan population data.

Country-clusters are based on Denevan (1992) and describe areas comprising one or several countries: Amazonia comprises Brazil, Guyana, and Suriname; Andes comprises Ecuador, Peru, and Bolivia; North America comprises Canada and the United States; Hispaniola comprises Haiti and the Dominican Republic; Honduras-Belize comprises Honduras and Belize; and Lowland South America comprise Paraguay and Uruguay. For the country clusters, population and area were totaled for entire set of constituent countries; homozygosity was computed as the area-weighted average of the homozygosity of the constituent countries. Source: Authors' calculations with data from Ashraf and Galor (2013) and Denevan (1992). See text for details.

Figure 11: *Density vs. Homozygosity with Updated Population Estimates (Quadratic)*

Notes. The plot shows the bivariate relationship between log of Population Density in 1500 CE and homozygosity predicted from migratory distance from Addis Ababa for countries or country clusters using alternately Ashraf and Galor (2013) McEvedy and Jones (1978) population data and Denevan (1992) data. The unchanged data or updated Denevan (1992) data are labeled points. The data points using Ashraf and Galor (2013) McEvedy and Jones (1978) population data to compute population density are shown as vertex-down triangles, which are directly above or below the updated points for the same countries or country clusters. The dashed line shows the quadratic relationship using the Ashraf and Galor (2013) McEvedy and Jones (1978) population estimates to compute population density. The dotted line shows the quadratic relationship for the Denevan population data.

Country-clusters are based on Denevan (1992) and describe areas comprising one or several countries: Amazonia comprises Brazil, Guyana, and Suriname; Andes comprises Ecuador, Peru, and Bolivia; North America comprises Canada and the United States; Hispaniola comprises Haiti and the Dominican Republic; Honduras-Belize comprises Honduras and Belize; and Lowland South America comprise Paraguay and Uruguay. For the country clusters, population and area were totaled for entire set of constituent countries; homozygosity was computed as the area-weighted average of the homozygosities of the constituent countries. Source: Authors' calculations with data from Ashraf and Galor (2013) and Denevan (1992). See text for details.
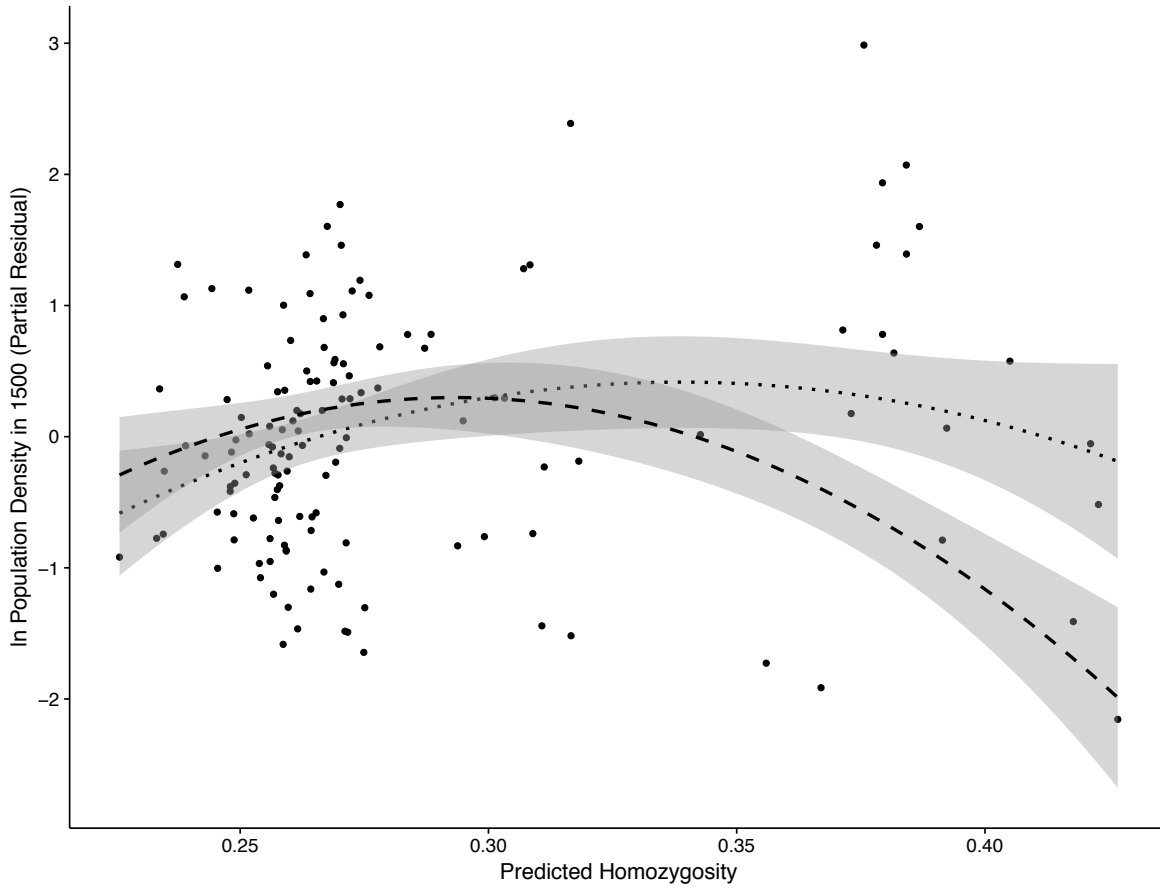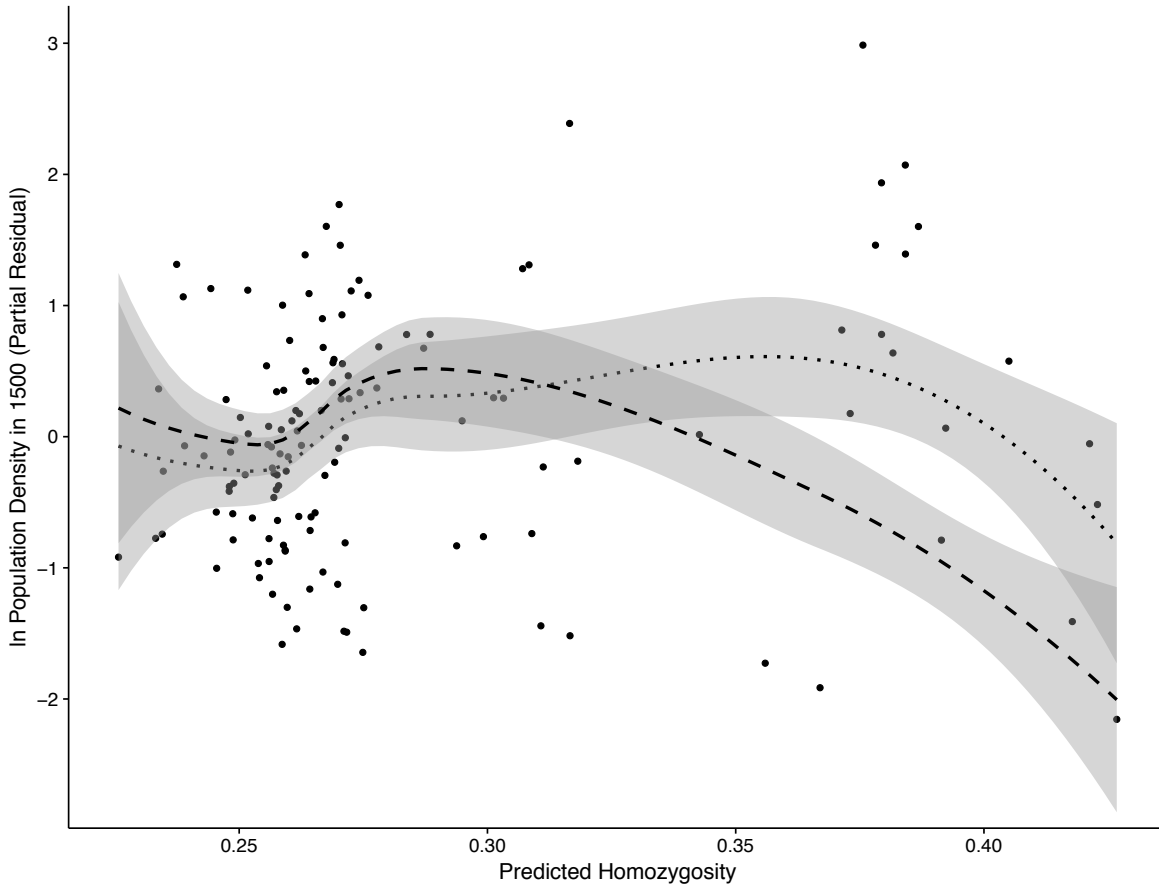
Figure 12: *Density vs. Homozygosity with Updated Population Estimates (Non-parametric)*
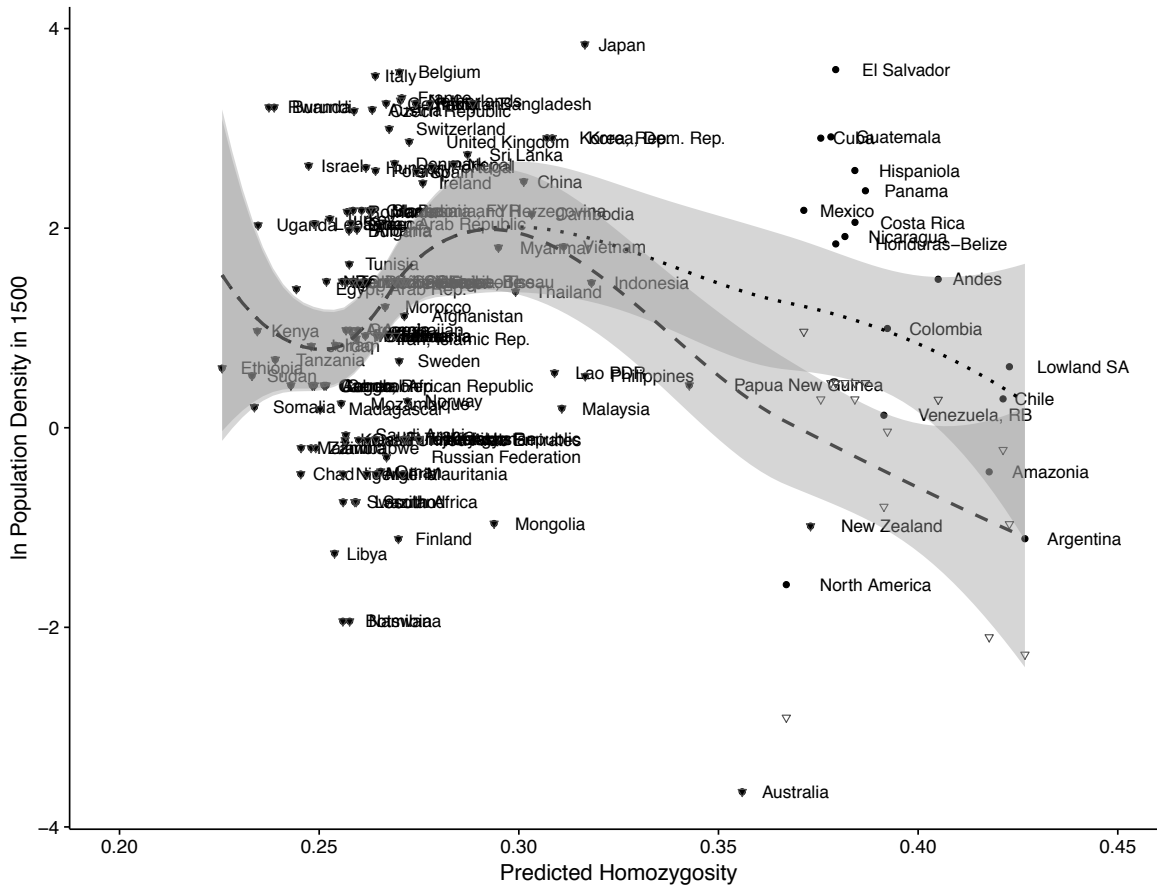
Notes. The plot shows the bivariate relationship between log of Population Density in 1500 CE and homozygosity predicted from migratory distance from Addis Ababa for countries or country clusters using alternately Ashraf and Galor (2013) McEvedy and Jones (1978) population data and Denevan (1992) data. The unchanged data or updated Denevan (1992) data are labeled points. The data points using Ashraf and Galor (2013) McEvedy and Jones (1978) population data to compute population density are shown as vertex-down triangles, which are directly above or below the updated points for the same countries or country clusters. The dashed line shows the non-parametric (loess) relationship using the Ashraf and Galor (2013) McEvedy and Jones (1978) population estimates to compute population density. The dotted line shows the loess relationship for the Denevan population data.

Country-clusters are based on Denevan (1992) and describe areas comprising one or several countries: Amazonia comprises Brazil, Guyana, and Suriname; Andes comprises Ecuador, Peru, and Bolivia; North America comprises Canada and the United States; Hispaniola comprises Haiti and the Dominican Republic; Honduras-Belize comprises Honduras and Belize; and Lowland South America comprise Paraguay and Uruguay. For the country clusters, population and area were totaled for entire set of constituent countries; homozygosity was computed as the area-weighted average of the homozygosities of the constituent countries. Source: Authors' calculations with data from Ashraf and Galor (2013) and Denevan (1992). See text for details.

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Figure 13: *Density vs. Homozygosity with Updated Population Estimates (Quadratic using partial linear model with covariates)*

Notes. The plot shows the relationship between log of Population Density in 1500 CE and homozygosity predicted from migratory distance from Addis Ababa for countries or country clusters using alternately Ashraf and Galor (2013) McEvedy and Jones (1978) population data and Denevan (1992) data with controls for, all in natural log, years since the neolithic transition, arable share of land area, absolute value of latitude, land area suitable for agriculture, but without continent indicators. The controls are introduced as the linear component of a partial linear model using the method of Yatchew (2003). Only the unchanged data or updated Denevan (1992) data are shown. Quadratic regressions through the partial-linear-model residuals are indicated with a dashed line for the Ashraf and Galor (2013) data and with a dotted line for the Denevan (1992) data.

Country-clusters are based on Denevan (1992) and describe areas comprising one or several countries: Amazonia comprises Brazil, Guyana, and Suriname; Andes comprises Ecuador, Peru, and Bolivia; North America comprises Canada and the United States; Hispaniola comprises Haiti and the Dominican Republic; Honduras-Belize comprises Honduras and Belize; and Lowland South America comprise Paraguay and Uruguay. For the country clusters, population and area were totaled for entire set of constituent countries; homozygosity was computed as the area-weighted average of the homozygosities of the constituent countries. Source: Authors' calculations with data from Ashraf and Galor (2013) and Denevan (1992). See text for details.
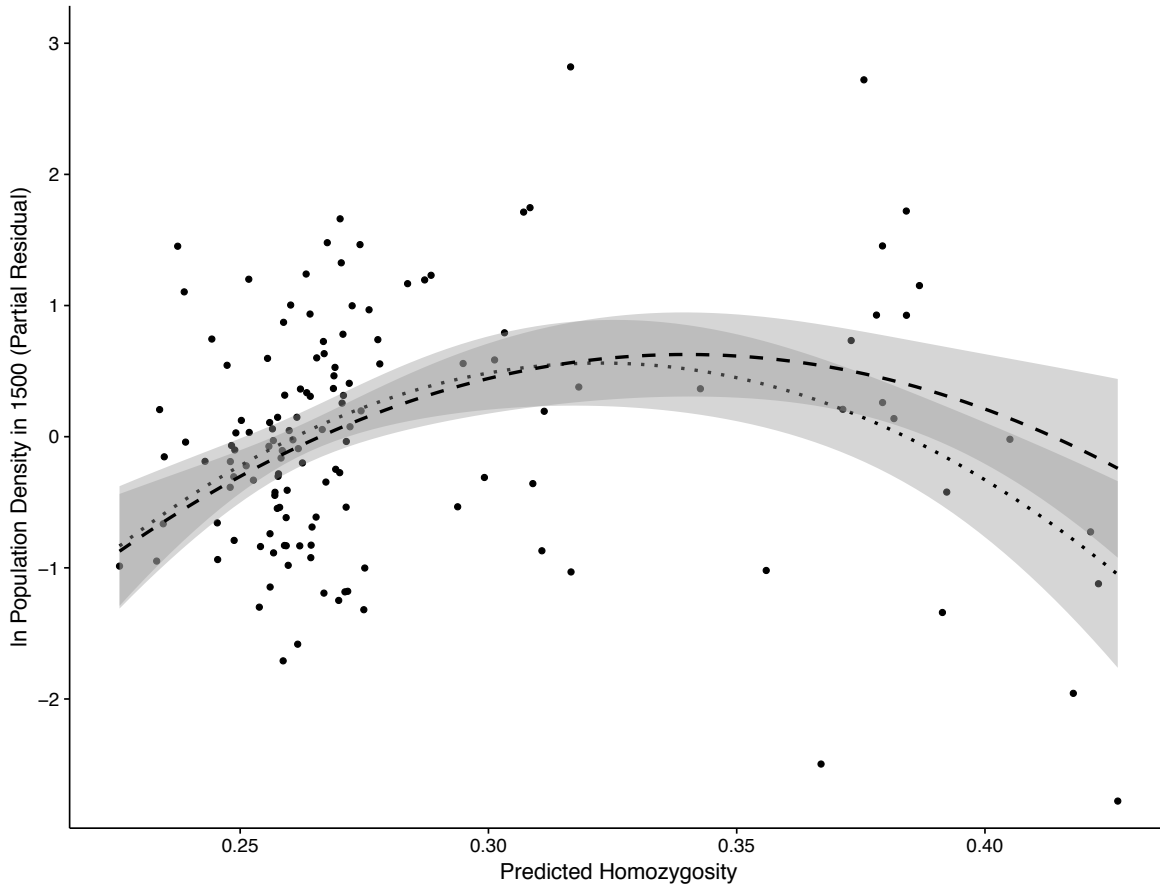
Figure 14: *Density vs. Homozygosity with Updated Population Estimates (Loess using partial linear model with covariates)*

Notes. The plot shows the relationship between log of Population Density in 1500 CE and homozygosity predicted from migratory distance from Addis Ababa for countries or country clusters using alternately Ashraf and Galor (2013) McEvedy and Jones (1978) population data and Denevan (1992) data with controls for, all in natural log, years since the neolithic transition, arable share of land area, absolute value of latitude, land area suitable for agriculture, but without continent indicators. The controls are introduced as the linear component of a partial linear model using the method of Yatchew (2003). Only the unchanged data or updated Denevan (1992) data are shown. Loess regressions through the partial-linear-model residuals are indicated with a dashed line for the Ashraf and Galor (2013) data and with a dotted line for the Denevan (1992) data.

Country-clusters are based on Denevan (1992) and describe areas comprising one or several countries: Amazonia comprises Brazil, Guyana, and Suriname; Andes comprises Ecuador, Peru, and Bolivia; North America comprises Canada and the United States; Hispaniola comprises Haiti and the Dominican Republic; Honduras-Belize comprises Honduras and Belize; and Lowland South America comprise Paraguay and Uruguay. For the country clusters, population and area were totaled for entire set of constituent countries; homozygosity was computed as the area-weighted average of the homozygosities of the constituent countries. Source: Authors' calculations with data from Ashraf and Galor (2013) and Denevan (1992). See text for details.
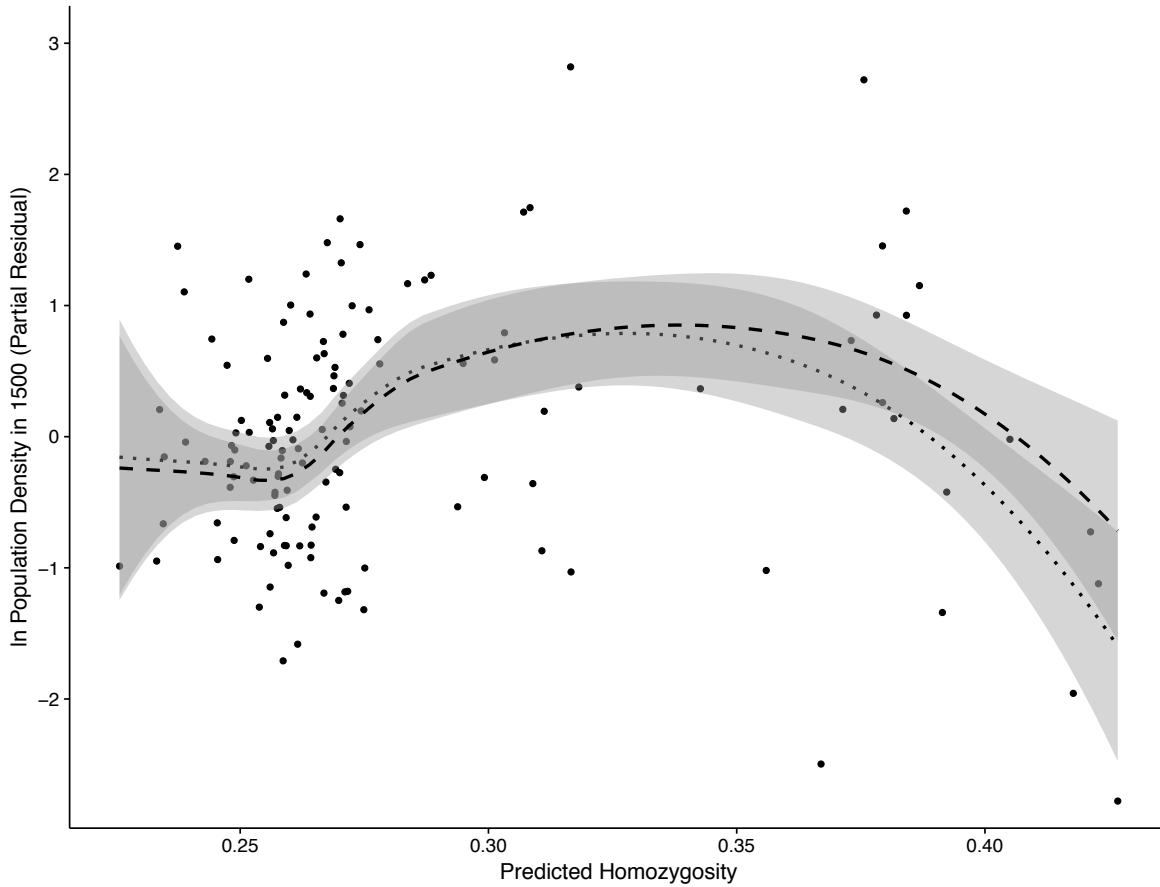
Figure 15: *Density vs. Homozygosity with Updated Population Estimates (Quadratic using partial linear model with covariates and continent fixed effects)*

Notes. The plot shows the relationship between log of Population Density in 1500 CE and homozygosity predicted from migratory distance from Addis Ababa for countries or country clusters using alternately Ashraf and Galor (2013) McEvedy and Jones (1978) population data and Denevan (1992) data, controlling for five continent indicators and, all in natural log, years since the neolithic transition, arable share of land area, absolute value of latitude, land area suitable for agriculture. The controls are introduced as the linear component of a partial linear model using the method of Yatchew (2003). Only the unchanged data or updated Denevan (1992) data are shown. Quadratic regressions through the partial-linear-model residuals are indicated with a dashed line for the Ashraf and Galor (2013) data and with a dotted line for the Denevan (1992) data.

Country-clusters are based on Denevan (1992) and describe areas comprising one or several countries: Amazonia comprises Brazil, Guyana, and Suriname; Andes comprises Ecuador, Peru, and Bolivia; North America comprises Canada and the United States; Hispaniola comprises Haiti and the Dominican Republic; Honduras-Belize comprises Honduras and Belize; and Lowland South America comprise Paraguay and Uruguay. For the country clusters, population and area were totaled for entire set of constituent countries; homozygosity was computed as the area-weighted average of the homozygosities of the constituent countries. Source: Authors' calculations with data from Ashraf and Galor (2013) and Denevan (1992). See text for details.

Figure 16: *Density vs. Homozygosity with Updated Population Estimates (Loess using partial linear model with covariates and continent fixed effects)*

Notes. The plot shows the relationship between log of Population Density in 1500 CE and homozygosity predicted from migratory distance from Addis Ababa for countries or country clusters using alternately Ashraf and Galor (2013) McEvedy and Jones (1978) population data and Denevan (1992) data, controlling for five continent indicators and, all in natural log, years since the neolithic transition, arable share of land area, absolute value of latitude, land area suitable for agriculture. The controls are introduced as the linear component of a partial linear model using the method of Yatchew (2003). Only the unchanged data or updated Denevan (1992) data are shown. Loess regressions through the partial-linear-model residuals are indicated with a dashed line for the Ashraf and Galor (2013) data and with a dotted line for the Denevan (1992) data.

Country-clusters are based on Denevan (1992) and describe areas comprising one or several countries: Amazonia comprises Brazil, Guyana, and Suriname; Andes comprises Ecuador, Peru, and Bolivia; North America comprises Canada and the United States; Hispaniola comprises Haiti and the Dominican Republic; Honduras-Belize comprises Honduras and Belize; and Lowland South America comprise Paraguay and Uruguay. For the country clusters, population and area were totaled for entire set of constituent countries; homozygosity was computed as the area-weighted average of the homozygosities of the constituent countries. Source: Authors' calculations with data from Ashraf and Galor (2013) and Denevan (1992). See text for details.

Figure 17: *Ancestry Adjustment*
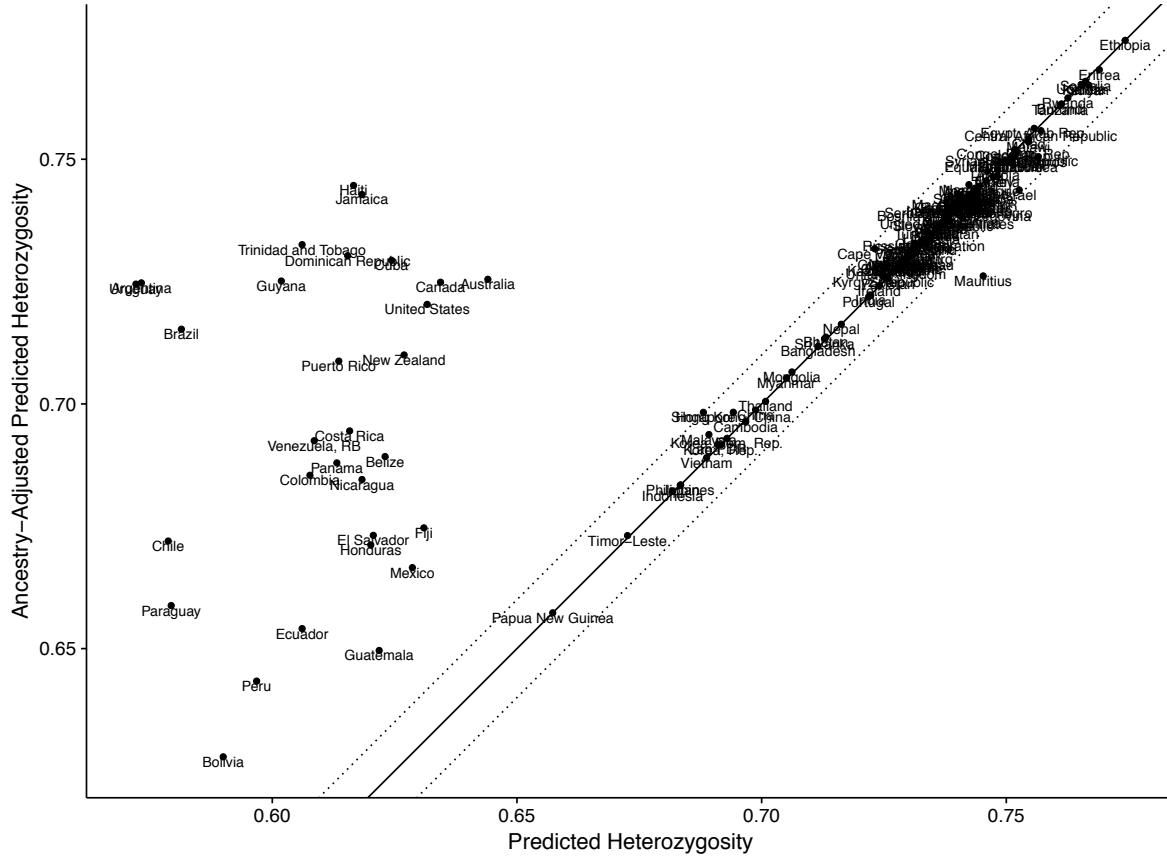
Notes. The horizontal axis shows heterozygosity predicted from migratory distance from Addis Ababa. The vertical axis shows heterozygosity predicted from migratory distance from Addis Ababa *adjusted for ancestry shifts based on post-1500 migration.* The 45-degree line indicates no difference between predicted heterozygosity and ancestry-adjusted predicted heterozygosity. Countries that Ashraf and Galor (2013) assume to be static, i.e., to have heterozygosity unchanged by migration since 1500 appear on the 45-degree line. Countries in the Western Hemisphere and Oceania in which post-1500 migration has increased population heterozygosity, for example, because of the African slave trade or settler immigration, appear above the 45-degree line.
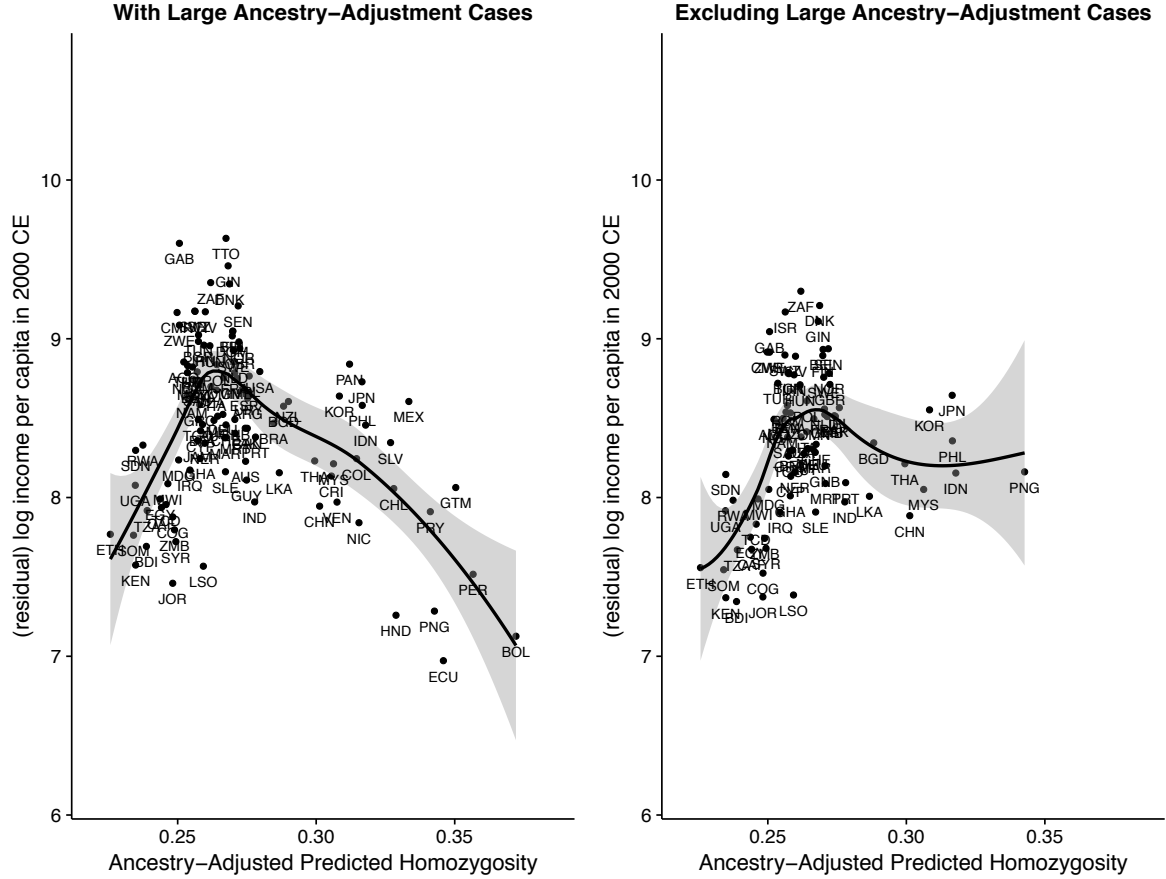
Source: Authors' calculations with data from Ashraf and Galor (2013). See text for details.

Figure 18: *Income per Capita in 2000 CE vs. Homozygosity*
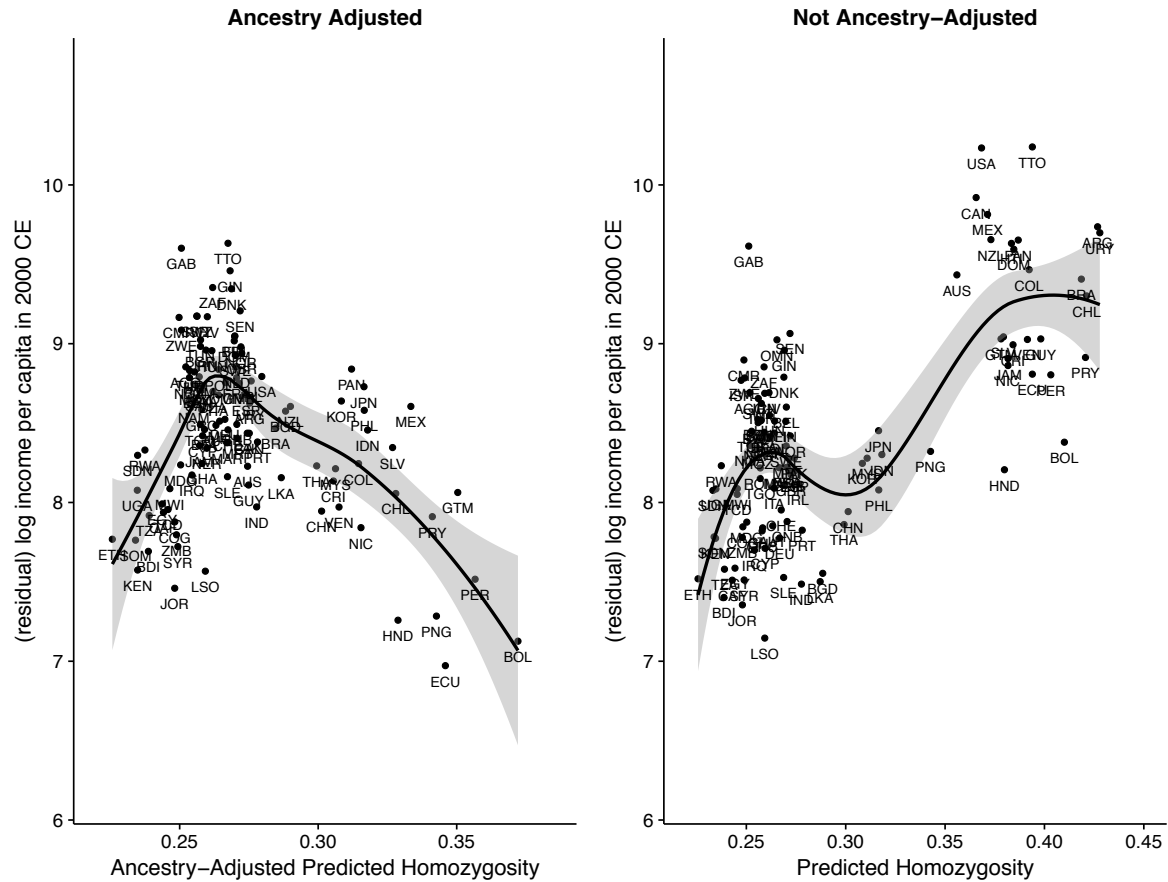
Notes. The plot shows the between log income per capita in 2000 CE and predicted homozygosity, controlling for five continent indicators, OPEC membership, four legal-origin indicators, social infrastructure, ethnolinguistic fractionalization, malaria risk, distance to navigable waterways, percent of the population living in tropical zones, and, all in natural log, years since the neolithic transition, arable share of land area, absolute value of latitude, land area suitable for agriculture. The controls are introduced as the linear component of a partial linear model using the method of Yatchew (2003). The left panel uses ancestry-adjusted homozygosity data that adjusts predicted homozygosity on the basis of the predicted 1500 CE homozygosity of the source populations that migrated to the country between 1500 CE and 2000 CE. The right panel uses homozygosity predicted by migratory distance from Addis Ababa. Authors' calculations with data from Ashraf and Galor (2013). See text for details.
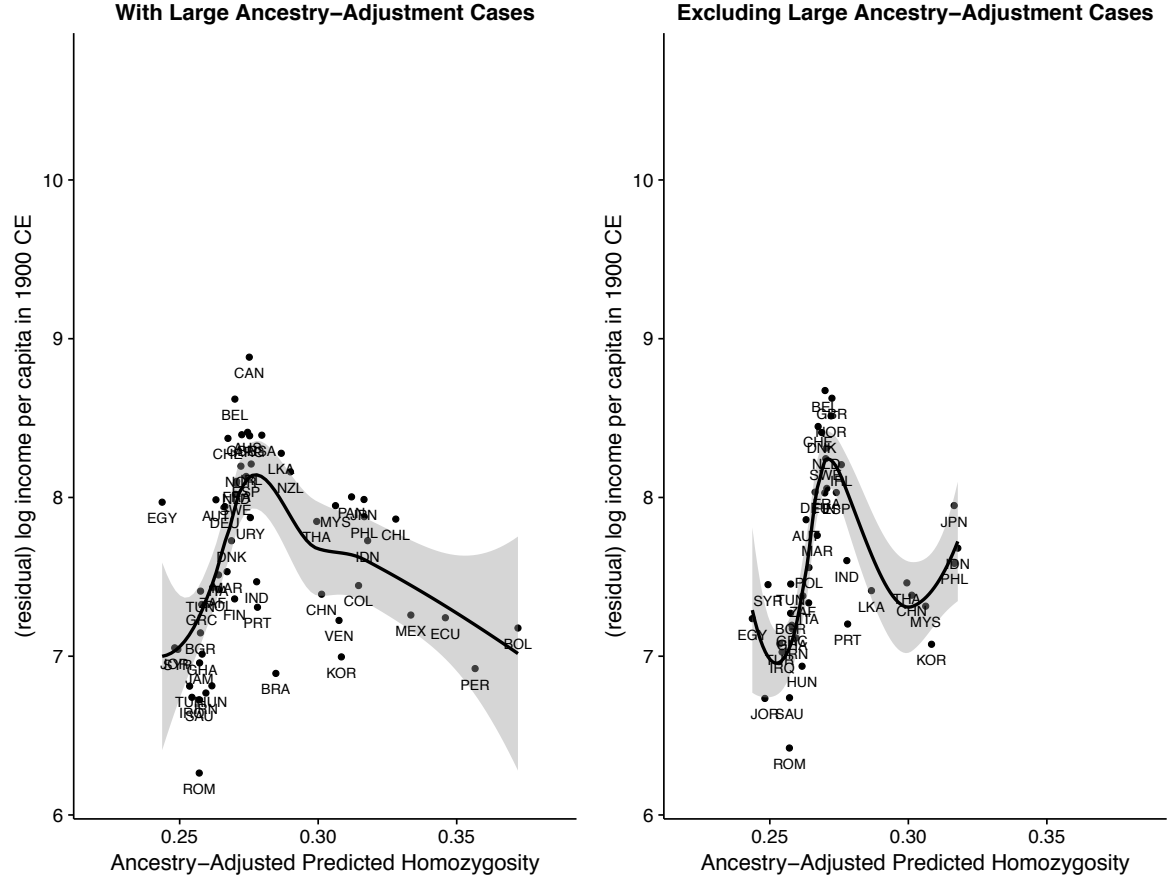
Figure 19: *Income per Capita in 2000 CE vs. Homozygosity*

Notes. The plot shows the between log income per capita in 2000 CE and homozygosity predicted from migratory distance from Addis Ababa for countries and adjusted for migration between 1500 CE and 2000 CE, controlling for five continent indicators, OPEC membership, four legal-origin indicators, social infrastructure, ethnolinguistic fractionalization, malaria risk, distance to navigable waterways, percent of the population living in tropical zones, and, all in natural log, years since the neolithic transition, arable share of land area, absolute value of latitude, land area suitable for agriculture. The controls are introduced as the linear component of a partial linear model using the method of Yatchew (2003). The left panel includes all data; the right panel is limited to cases for which the absolute difference between predicted homozygosity and ancestry-adjusted predicted homozygosity was less than 0.01 units.

Authors' calculations with data from Ashraf and Galor (2013). See text for details.
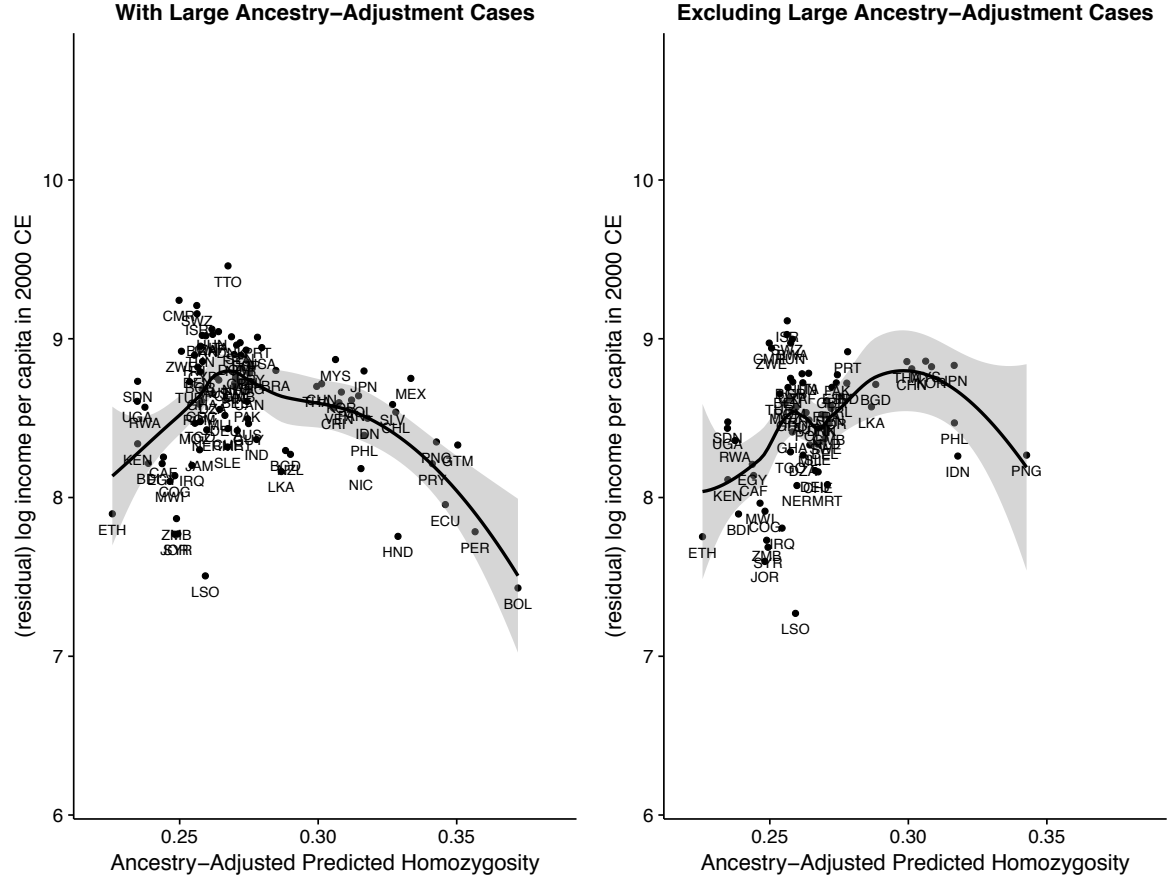
Figure 20: *Income per Capita in 1900 CE vs. Homozygosity*

Notes. The plot shows the between log income per capita in 1900 CE and homozygosity predicted from migratory distance from Addis Ababa for countries and adjusted for migration between 1500 CE and 2000 CE, controlling for five continent indicators, malaria risk, distance to navigable waterways, percent of the population living in tropical zones, and, all in natural log, years since the neolithic transition, arable share of land area, absolute value of latitude, land area suitable for agriculture. The controls are introduced as the linear component of a partial linear model using the method of Yatchew (2003). The left panel includes all data; the right panel is limited to cases for which the absolute difference between predicted homozygosity and ancestry-adjusted predicted homozygosity was less than 0.01 units.
Authors' calculations with data from Ashraf and Galor (2013) and Bolt et al. (2018). See text for details.

Figure 21: *Income per Capita in 2000 CE vs. Homozygosity: Control for schooling*

Notes. The plot shows the between log income per capita in 2000 CE and homozygosity predicted from migratory distance from Addis Ababa for countries and adjusted for migration between 1500 CE and 2000 CE, controlling for average years of schooling, five continent indicators, OPEC membership, four legal-origin indicators, social infrastructure, ethnolinguistic fractionalization, malaria risk, distance to navigable waterways, percent of the population living in tropical zones, and, all in natural log, years since the neolithic transition, arable share of land area, absolute value of latitude, land area suitable for agriculture. The controls are introduced as the linear component of a partial linear model using the method of Yatchew (2003). The left panel includes all data; the right panel is limited to cases for which the absolute difference between predicted homozygosity and ancestry-adjusted predicted homozygosity was less than 0.01 units.
Authors' calculations with data from Ashraf and Galor (2013). See text for details.