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The Roots of Global Inequality: The Role of Biogeography and Genetic Diversity

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ABSTRACT *This paper adds further evidence supporting Jared Diamond's hypothesis that global technological differences in the pre-modern era were fundamentally due to bio-geographic factors: the time elapsed since the onset of agriculture and husbandry, the size of the population relative to the territories, the shape of continents. An alternative hypothesis, that genetic diversity within populations is the ultimate cause of global inequalities, is also examined. Results show how there is no robust evidence supporting a possible effect of genetic diversity on international differences in population density and technology in the pre-modern era.*

1. Introduction

The era of the great geographic discoveries, from the end of the fifteenth century, represented a main caesura in the history of humanity. Europeans explored, conquered and colonised different parts of the globe, thus definitively modifying the destiny of those territories and of the peoples that inhabited them. The geographic explorations also revealed a striking fact: the existence of an incomparable technological divide between the populations of Eurasia and the majority of those inhabiting the other continents. At the beginning of the modern era, the world's most advanced technological regions were in Eurasia: China, the technological leader, Europe and, in some respects, India (Jones, 1981; Landes, 1998).¹ The Americas, Oceania and most of sub-Saharan Africa were incommensurably more backward. What were the causes of those differences?

For a long time, the most frequent answer was that technological and cultural differences among populations were the result of innate differences between human 'races' (Marks, 1995, pp. 63–76). In contrast to this view, J. Diamond (1997) proposed that the differences in technology levels among the populations inhabiting the diverse continents were fundamentally due to some biogeographic factors. Diverse climates, the availability of domesticable plants and animals and the geographic characteristics of the territories favoured, in some regions, an early transition from foraging to agriculture and husbandry. In settled agrarian societies, population size notably increased and this, in turn, led to the formations of more complex societies that evolved into cities and states. Increasing social complexity was accompanied (and sustained) by the accumulation of knowledge and technology. The diffusion of technological innovations was also influenced by the geographical and ecological barriers to the movements of people and, hence, of ideas. For its biogeographic and geographic

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characteristics, Eurasia had a significant advantage with respect to other continents (Diamond, 1997; Harris, 1977).

From the first agricultural settlements in the Middle East, around 11,000 years BCE, as well as in India and China, a cumulative process of technological evolution led to a dramatic divide between Eurasia and the rest of the world. Even though specific historical factors influenced the evolution of societies, geographical and bio-geographical factors initially played a fundamental role in shaping the differences between continents. Diamond's argumentations have been empirically supported by Olsson and Hibbs (2005), who showed how the bio-geographic factors suggested by Diamond accounted for the different timings of agricultural transition, predicting current disparities in international economic development. In addition, the timing to agricultural transition is a strong predictor of cross-country differences in economic development, urbanisation and advances in technology around 1500 CE (Ang, 2015; Chanda & Putterman, 2007; Putterman, 2008). Finally, studies demonstrated how the east-west orientation of the Eurasian landmass aided human migrations and the spread of domesticable plants and animals and, consequently, of technological innovations (Laitin, Moortgat, & Robinson, 2012; Ramachandran & Rosenberg, 2011)

Recently, the idea that global inequalities in economic development are, to some extent, related to deep rooted factors and, ultimately to human nature, also emerged in social sciences. A growing body of research suggests, in fact, that genes may have a role in long-term economic development (Ashraf & Galor, 2013, 2017; Spolaore & Wacziarg, 2009, 2013). A thesis put forward by Ashraf and Galor (2013) considers 'populations' genetic diversity' as the ultimate cause of historical and current international economic disparities.

This paper's aim is twofold. First, it tests Diamond's (1997) thesis that worldwide technological differences, at the onset of the modern era, were fundamentally due to the timing of transition from foraging to farming, population density and continental axis orientation. In contrast to related studies, in a Boserupian perspective, this paper focuses on the relationship between population density and international technological disparities in 1500 CE. Furthermore, the paper tests the alternative explanation offered by Ashraf and Galor (2013), according to which population genetic diversity is the ultimate cause of international inequality in both the pre-modern era and in current times. Results show how the geographic thesis is supported by both data and historical evidence, while the genetic explanation by Ashraf and Galor (2013) does not have robust empirical support.

This paper proposes that agriculture development was a fundamental, but not unique, factor in influencing technological innovation. The density of population, and networks between populations, also played a major role in determining the rate of innovation. The remainder of the paper is as follows: Section 2 presents the theoretical and historical framework, examining the long-lasting consequences of Neolithic revolution on population growth and technological advancement; Section 3 contains the empirical analysis; Section 4 concludes.

2. The ripple effects of Neolithic revolution

2.1. *The effects of Neolithic revolution*

The Neolithic transition from hunting and gathering to agriculture and husbandry represented a breakthrough event in the history of mankind. Food production based on the domestication of some crops and animal species arose, independently, in different eras in at least nine areas in all continents, except Australia. Agriculture started to develop in the Fertile crescent around 11,000 years ago (YA), around 9000 YA along the Yangzi and Yellow River Basins, between 9000–6000 in New Guinea's highlands, and between 5000–4000 YA in some areas of Central and South America (Bellwood & Oxenham, 2008; Diamond & Bellwood, 2003). The location of the centres where agriculture originated was largely determined by the availability of plants or animals suitable for domestication (Aubaile, 2012; Diamond, 1997, 2002), even though the causes of the shift from hunting and gathering to agriculture and husbandry are a matter of debate (Weisdorf, 2005).

For the first farmers, agricultural activities were much more time-consuming and physically exhausting than gathering and hunting. For a certain phase, in fact, the transition to agriculture led to a deterioration of living and health conditions – as revealed by skeletons of the first farmers, that show pathological changes such as a drastic reduction of stature, skeletal and vitamins-related disorders – and was accompanied by the spread of some communicable diseases related to the animal species that were bred (Armélagos & Harper, 2005; Murphy, 2007, pp. 124–28). These facts suggest that the transition to agriculture was, to some extent, driven by necessity. According to some scholars, the ‘necessity’ was represented by the extinction of the Pleistocene megafauna due to the intensification of hunting, or to demographic pressure that forced populations to exploit other livelihood strategies (Cohen, 1977; Harris, 1977). Even though the diverse theories may explain the birth of agriculture in certain regions, none of them is universally applicable (Weisdorf, 2005). Schematically, however, it can be said that agriculture would not have been possible without some basic prerequisites. The first prerequisite was the right sort of plants and animals potentially suitable for domestication. The second was represented by the right climatic conditions that, in some regions, were provided by the mini-Ice Age, or Younger Dryas interval, followed by the long period of climatic stability that persists up to this day, and by the cultural changes required to establish and develop sedentary societies. Finally, the third prerequisite was the steady decline in availability of the main traditional food resources, which represented the stimulus to push people from a traditional lifestyle to a new, and untested, subsistence method (Diamond, 2002; Harris, 1977; Murphy, 2007).

From its centres of origin, agriculture progressively spread across other regions. Two main models have been proposed to explain this process. The first is that of cultural diffusion, according to which, hunting and gathering populations progressively acquired knowledge and adopted agricultural technology. The second model is that of the *demic diffusion*, in which the farmers themselves moved, taking with them agricultural practices (Cavalli-Sforza, Menozzi, & Piazza, 1994; Jobling, Hollox, Hurles, Kivisild, & Tyler-Smith, 2014, pp. 377–404). However, settled agriculture led to major demographic and societal transformations. While hunter-gatherer societies were composed of small groups of individuals, agriculture, particularly grain production, and husbandry permitted the storage of foodstuffs. This allowed settled farming societies to become demographically larger. Archaeological records indicate, in fact, that the Neolithic transition led to an increase in population. The so-called Neolithic demographic transition (NDT) was characterised by a sharp increase in birth-rates, in female fertility and population growth rate, for a period of about a millennium, following the onset of the transition to agriculture (Bellwood & Oxenham, 2008; Bocquet-Appel, 2008). During the transition period, a major demographic shift, supported by an abrupt increase in the proportion of juvenile skeletons found in burials (Bocquet-Appel, 2011), has been documented in different homeland areas of agriculture. For instance, Kuijt (2008) estimated an increase by a factor of about 60 in the mean populations of settlements in the south-central Levant between 9500 to 6500 BCE ca. Large increases in population size following agricultural transition have been documented for China, south-eastern Asia, Europe and western Africa (Bellwood & Oxenham, 2008; Gignoux, Henn, & Mountain, 2011). The considerable increase in population between 11,000–3500 YA generated previously unknown forms of socio-economic and political-organisation, such as village units and, later, chiefdoms. As clearly stated by Bocquet-Appel (2008, p. 46):

the NDT, because of the unprecedented demographic growth it generated, induced incalculably more complex social, political, economic and ideological relationships compared to the relatively simple community-based forager societies, which had remained practically unchanged for perhaps tens of thousands of years. The NDT formed the basis of the world of preindustrial populations.

The differences in social organisation between hunter-gatherers and pastoralists and agriculturalists were profound. Hunter-gatherers had egalitarian social systems based on reciprocity, in which the basic social unit was the band, a group of about 100 or more extended family members (Bocquet-Appel & Bar-Yosef, 2008, p. 2). When proto-agriculturalists and pastoralists commenced

domesticating animals and plants, thus settling-down, the social structure became tribal, that is stratified and composed of several extended family groups or clans. As agricultural production increased, chiefdoms emerged; stratified societies in which each individual fit into a hierarchy, and where wealth and power were hereditary (Foster Mcarter, 2007, pp. 122–15).

Social organisation and demographic growth progressively led to new forms of economic exchange. Reciprocity became increasingly difficult to maintain as people started to specialise in specific activities. Probably, in some cases, Neolithic villagers organised redistribution systems (Foster Mcarter, 2007). However, these systems progressively disappeared when societies became more stratified, with social, religious and political hierarchies. As social organisation became more complex, so did the exchange systems: trade networks became intense and wider. Farming had a crucial impact on social organisation and technology development: for the first time in history, food production and sedentary lifestyles made labour specialisation possible, with some individuals permanently involved in activities different to food-production (Diamond, 1997; Putterman, 2012).

Urban development required large agricultural production. In fact, the earliest civilisations and urban centres arose in fertile regions, such as the floodplains of large rivers: in the fourth millennium BCE in the valleys of the Tigris and Euphrates in Mesopotamia, and of the Nile in Egypt; in the third millennium BCE in the valley of the Indus in Pakistan, and in the second millennium BCE in the valley of the Yellow River in China. In Mesoamerica the most influential early civilisation, that of the Olmec, flourished between 1200 and 400 BCE. Its development was also made possible by earlier advances in agriculture (Bulliet, Crossley, Headrick, Hirsch, & Lyman, 2008, pp. 78–80).

Agricultural and related activities, such as the building of channels or wells for irrigation or other collective works, required a high number of individuals and complex social orders. Archaeological records demonstrate how, in many cases, early Neolithic settlements became large urban centres. The towns of Çatalhöyük in Anatolia (≈7500 BCE) occupied about 32 acres, while Jericho in Palestine (≈8000–7000 BCE) extended to 10 acres with about 2000 inhabitants (Headrick, 2009, p. 13). In the Indus Valley, between 2600 to 1900 BCE, major urban centres flourished. The city of Harappa had a circumference of 3.5 miles and, probably, a population of 35,000 individuals; Mohenjo-daro was several times larger (Bulliet et al., 2008, p. 50). Not all agricultural urban settlements, however, evolved into organised political formations and states. For example, Bandy (2008) reported how, in 36 agricultural areas, 33 developed into urban centres with least 300 people, but only in eight cases did villages then evolve into primary states. These states were all in Eurasia and Mesoamerica, namely: The Basin of Mexico; Central Henan, China; the Indus Valley, Pakistan; Mesopotamia; the Nile Valley, Egypt; S. Titicaca Bolivia; the Moche Valley, Peru; and the Valley of Oaxaca, Mexico. With the exception of China, in the cases studied by Bandy (2008), state formation took place between 1000 and 2500 years after the local onset of agricultural village life.

It is important to recall, however, how in Eurasia and Mesoamerica not only the timing, but also the patterns of agricultural and urban development differed. The differences were due to diverse factors, among which the number and the types of domesticated animals and plants were decisive. In Eurasia, the domestication of sheep and goats was soon followed by that of pigs, cattle, camels, donkeys and horses. All these animals were integrated into the agricultural system, and provided the basis for additional technological advances such as ploughing and transport. In Mesoamerica, the wheel was never used as a transport tool, probably for lack of pack animals. So, America remained behind, not only in transport technology but also in those developments – such as grinding or lifting – based on wheels or pulleys (Harris, 1977).

As previously seen, in the Middle East, China and India, the transition toward settled agriculture started notably earlier than in other world regions. Not only were there many domesticable species of animals and plants, but they were also more productive than those in other parts of the world. Furthermore, in Eurasia, the east-west orientation of continental main axis, and the absence of insurmountable geographic barriers, favoured the diffusion of domestic species, but also of people and ideas. In other continents, instead, the south-north axis, and very different and hostile environments, made this process of diffusion much more difficult (Crosby, 1986; Diamond, 1997). The influence of the shape of landmasses on migrations, and consequently on technology diffusion, has

been confirmed by Ramachandran and Rosenberg (2011). Using genotype data from 68 indigenous populations, they found that genetic differentiation between Native American populations, along latitudinal and longitudinal axes, is greater than corresponding differentiation in Eurasia, indicating that the east-west orientation of Eurasia made migrations easier than in the Americas.

The early agriculture development of Eurasia had ripple consequences on subsequent demographic growth, urbanisation, state formation and technological development, including investment in military technologies such as guns or vessels. Countries in which the transition to agriculture started earlier were, on average, more densely populated and had higher per capita GDP and technology levels in 1500 (Ang, 2015; Putterman, 2008). Analogously, countries with longer histories of state-level institutions reached comparatively higher levels of economic development in the course of history (Bockstette, Chanda, & Putterman, 2002; Chanda & Putterman, 2007).

2.2. Population density before 1500 CE

For the pre-modern era, population estimates are available for some countries. According to Maddison (2010), in the year 1 CE the world population was about 226 million people, 75 per cent of which lived in Asia, 11 per cent in Western Europe and 8 per cent in Africa. The Americas and Australia represented a very marginal share of the world's population. McEvedy and Jones (1978) provided estimates for the populations of continents, and for some countries at current (1975) borders, from 400 BCE onward. For year 1 they estimated a world population of about 170 million people, and of about 420 million people for 1500. The continental distribution of population is reported in Table 1 (see the Supplementary Materials for alternative estimates). Given the degree of uncertainty, these figures should be viewed with caution, even though data by McEvedy and Jones (1978) have been used by numerous studies on long-run economic development, including those by Ashraf and Galor (2013) and Chanda and Putterman (2007).

The figures show striking differences in the population density of continents around 1500. Eurasia accounted for about 40 per cent of the landmass and 85 per cent of world population. The higher population density of Eurasia has been explained by the early adoption and diffusion of agriculture. Thus, the ultimate determinants of population density may be traced back to those bio-geographic factors, such as climate and environment, soil characteristics or the presence of domesticated animals and plants, that influenced agriculture development (Diamond, 1997). In the case of the Americas, it is possible that not only bio-geography, but also the late peopling of the continents by *Homo Sapiens* influenced subsequent demographic development (Frankema, 2015). America was, in fact, the continent last peopled by *H. Sapiens*. Genetic data support three migration waves from Beringia towards America. The first migration date was 20–15,000 years ago (YA). Two additional migration flows probably occurred around 4500 and 1000 YA (Reich et al., 2012). The founding population, during the peopling of the Americas, was very small. Based on genetic data, it has been estimated that the Americas could have been founded by as few as 80 individuals (Fagundes et al., 2008; Hey, 2005).

Table 1. Population density in the years 1, 1000 and 1500 and area of continents

	Density (pop/km ²)			World share (%)	
	1 CE	1000 CE	1500 CE	Area	Population in 1500
Africa	0.55	1.10	1.53	22.6	10.9
America	0.11	0.23	0.35	30.2	3.3
Asia	2.61	4.20	6.36	33.2	66.2
Europe	3.23	3.75	8.44	7.2	19.1
Oceania	0.11	0.17	0.22	6.8	0.5

Source: Data from McEvedy and Jones (1978).

The very low population density of Australia before European colonisation may be explained, instead, by bio-geographical factors. Australia is classified as having three climatic zones: the temperate south, the central deserts and the monsoonal north. Much of Australia is desert; up to two-thirds of the continent is defined as arid: the climate is dry, rainfall very scarce and the soil poor in nutrients. Unlike the Papuans and the inhabitants of the northern and eastern Torres Islands, the Aborigines of Australia and Tasmania did not know agriculture and husbandry, and this impacted on their demographic growth (Clarke, 2003, p. 14). It has been estimated that in 1788 the population of Australia was of about 800,000 Aborigines (Hunter & Carmody, 2015).

The low density of sub-Saharan Africa may also be largely attributed to bio-geographic factors, even though the picture is much more complex than that of America or Oceania. Poor African soils, fickle rainfalls, the hostile environments of tropical forests and dry areas, together with the diffusion of endemic diseases, created an environment not conducive to agricultural societies (Iliffe, 1995, p. 1). Notwithstanding this, prior to 1500, with respect to population density, urbanisation and trade, some regions of Africa – namely West Africa and Ethiopia – were not so dissimilar to many areas of Eurasia and were certainly much more developed than the Americas and Oceania (Ehret, 2014; Inikori, 2014), except for Mesoamerica and Andean civilisations. However, until the twentieth century, sub-Saharan Africa remained an under-populated region.²

3. The empirical analysis

3.1 *Neolithic transition and population density*

In this section, we test Diamond's (1997) hypothesis that technological development in the pre-modern era was influenced by three main factors: the onset of agriculture, population density and the axis orientation of continents. Preliminarily, it can be noted how the transition to agriculture did not influence technology directly but indirectly, triggering demographic and social development. The first step of our empirical strategy is, thus, aimed at assessing the link between agriculture and population density; as a second step, the link between population and technology is analysed.³

In our analysis, population density in the years 1 and 1000 CE is computed on McEvedy and Jones' (1978) data. Although Maddison (2010) has provided more recent estimates on world population, we prefer McEvedy and Jones' data, since they were used in related studies, particularly that of Ashraf and Galor (2013), that we refer to. In addition, for the considered years, in Maddison's dataset the number of observations is notably lower than in McEvedy and Jones' study (1978), especially for African and Asian countries, and this inevitably influences the reliability of estimates. Population density is regressed on the timing since Neolithic transition (Putterman, 2006, 2008), controlling for absolute latitude and land suitability for agriculture (Michalopoulos, 2012). For descriptions of variables and sources, see the Supplementary Materials.

Regressions results are reported in Table 2. The full specification explains 52 per cent of the variance in population density in year 1 and 48 per cent in 1000 CE. The link between transition years and density is highly significant. The timing of agricultural transition has a greater impact, in terms of coefficient magnitude, on density than agricultural suitability and latitude. The reason is straightforward: prior to 1500 many regions of the world suitable for agriculture, such as large parts of North America, were still underpopulated and/or inhabited by hunter-gatherer populations: soil suitability was an important factor for agriculture development, although insufficient alone. Overall, these findings are consistent with the above-cited archaeological and historical evidence, and with research showing how the timing of agriculture transition is a strong predictor of population density in the pre-modern era (Putterman, 2008).

3.2 *Testing Diamond's hypothesis*

This section focuses on the link between population density and technology levels in 1500 CE. Our approach follows the work of Klasen and Nestmann (2006), who used population density in years

Table 2. Transition to agriculture and population density in 1 and 1000 CE

	Log population density 1		Log population density 1000	
Const	-15.7*** (1.62)	-15.5*** (1.67)	-11.8*** (1.12)	-12.1*** (1.12)
log Neolithic transition	1.93*** (0.192)	1.88*** (0.213)	1.54*** (0.134)	1.65*** (0.148)
log Land suitability	0.438*** (0.079)	0.434*** (0.080)	0.430*** (0.061)	0.436*** (0.060)
log Latitude		0.0741 (0.093)		-0.188* (0.099)
N	129	129	143	143
Adj. R ²	0.52	0.52	0.47	0.48

Notes: OLS estimates. Heteroskedasticity-robust standard errors in parentheses – *significant at 10 per cent; *** $p < 0.01$, ** $p < 0.05$, * $p < 0.1$.

0 and 1000 to explain economic development in 1500. Technology in 1500, measured by the index proposed by Comin, Easterly, and Gong (2010), is regressed on population density in years 1 and 1000 CE and on a set of geographical variables: absolute latitude; the orientation of continental axis; terrain roughness; average elevation of countries; and mean distance from the nearest waterway (for a detailed description, see Supplementary Materials). All the control variables, excepting axis, are in natural logarithms. Specifications also control for continental dummies; following Diamond (1997), we consider Europe and Asia as a unique continent.⁴ Estimates for year 1 and 1000 CE are reported in Tables 3 and 4, respectively. The effect of population density on technology is positive and significant at the 1 per cent level. It is worth noting how the magnitudes of the density coefficients in years 1 and

Table 3. Testing Diamond's hypothesis (I)

	Dependent variable: Technology in 1500 CE					
	(1)	(2)	(3)	(4)	(5)	(6)
Const	0.527*** (0.022)	0.209*** (0.078)	0.0054 (0.056)	-0.0273 (0.097)	0.0686 (0.048)	0.0925 (0.068)
log Pop. density 1 CE	0.126*** (0.010)	0.0996*** (0.011)	0.0667*** (0.012)	0.0818*** (0.013)	0.0365*** (0.012)	0.0409*** (0.012)
log Latitude		0.108*** (0.025)	0.0643*** (0.020)	0.0706*** (0.020)	0.0575*** (0.016)	0.0663*** (0.017)
Axis			0.198*** (0.036)	0.192*** (0.036)		
log Elevation				-0.0481 (0.045)		-0.0630 (0.041)
log Roughness				-0.0280 (0.039)		0.0279 (0.033)
log Water distance				0.0449* (0.024)		0.0216 (0.020)
Africa					0.180*** (0.037)	0.178*** (0.047)
Eurasia					0.478*** (0.039)	0.449*** (0.042)
Oceania					-0.0875*** (0.024)	-0.0913** (0.043)
n	107	107	105	104	107	104
Adj. R ²	0.41	0.53	0.67	0.71	0.80	0.80

Notes: OLS estimates. Heteroskedasticity-robust standard errors; *** $p < 0.01$, ** $p < 0.05$, * $p < 0.1$.

Table 4. Testing Diamond's hypothesis (II)

Dependent variable: Technology in 1500 CE						
	(1)	(2)	(3)	(4)	(5)	(6)
const	0.435*** (0.024)	0.0713 (0.074)	-0.0728 (0.046)	-0.0437 (0.090)	0.0395 (0.045)	0.0832 (0.060)
log Pop. density 1000 CE	0.125*** (0.012)	0.108*** (0.010)	0.0762*** (0.012)	0.0841*** (0.014)	0.0410*** (0.011)	0.0450*** (0.012)
log Latitude		0.128*** (0.023)	0.0803*** (0.020)	0.0943*** (0.021)	0.0577*** (0.016)	0.0726*** (0.018)
Axis			0.188*** (0.036)	0.173*** (0.038)		
log Elevation				-0.0832** (0.040)		-0.0859** (0.038)
log Roughness				0.0187 (0.037)		0.0487 (0.032)
log Water distance				0.0521** (0.023)		0.0333 (0.020)
Africa					0.153*** (0.0378)	0.164*** (0.0476)
Eurasia					0.481*** (0.039)	0.449*** (0.042)
Oceania					-0.0851*** (0.024)	-0.0668** (0.033)
n	116	116	113	111	116	111
Adj. R ²	0.37	0.53	0.67	0.70	0.79	0.79

Notes: OLS estimates. Heteroskedasticity-robust standard errors; *** $p < 0.01$, ** $p < 0.05$, * $p < 0.1$.

1000 CE are similar. Continental axis orientation and latitude also affect technology in all specifications with rather stable coefficients. The coefficient of latitude indicates that there is a detrimental effect on technological progress as we approach the equatorial bands, while continental axes support the prediction of the Eurasian advantage in terms of axis (continental) orientation, which favoured communication and the diffusion of innovations. The mean elevation of countries is negatively and significantly related to technology in 1000 CE, but not significantly in year 1; distance from waterways is positively linked to technology but its significance depends on the diverse specifications, while terrain roughness is not significant. Overall, the full specifications explain about 80 per cent of cross-country variations in technology index in the considered years. Our results are consistent with those of Klasen and Nestmann (2006), that greater population density spurs technological change, and add empirical support to Diamond's (1997) hypothesis on continental differences in technology during the pre-modern era.

3.3. Endogeneity issues

In economics, the relationship between technology and demography has been addressed within two main paradigms. The first is the Malthusian one, according to which population growth is limited by food resources: population grows geometrically, while food production linearly (Malthus, 1798). Therefore, in the absence of any technological advancement that keeps up with population growth, societies cannot escape from subsistence crises. The second paradigm is the Boserupian one, according to which the growth of a population is the engine of technological change (Boserup, 1965, 1981). In Boserup's view, an increase in population, that modifies the relationship between people and resources, provides an incentive to invent new techniques or to find new resources. Population levels thus determine the pace of innovation, which in turn fosters demographic growth, in an interlinked process that allows economies to escape from the Malthusian trap.

Table 5. Controlling for endogeneity (TSLS)

Dependent variable: Technology in 1500 CE						
	(1)	(2)	(3)	(4)	(5)	(6)
const	0.340*** (0.093)	0.118 (0.114)	0.217*** (0.078)	0.110 (0.085)	0.0428 (0.119)	0.126* (0.072)
log Pop. density 1 CE	0.177*** (0.021)	0.142*** (0.018)	0.0978*** (0.023)			
log Pop. density 1000 CE				0.186*** (0.023)	0.155*** (0.020)	0.113*** (0.026)
log Latitude	0.0688** (0.030)	0.0651*** (0.022)	0.0566*** (0.018)	0.106*** (0.029)	0.110*** (0.026)	0.0842*** (0.024)
Axis		0.145*** (0.039)			0.102** (0.052)	
log Elevation		-0.0677 (0.051)	-0.0673 (0.044)		-0.0902* (0.049)	-0.0770* (0.041)
log Roughness		-0.0264 (0.043)	-0.0009 (0.040)		0.0168 (0.044)	0.0187 (0.038)
log Water distance		0.0799*** (0.028)	0.0552** (0.027)		0.0862*** (0.027)	0.0654** (0.026)
Africa			0.0713 (0.055)			0.0632 (0.056)
Eurasia			0.320*** (0.074)			0.294*** (0.083)
Oceania			-0.0782*** (0.023)			-0.0154 (0.046)
n	104	102	103	110	107	108
First stage F	60.1	56.9	33.3	72.6	72.3	37.3
Adj. R ²	0.50	0.67	0.76	0.51	0.64	0.74

Notes: Instrument: Log of agriculture transition; Heteroskedasticity-robust standard errors; *** $p < 0.01$, ** $p < 0.05$, * $p < 0.1$. First stage- f-statistics for weak instruments.

However, since technological progress is cumulative, technology in each period tends to be affected by its previous levels. Having previously described the feedback loop involving technology and population density, neither can it be excluded that a potential endogeneity problem exists. The endogeneity of technology may be econometrically addressed by selecting a proper instrument that allows us to identify the effect that population density has on it.

Unfortunately, the task is not so easy to accomplish, since it is difficult to find proper instruments for population density. A viable instrument is the log of years since agricultural transition, which clearly affected technology in 1500, as previously demonstrated, through the population density channel. The exogeneity of this instrument is given by the fact that the transition from foraging to farming was the result of diverse factors: bio-geographic, climatic, cultural, and the increased hunting of megafauna. Table 5 reports the results of the second stage of the instrumental variable (IV) estimations, in which the log of agricultural transition is employed as an instrument for population density. The first stage F-statistic indicates the validity of the used instrument.

In all specifications, (exogenous) population density is a powerful predictor of technology in 1500. The geographic controls are also significant as in the previous OLS estimates and with the expected signs and, overall, the regressions explain a large fraction of cross-country variations in technology levels. Overall, the empirical analysis contributes to support Diamond's hypothesis on the ultimate determinants of worldwide technology disparities.

3.4. Testing the effect of genetic diversity

In a seminal article, Ashraf and Galor (2013) proposed that global economic inequality, both in pre-modern times and today, has its deep roots in the genetic diversity of populations. A common measure

of population genetic diversity is the *expected heterozygosity*, defined as the probability that two randomly drawn alleles, or gene variants, of a DNA locus (either within a population or between two different populations) are different. The expected heterozygosity H_e , is given by $1 - \sum p_i^2$, where p_i is the observed frequency of the i^{th} allele at the locus. The ‘mean expected heterozygosity’, that is H_e averaged over all loci sampled, is one of the most widely used measures of genetic variation (Jobling et al., 2014; Nei, 1987). Studies have shown how within-population heterozygosity decreases approximately linearly with increasing over-land distance from Africa (Harpending & Rogers, 2000; Prugnolle & Manica, 2005). This pattern in heterozygosity has been interpreted as reflecting the worldwide expansion of *Homo Sapiens* after dispersion out-of-Africa (~60,000 YA). According to the ‘serial founder effect’ (SFE) model, the peopling of the world by *H. Sapiens* took place through an iterative process, in which new territories were colonised by small groups of individuals (founders) from larger populations, thus determining successive population bottlenecks and a decay of genetic diversity (Ramachandran et al., 2005). The highest heterozygosity is found, in fact, in African populations, the lowest in Oceania and in Native American populations, while its level is intermediate in Eurasia.

The SFE model assumes limited migrations and no admixture with archaic hominins, such as Neanderthals and Denisovans. It is now recognised that admixture and migrations affected *H. Sapiens* evolutionary history (Sugden & Ramachandran, 2016). Recently, Pickrell and Reich (2014) demonstrated, through simulations, that the decline in genetic diversity with distance from Africa may be produced by models different to SFE, based on archaic and recent admixtures alone. Studies, however, support the SFE model in explaining the global pattern of heterozygosity, showing how recent admixtures have played a major role at the regional level, where, in fact, heterozygosity is uncorrelated with distance from Africa (Hunley & Cabana, 2016; Hunley, Gwin, & Liberman, 2016).

Ashraf and Galor (2013) took data on the expected heterozygosity of 53 world-wide populations from the Human Genome Diversity Panel (Cann et al., 2002). These populations were grouped in 21 countries and, for each of them, Ashraf and Galor computed an ‘observed diversity’ index as the mean of the expected heterozygosity of the respective populations. Based on the SFE model, they then computed ‘predicted heterozygosity’ for 145 countries based on the migratory distance from East Africa: the underlying hypothesis is that migratory distance affects population density exclusively through the serial founder effect process on genetic diversity. In Ashraf and Galor’s (2013) dataset, migratory distance from Addis Ababa and predicted genetic diversity are therefore *perfectly* correlated, and could be used interchangeably in the analysis (for a discussion, see Tang, 2016, Online appendix A). Figure 1 presents the world map of predicted heterozygosity.

In accordance with the Malthusian argument, that higher productivity is reflected by a larger population, Ashraf and Galor (2013) used population density in years 1, 1000 and 1500 CE to proxy economic development in the pre-modern era. Per capita income in the year 2000 was instead used as an indicator of current development levels. Through multiple regressions, they found a significant hump-shaped relationship between predicted genetic diversity and population density in the pre-modern era; the same relationship was also found between the genetic diversity of contemporary national populations and current income per capita. Ashraf and Galor (2013), maintained that this non-linear relationship is highly statistically significant and robust to diverse control variables, including continental dummies and the bio-geographic determinants of technological development proposed by Diamond (1997). They concluded that the hump-shaped effect of genetic diversity on development outcomes reflects the trade-offs between the detrimental and beneficial effects of diversity on productivity. In their words:

While the low degree of diversity among Native American populations and the high degree of diversity among African populations have been detrimental forces in the development of these regions, the intermediate levels of genetic diversity prevalent among European and Asian populations have been conducive for development. (Ashraf & Galor, 2013, p. 43)

According to the authors, their research ‘highlights one of the deepest channels in comparative development, pertaining not to factors associated to the onset of complex agricultural societies as in the influential hypothesis of Diamond (1997), but to conditions innately related to the very dawn of humankind itself’ (Ashraf & Galor, 2013, p. 2).

As was predictable, Ashraf and Galor’s (2013) article raised harsh criticisms regarding both methodological and genetic grounds (Creanza & Feldman, 2016; D’Alpoim Guedes et al., 2013; Feldman, 2014; Gelman, 2013). The statistical robustness of Ashraf and Galor’s results was examined by Rosenberg and Kang (2015). After considering genetic data for 237 populations of 39 countries, they found that the quadratic relationship between expected genetic diversity and population density in 1500 is no longer significant (for a response to criticisms see Ashraf & Galor, 2017). Furthermore, Tang (2016) showed how the results of Ashraf and Galor’s regressions are not robust when a dummy for Eurasia is controlled for: when including this dummy, genetic diversity loses its significance in explaining economic development.

To test Ashraf and Galor’s (2013) genetic hypothesis we used their dataset, available online. Figure 2 plots the relationship between predicted genetic homogeneity (that is, 1 minus genetic diversity), and the log of population density in 1500, over the entire sample of the above-mentioned dataset. The bell-shaped relationship among the variables is evident. It can be noted how this relationship derives from two main clusters: one composed of the countries of the Americas plus Oceania (high genetic homogeneity), the other of African countries (high diversity).

It is worth noting that there is a wide range of variation in population density for each level of predicted genetic diversity. For example, Lebanon and the Democratic Republic of Congo have the same genetic diversity level but, in 1500, population density in Lebanon was fivefold that of Congo. In Italy, predicted diversity is slightly higher than that of Mali, while population density is 54 times higher. The disproportions in population density among countries with similar genetic homogeneity levels are apparent in Figure 2.

First we replicated one of Ashraf and Galor’s estimates, namely the one in which they examined Diamond’s explanation (Ashraf & Galor, 2013, Table A.6). This is a relevant point in the authors’ argumentation that genetic-rooted factors influenced economic development. The results of our replication exercise are reported in Table 6 (columns 1–4) and show the significant quadratic effect of genetic diversity variables on population density.⁵ The robustness of these results is tested extending the sample by adding four observations (columns 5–8). These additional observations regard Australia, Canada, United States and New Zealand, and data were taken from Hibbs and Olsson (2004). The addition of these four observations changes previous results: when Neolithic transition is excluded from the specifications, genetic diversity is no longer significant, while the variables related to agriculture and bio-geography remain significant.

These changes in the results may be explained by the inclusion of the observations for Oceania and North America, two world regions scarcely populated in the pre-modern era (in Figure 1, in fact, these countries compose a cluster for very low population density). In our opinion, there is no compelling reason to exclude these countries from the analysis, given that data are easily available and consistent with those already used.⁶ Since the inclusion of four observations notably changes the results, it is reasonable to conclude that the impact of genetic diversity on population density in Ashraf and Galor (2013) is not robust to changes in sample.

Secondly, we replicated one of the baseline regressions that Ashraf and Galor used to demonstrate the ‘independent and combined effects of the genetic diversity, transition timing, and land productivity channels’ on population density in 1500 (Ashraf & Galor, 2013, p. 26). We used their dataset *without any* modification. Column 1 of Table 7 reports Ashraf and Galor’s (2013, p. 26) same specification, that shows the quadratic effect of genetic diversity on population density. The robustness of the estimate is, then, progressively tested excluding the other variables from specification. The results again show how, when the Neolithic transition timing variable is excluded, genetic diversity has no effect on population density (columns 2–3). This contradicts the hypothesis of an effect of genetic diversity on economic development independent from agriculture transition timing.

Table 6. Testing the role of genetic diversity (I)
Dependent variable: log of population density in 1500 CE

	Ashraf and Galor (2013) sample				Extended sample			
	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)
Constant	-85.22*** (21.01)	-87.01*** (23.99)	-59.30*** (21.44)	-72.83*** (24.89)	-75.35*** (21.16)	-41.37 (27.87)	-31.76 (25.18)	-38.72 (27.15)
Predicted diversity	216.8*** (62.65)	252.1*** (72.11)	174.4*** (63.65)	212.1*** (74.15)	182.7*** (63.45)	111.6 (84.11)	91.40 (75.11)	114.0 (81.36)
Predicted diversity sqr.	-154.7*** (46.10)	-180.7*** (53.39)	-125.1*** (46.69)	-151.6*** (54.69)	-128.0*** (46.90)	-74.11 (62.61)	-62.13 (55.52)	-79.46 (60.19)
log Neolithic transition	1.300*** (0.151)				1.453*** (0.164)			
log Arable land	0.437*** (0.104)	0.431*** (0.102)	0.441*** (0.095)	0.411*** (0.099)	0.340*** (0.112)	0.419*** (0.111)	0.328*** (0.111)	0.350*** (0.110)
log Latitude	-0.212*** (0.106)	-0.426*** (0.124)	-0.496*** (0.152)	-0.487*** (0.158)	-0.242*** (0.104)	-0.380*** (0.136)	-0.621*** (0.161)	-0.606*** (0.164)
log Land suitability	0.288** (0.126)	0.184 (0.124)	0.297** (0.129)	0.242* (0.126)	0.403*** (0.134)	0.360** (0.181)	0.444*** (0.150)	0.453*** (0.146)
Climate		0.622*** (0.135)		0.419 (0.267)		0.301* (0.165)		-0.125 (0.187)
Axis		0.281 (0.276)		0.0397 (0.221)		0.584** (0.261)		-0.258 (0.226)
Size		-0.0065 (0.012)		-0.005 (0.010)		-0.0025 (0.014)		0.0004 (0.010)
Plants			0.0148 (0.017)	-0.0053 (0.022)			0.0093 (0.018)	0.0161 (0.022)
Animals			0.154** (0.060)	0.121* (0.069)			0.222*** (0.069)	0.251*** (0.076)
n	96	96	96	96	100	100	100	100
Adj. R ²	0.74	0.70	0.70	0.72	0.74	0.57	0.69	0.70

Notes: OLS estimates. Ashraf and Galor (2013) data. The extended sample includes: Australia, New Zealand, Canada and the United States. Heteroskedasticity-robust standard errors; *** p < 0.01, ** p < 0.05, * p < 0.1.

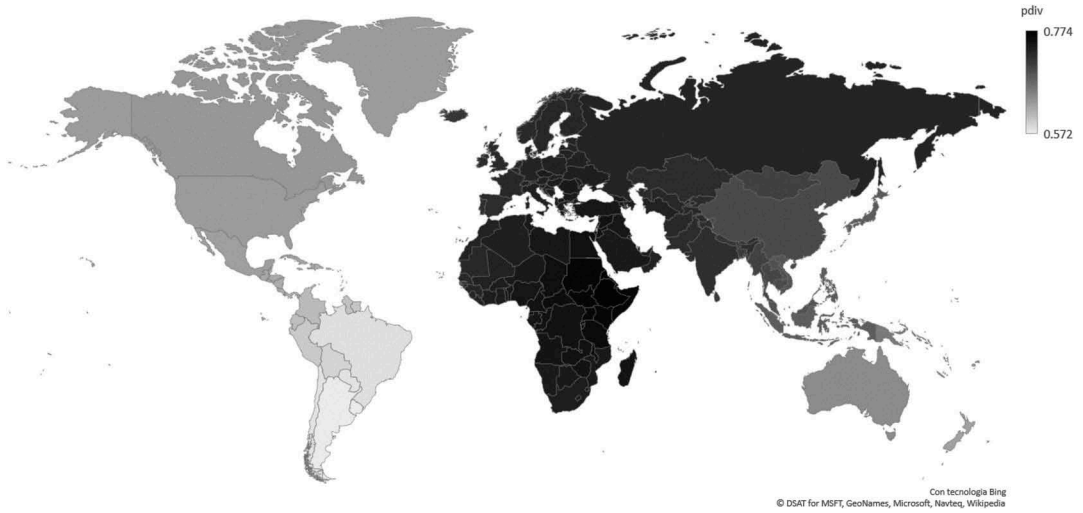


Figure 1. World map of predicted genetic diversity.

Note: World map in Miller projection. Source: Data from Ashraf and Galor (2013).

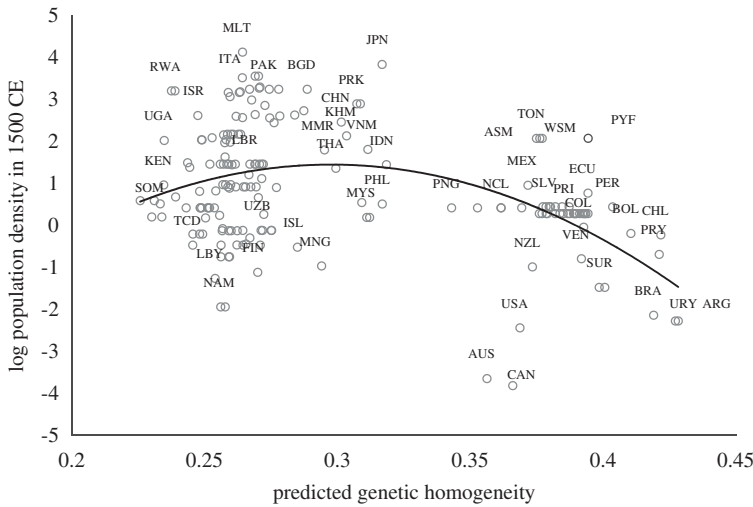


Figure 2. Predicted genetic diversity and population density in 1500 CE.

Source: data from Ashraf and Galor (2013), full sample.

Analogous findings are obtained in regressions that include observed genetic diversity, predicted diversity, migratory distance from Addis Ababa and continental dummies (Supplementary Materials, Tables A2–A3).⁷

The final step of our analysis consisted of including predicted genetic diversity among the explanatory variables of technology in 1500. If, as Ashraf and Galor maintained, genetic diversity predicts population density, it is possible to suppose that it also predicts technology. This stems from Ashraf & Galor’s (2011, 2013) same arguments that, during the Malthusian era, improvements in the technological environment led to a larger population. Figure 3 plots the relationship between predicted genetic homogeneity and technology in 1500. Even in this case, a hump-shaped relationship emerges, as well as two clusters: the Americas and the countries of Oceania are grouped together, and appear clearly distinct from the rest.

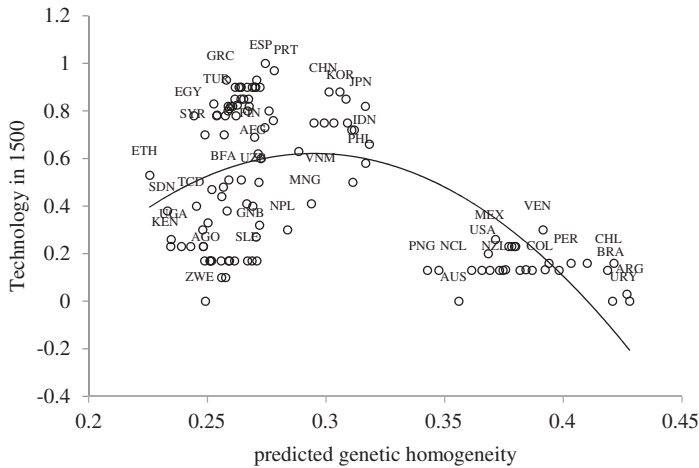


Figure 3. Predicted genetic diversity and technology in 1500 CE.

Source: Technology index from Comin et al. (2010), predicted genetic homogeneity from Ashraf and Galor (2013).

Table 7. Testing the role of genetic diversity (II)

Dependent variable: log of population density in 1500 CE			
	(1)	(2)	(3)
Constant	-76.85*** (28.10)	-32.11 (28.91)	-45.33 (33.33)
Predicted diversity	199.7** (78.33)	90.83 (81.87)	129.1 (94.71)
Predicted diversity sqr.	-146.2*** (55.04)	-63.65 (57.53)	-94.56 (66.79)
log Neolithic transition	1.235*** (0.224)		
log Arable land	0.393*** (0.097)	0.400*** (0.115)	
log Latitude	-0.417*** (0.119)	-0.512*** (0.133)	
log Land suitability	0.257*** (0.0935)	0.211* (0.118)	
Africa	0.694 (0.771)	1.161 (1.243)	2.217* (1.255)
Europe	0.924 (0.829)	2.701** (1.249)	3.507*** (1.239)
Asia	0.277 (0.810)	2.216* (1.226)	2.717** (1.204)
Americas	-0.238 (0.742)	0.746 (1.113)	1.344 (1.130)
n	145	145	145
Adj. R ²	0.69	0.61	0.37

Notes: OLS estimates. A. Column (1) replicates Ashraf and Galor (2013) Table 3 col. (6). Heteroskedasticity-robust standard errors; **** p < 0.01, ** p < 0.05, * p < 0.1

We included predicted genetic diversity in the regressions with technology in 1500 as a dependent variable (Table 8). Column 2 reports the results when geographical variables are added: the genetic channel loses its significance, while the effect of latitude and continental axis is confirmed. The last columns include population density, which remains highly significant in

Table 8. Genetic diversity, population density and technology in 1500

Dependent variable: Technology in 1500 CE				
	(1)	(2)	(3)	(4)
const	-22.7*** (3.94)	-1.93 (3.99)	1.27 (4.55)	-0.800 (4.21)
Predicted diversity	66.1*** (11.8)	2.84 (12.0)	-5.64 (13.6)	0.533 (12.6)
Predicted diversity sqr.	-46.9*** (8.75)	-0.497 (8.88)	5.32 (9.97)	0.627 (9.25)
log Pop. density 1 CE			0.0544*** (0.014)	
log Pop. density 1000 CE				0.0626*** (0.015)
Axis		0.207*** (0.038)	0.162*** (0.040)	0.162*** (0.037)
log Latitude		0.0825*** (0.019)	0.0898*** (0.019)	0.0962*** (0.019)
log Elevation		-0.0229 (0.026)	-0.0435 (0.027)	-0.0449* (0.026)
log Water distance		-0.0390** (0.018)	0.0063 (0.019)	0.0043 (0.019)
n	121	113	102	109
Adj. R ²	0.34	0.68	0.73	0.72

Notes: OLS estimates. Heteroskedasticity-robust standard errors; - *** p < 0.01, ** p < 0.05, * p < 0.1.

spite of the presence of genetic diversity among the regressors, thus suggesting that population density was a major

factor affecting cross-country variations in technological levels in the pre-modern era. These results, again, reject Ashraf and Galor's (2013) genetic hypothesis, while supporting the bio-geographical one.

5. Conclusion

At around 1500, the abysmal technological divide that existed between Europe and parts of Asia and the rest of the world is one of the most astonishing historical facts. The most advanced technologies at that time were in Eurasia, while in the other continents, with few exceptions, populations used much more rudimentary tools, in many cases similar to those used in the Neolithic or the upper Palaeolithic eras. In 1500, much of the world was still inhabited by hunter-gatherers. It was as if people were living not only in different continents, but also in different times. What were the causes of those differences?

Based on J. Diamond's (1997) great narrative, we showed how the international disparities in technological levels in 1500 CE are predicted by population density in years 1 and 1000 CE, by the axes of continents, latitude and some geographical factors. In turn, population density is strongly linked to the timing of the Neolithic transition: countries that adopted agriculture earlier had larger populations in 1 and 1000 CE. Overall, these findings are consistent with the historical evidence and with related studies on the deep determinants of economic and technology development (Ang, 2015; Chanda & Putterman, 2007; Putterman, 2008).

We also examined the thesis according to which global inequality has its deep roots in factors inherent to human nature, more precisely the level of genetic diversity within societies. This thesis was recently proposed by Ashraf and Galor (2013), who maintained that the 'predicted genetic diversity' of populations has a hump-shaped relationship with economic development, both in the pre-modern era and today. They argued that there is an 'optimal degree of genetic diversity' that has

been conducive to long-term economic development. This ‘optimal degree of diversity’ is that found in Eurasian populations, while the high genetic diversity of sub-Saharan Africans, and the low diversity of indigenous Australians and Americans, have been detrimental for development. By using Ashraf and Galor’s (2013) data, we found that their results are not robust to changes in sample size and to diverse specifications. In addition, genetic diversity is not a robust predictor of technological differences in 1500 when regressions control for population density and continental axes. These results are in line with other studies that critically re-examined the link between populations’ genetic endowment and long-run development (Campbell & Pyun, 2017; Rosenberg & Kang, 2015; Tang, 2016).

The impact of Neolithic transition on demographic growth and urbanisation in Eurasia is documented historically and scientifically (Bocquet-Appel & Bar-Yosef, 2008; Bocquet-Appel, 2008, 2011). Likewise, the low demographic density of the Americas, Oceania and sub-Saharan Africa, in the pre-colonial age, has been attributed to bio-geographical constraints that impeded the birth or diffusion of agriculture (Diamond, 1997; Harris, 1977). In the case of the Americas, the late peopling of the continent may have also contributed to the low population density (Frankema, 2015). In those regions of Africa or Central America where agriculture and husbandry were practised, demographic density was not lower than that of many Eurasian regions (Weil, 2014; Whitmore, Turner, & Johnson, 1990). There is no scientific evidence, however, supporting Ashraf and Galor’s thesis that, in pre-modern times, international differences in population density (their proxy of economic development) fundamentally reflected the level of genetic diversity within societies (D’Alpoim Guedes et al., 2013; Rosenberg & Kang, 2015).

Agriculture was a crucial factor for technology development, even though it was not sufficient alone. Research on worldwide traditional societies documents, in fact, how the size and density of populations, and social interconnections among populations, have been decisive factors for cultural and technological evolution (Richerson, Boyd, & Bettinger, 2009; Shennan, 2008). In many regions of the world, an adverse geography strongly limited the possibility of establishing social and economic connections among diverse populations, thus hampering innovation and the diffusion of knowledge and technologies. The cases of some traditional societies, such as the Dani of Papua New Guinea (Archbold, 1941; Brown, 1978) and the Tasmanians (Davidson & Roberts, 2008; Henrich, 2004), offer paradigmatic examples of the adverse effects of isolation on technological advancement. Influencing agricultural development and social connections, geography played a fundamental role in shaping the trajectories of societies. In human history, culture and genes interacted and co-evolved (Cochran & Harpending, 2009; Gintis, 2011; Richerson & Boyd, 2005). The spread of lactose-tolerance, a genetic mutation related to animal husbandry, is one of the best examples of culture-genes co-evolution. Although culture-gene interaction may be a promising field of research also for economics, the hypothesis that social complexity may be traced to genetic factors remains to be proved.

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Disclosure statement

No potential conflict of interest was reported by the authors.

Notes

1. The causes of the ‘great divergence’ between western Europe and China are the matter of intense historiographical debate (Hoffman, 2015; Jones, 1981).
2. Estimations of African population present a degree of uncertainty even for recent times; see Frankema and Jerven (2014).
3. This is a major difference between our analysis and that of Ang (2015), in which the Neolithic transition timing is used as a regressor to explain cross-country technology adoption levels in the pre-modern era.
4. Results, however, do not change when dummies for Europe and Asia are considered separately.
5. Ashraf and Galor computed bootstrapped standard errors to account for the presence of a generated regressor. However, the results do not change when heteroskedasticity-robust standard errors are employed.
6. In fact, Olsson and Hibbs (2005, p. 929) excluded these countries, because they considered the effects of bio-geography on current economic development.
7. Spolaore and Wacziarg (2009) also maintained that there is a causal link between a population’s genetic distance from the United States and its per capita income, proposing that genetic distance proxies a range of cultural traits which could impact on the transmission of technology. In line with our results, Campbell and Pyun (2017) demonstrated how the correlation between genetic distance and GDP per capita disappears when geographical controls are considered.

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