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How Deep Are the Roots of Economic Development?†

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The empirical literature on economic growth and development has moved from the study of proximate determinants to the analysis of ever deeper, more fundamental factors, rooted in long-term history. A growing body of new empirical work focuses on the measurement and estimation of the effects of historical variables on contemporary income by explicitly taking into account the ancestral composition of current populations. The evidence suggests that economic development is affected by traits that have been transmitted across generations over the very long run. This article surveys this new literature and provides a framework to discuss different channels through which intergenerationally transmitted characteristics may impact economic development, biologically (via genetic or epigenetic transmission) and culturally (via behavioral or symbolic transmission). An important issue is whether historically transmitted traits have affected development through their direct impact on productivity, or have operated indirectly as barriers to the diffusion of productivity-enhancing innovations across populations. (*JEL* J11, O33, O47, Z13)

> *"The further backward you look, the further forward you can see"* (attributed to Winston Churchill).[1]

1. *Introduction*

Why is income per capita higher in some societies and much lower in others? Answers to this perennial question have evolved over time. Decades ago, the emphasis was on the accumulation of factors of production and exogenous technological progress. Later, the focus switched to policies and incentives endogenously affecting factor accumulation and innovation. More recently, the attention has moved to the institutional framework underlying these policies and incentives. Pushing

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[1] This is the usual form of the quote attributed to Winston Churchill—for instance, by Queen Elizabeth II in her 1999 Christmas Message. According to Langworth (2008, 577), Churchill's words were "the longer you can look back, the farther you can look forward."

back the debate one more degree, a key question remains as to why the proximate determinants of the wealth of nations vary across countries. A burgeoning literature seeks to better understand the deep causes of development, rooted in geography and history.

As the empirical literature has moved from studying the proximate determinants of growth and development to analyzing ever deeper, more fundamental factors, important questions have arisen: How much time persistence is there in development outcomes? How far back in time should we go in order to understand contemporary economic development? Through what specific mechanisms do long-term geographic and historical factors affect outcomes today? If economic development has deep historical roots, what is the scope for policy to affect the wealth of nations? This article discusses the current state of knowledge on these issues, focusing on recent empirical work shedding light on the complex interactions among geography, history, and comparative development. Throughout, we illustrate the major milestones of the recent literature in a unified empirical framework for understanding variation in economic development.

Our starting point is the long-standing debate on geography and development. There is no doubt that geographic factors, such as latitude and climate, are highly correlated with development, but the interpretation of this correlation remains hotly debated. While some of the effects of geography may operate directly on current productivity, there is mounting evidence that much of the correlation operates through indirect mechanisms, i.e., through the historical effects of initial geographic conditions on the spatial distribution of human characteristics, such as institutions, human capital, social capital, and cultural traits, affecting income and productivity over the long run.[2] We review the literature on the legacy of geographic conditions in section 2.

A major theme emerging from the recent literature is that key human characteristics affecting development are transmitted from one generation to the next within populations over the long run, explaining why deep historical factors still affect outcomes today. A growing body of new empirical work has focused on the measurement and estimation of long-term effects of historical variables on contemporary income by explicitly taking into account the ancestral composition of current populations (Spolaore and Wacziarg 2009; Putterman and Weil 2010; Comin, Easterly, and Gong 2010; Ashraf and Galor 2013). We survey contributions to this new literature in section 3.

In section 4, we provide a general taxonomy to discuss different channels through which inherited human characteristics may impact economic development. Our discussion builds on an extensive evolutionary literature on the complex interactions among genetic, epigenetic, and cultural transmission mechanisms, and on the coevolution of biological and cultural traits (Cavalli-Sforza and Feldman 1981; Boyd and Richerson 1985; Richerson and Boyd 2005; Jablonka and Lamb 2005), as well as on a growing literature on cultural transmission and economic outcomes (e.g., Bisin and Verdier 2000, 2001; Tabellini 2008, 2009; Alesina, Giuliano, and Nunn 2013). An important issue is whether historically transmitted characteristics affect economic development through their direct impact on productivity, or operate indirectly as barriers to the diffusion of technological and institutional innovations across populations.

[2] For recent discussions of these issues from different perspectives, see Galor (2005, 2011) and Acemoglu, Johnson, and Robinson (2005).

2. *Geography and Development*

2.1 *Long-Term Effects of Geography*

The hypothesis that geographic factors affect productivity and economic development has a long pedigree, going back to Machiavelli (1531), Montesquieu (1748), and Marshall (1890). A vast empirical literature has documented high correlations between current levels of income per capita and a series of geographic and biological variables, such as climate and temperature (Myrdal 1968; Kamarck 1976; Masters and McMillan 2001; Sachs 2001), the disease environment (Bloom and Sachs 1998; Sachs, Mellinger, and Gallup 2001; Sachs and Malaney 2002), natural resources (Sachs and Warner 2001), and transportation conditions (Rappaport and Sachs 2003).

In order to illustrate the main empirical findings of the contributions discussed herein, we punctuate this paper with our own empirical results based on a unified data set, regression methodology and sample. This analysis is not meant to be an exhaustive recapitulation of existing results, but simply to illustrate some important milestones in the recent literature. We use, alternately, log per capita income in 2005 (from the Penn World Tables version 6.3) as a measure of contemporary economic performance, and population density in 1500 (from McEvedy and Jones 1978) as a measure of economic performance in 1500, and regress these on a variety of proposed determinants of development, starting here with geographic factors.[3]

[3]As is well known, in the preindustrial, Malthusian era population density is the appropriate measure of a society's economic performance since any technological improvement leads to increases in population rather than to increases in per capita income. For a theoretical and empirical analysis of the relationship between population size, population density, and long-term growth in Malthusian times, see Kremer (1993). For in-depth discussions of this topic, see Galor (2005) and the recent contribution by Ashraf and Galor (2011a).

Table 1, column 1 shows that a small set of geographic variables (absolute latitude, the percentage of a country's land area located in tropical climates, a landlocked country dummy, an island country dummy) can jointly account for 44 percent of contemporary variation in log per capita income, with quantitatively the largest effect coming from absolute latitude (excluding latitude causes the R^2 to fall to 0.29). This result captures the flavor of the above-cited literature documenting a strong correlation between geography and income per capita.

While the correlation between geography and development is well established, the debate has centered around causal mechanisms. A number of prominent economists, including Myrdal (1968), Kamarck (1976), and Sachs and coauthors, argue that geographic factors have a direct, contemporaneous effect on productivity and development. In particular, Sachs (2001) claims that economic underdevelopment in tropical countries can be partly explained by the current negative effects of their location, which include two main ecological handicaps: low agricultural productivity and a high burden of diseases. Tropical soils are depleted by heavy rainfall, and crops are attacked by pests and parasites that thrive in hot climates without winter frosts (Masters and McMillan 2001). Warm climates also favor the transmission of tropical diseases borne by insects and bacteria, with major effects on health and human capital. In sum, according to this line of research, geography has direct current effects on productivity and income per capita.

Other scholars, in contrast, claim that geography affects development indirectly through historical channels, such as the effects of prehistoric geographic and biological conditions on the onset and spread of agriculture and domestication (Diamond 1997; Olsson and Hibbs 2005), and the effects of crops and germs on the settlement of European colonizers after 1500 (Engerman

TABLE 1
GEOGRAPHY AND CONTEMPORARY DEVELOPMENT
(*Dependent variable: log per capita income, 2005; estimator: OLS*)

Sample:	Whole World	Olsson–Hibbs sample[a]	Olsson–Hibbs sample[a]	Olsson–Hibbs sample[a]	Olsson–Hibbs sample[a]	Old World only
	(1)	(2)	(3)	(4)	(5)	(6)
Absolute latitude	0.044	0.052				
	(6.645)***	(7.524)***				
Percent land area in the tropics	–0.049	0.209	–0.410	–0.650	–0.421	–0.448
	(0.154)	(0.660)	(1.595)	(2.252)**	(1.641)	(1.646)
Landlocked dummy	–0.742	–0.518	–0.499	–0.572	–0.505	–0.226
	(4.375)***	(2.687)***	(2.487)**	(2.622)**	(2.523)**	(1.160)
Island dummy	0.643	0.306	0.920	0.560	0.952	1.306
	(2.496)**	(1.033)	(3.479)***	(1.996)**	(3.425)***	(4.504)***
Geographic conditions (Olsson–Hibbs)[b]			0.706		0.768	0.780
			(6.931)***		(4.739)***	(5.167)***
Biological conditions (Olsson–Hibbs)[c]				0.585	–0.074	0.086
				(4.759)***	(0.483)	(0.581)
Constant	7.703	7.354	8.745	8.958	8.741	8.438
	(25.377)***	(25.360)***	(61.561)***	(58.200)***	(61.352)***	(60.049)***
Observations	155	102	102	102	102	83
Adjusted R^2	0.440	0.546	0.521	0.449	0.516	0.641

Notes:
[a]The Olsson and Hibbs sample excludes the neo-European countries (Australia, Canada, New Zealand, and the United States) and countries whose current income is based primarily on extractive wealth (Olsson and Hibbs 2005).
[b]First principal component of number of annual or perennial wild grasses and number of domesticable big mammals (all variables from Olsson and Hibbs 2005)
[c]First principal component of absolute latitude; climate suitability to agriculture; rate of East–West orientation; size of landmass in millions of sq km (all variables from Olsson and Hibbs 2005).
Robust *t* statistics in parentheses.
***Significant at the 1 percent level.
**Significant at the 5 percent level.
*Significant at the 10 percent level.

and Sokoloff 1997 and 2002; Acemoglu, Johnson, and Robinson 2001, 2002; Easterly and Levine 2003).

Diamond (1997) famously argues that the roots of comparative development lie in a series of environmental advantages enjoyed by the inhabitants of Eurasia at the transition from a hunter–gatherer economy to agricultural and pastoral production, starting roughly in 10,000 BC (the Neolithic Revolution). These advantages included the larger size of Eurasia, its initial biological conditions (the diversity of animals and plants available for domestication in prehistoric times), and its East–West orientation, which facilitated the spread of agricultural innovations. Building on these geographic advantages, Eurasia experienced a population explosion

and an earlier acceleration of technological innovation, with long-term consequences for comparative development. According to Diamond, the proximate determinants of European economic and political success ("guns, germs, and steel") were therefore the outcomes of deeper geographic advantages that operated in prehistoric times. The descendants of some Eurasian populations (Europeans), building on their Neolithic advantage, were able to use their technological lead (guns and steel) and their immunity to old-world diseases (germs) to dominate other regions in modern times—including regions that did not enjoy the original geographic advantages of Eurasia.

In order to test Diamond's hypotheses, Olsson and Hibbs (2005) provide an empirical analysis of the relation between initial biogeographic endowments and contemporary levels of development.[4] They use several geographic and biological variables: the size of continents, their major directional axis (extent of East–West orientation), climatic factors, and initial biological conditions (the number of animals and plants suitable to domestication and cultivation at each location 12,000 years ago). We revisit their empirical results in columns 2 through 5 of table 1. In order to reduce the effect of post-1500 population movements, the Olsson–Hibbs sample excludes the neo-European countries (Australia, Canada, New Zealand, and the United States), as well as countries whose current income is based primarily on extractive wealth. Column 2 replicates the estimates of column 1 using this restricted sample—the joint explanatory power of geographic variables rises to 55 percent, since the new sample excludes regions that are rich today as a result of the guns, germs, and steel of colonizing Europeans rather than purely geographic factors.

Columns 3–5 add the two main Olsson–Hibbs geographic variables, first separately and then jointly: a summary measure of biological conditions and a summary measure of geographic conditions.[5] Both geographic and biological conditions variables are highly significant when entered separately. When entered jointly, the geographic conditions variable remains highly significant and the overall explanatory power of the regressors remains large (52 percent). These empirical results provide strong evidence in favor of Diamond's hypotheses, while suggesting that the geographic component of the story is empirically more relevant than the biological component. Column 6 goes further in the attempt to control for the effect of post-1500 population movements, by restricting the sample to the Old World (defined as all countries minus the Americas and Oceania). The effect of geography now rises to 64 percent—again highly consistent with Diamond's idea that biogeographic conditions matter mostly in the Old World.[6]

[4] See also Hibbs and Olsson (2004).

[5] These are the first principal components of the above-listed factors. Since latitude is a component of the geographic conditions index, we exclude our measure of latitude as a separate regressor in the regressions that include geographic conditions.

[6] Olsson and Hibbs also find that geographic variables continue to be positively and significantly correlated with income per capita when they control for measures of the political and institutional environment. They show that such political and institutional measures are positively correlated with geographic and biogeographic conditions, consistent with the idea that institutions could mediate the link between geography and development. As they notice (934), controlling for political–institutional variables raises well-known issues of endogeneity and reverse causality (for instance, richer countries can have the resources and ability to build better institutions). They write: "Researchers have struggled with the joint endogeneity issue, proposing various instrumental variables to obtain consistent estimates of the proximate effects of politics and institutions on economic performance, along with the related question of how much influence, if any, natural endowments exert on economic development independent of institutional development. None of these attempts is entirely persuasive in our view." We return to these important issues below.

2.2 *The Legacy of the Neolithic Transition*

The long-term effects of geographic and biogeographic endowments also play a central role in the analysis of Ashraf and Galor (2011a). While their main goal is to test a central tenet of Malthusian theory (that per capita income gains from technological improvements in the preindustrial era were largely dissipated through population growth), their approach leads them to provide further evidence relating to Diamond's hypotheses and the legacy of geography. Ashraf and Galor demonstrate that the spread of agriculture (the Neolithic transition) was driven by geographic conditions (climate, continental size and orientation) and biogeographic conditions (the availability of domesticable plant and big mammal species). They empirically document how geographic factors influenced the timing of the agricultural transition. They also show that biogeographic variables, consistent with Olsson and Hibbs (2005), are strongly correlated with population density in 1500, but argue that the only way these variables matter for economic performance in preindustrial times is through their effect on the timing of the adoption of agriculture. This paves the way to using biogeographic factors as instruments for the timing of the Neolithic transition in a specification explaining population density in 1500.

Table 2 illustrates these findings in our unified empirical setup. In column 1, we regressed the number of years since the Neolithic transition (obtained from Chanda and Putterman 2007) on a set of geographic variables—i.e., this is the first stage regression.[7] These geographic conditions account for 70 percent of the variation in the date of adoption of agriculture, and most enter with a highly significant coefficient. Column 2 shows the reduced form—again, geographic factors account for 44 percent of the variation in population density in 1500, consistent with the results of table 1 for the contemporary period.[8]

Ashraf and Galor (2011a) argue that, while geographic factors may have continued to affect economic development after the introduction of agriculture, the availability of prehistoric domesticable wild plant and animal species did not influence population density in the past two millennia other than through the timing of the Neolithic transition. Therefore, they use these variables, obtained from the Olsson and Hibbs (2005) data set, as instruments to estimate the effect of the timing of the Neolithic transition on population density. The results of column 3 (OLS) and column 4 (IV) of table 2 illustrate their findings: years since the agricultural transition has a strong, statistically significant positive effect on population density in 1500. Interestingly, the IV effect is quantitatively larger than the OLS estimate.[9] The magnitude of the effect is large, as a one standard

[7] For comparability we use the same set of variables as above, except instead of the Olsson–Hibbs summary indices of geographic and biological conditions, we directly include the number of annual or perennial wild grasses and the number of domesticable big mammals, so as to maintain consistency with Ashraf and Galor (2011a).

[8] Interestingly, the effect of latitude is negative. Ashraf and Galor (2011a) indeed observe that: "in contrast to the positive relationship between absolute latitude and contemporary income per capita, population density in preindustrial times was on average higher at latitudinal bands closer to the equator." Thus, the effects of geographic factors have varied over different periods of technological development, in line with the idea that the effects of geography on development are indirect.

[9] Ashraf and Galor (2011a) argue that, in regressions of this type: "reverse causality is not a source of concern, (. . .) [but] the OLS estimates of the effect of the time elapsed since the transition to agriculture may suffer from omitted variable bias (. . .)" (2016). The sign of the expected OLS bias therefore depends on the pattern of correlations between the omitted factors, the dependent variables and the included regressors. Finding an IV effect that is larger than the OLS effect is also broadly consistent with IV partly addressing measurement error in years since the agricultural transition, although care must be exercised with this inference in the multivariate context.

TABLE 2
GEOGRAPHY AND DEVELOPMENT IN 1500 AD

Dependent Variable:	Years since agricultural transition	Population density in 1500	Population density in 1500	Population density in 1500
Estimator:	OLS	OLS	OLS	IV
	(1)	(2)	(3)	(4)
Absolute latitude	–0.074 (3.637)***	–0.022 (1.411)	0.027 (2.373)**	0.020 (1.872)*
Percent land area in the tropics	–1.052 (2.356)**	0.997 (2.291)**	1.464 (3.312)***	1.636 (3.789)***
Landlocked dummy	–0.585 (2.306)**	0.384 (1.332)	0.532 (1.616)	0.702 (2.158)**
Island dummy	–1.085 (3.699)***	0.072 (0.188)	0.391 (0.993)	0.508 (1.254)
Number of annual or perennial wild grasses	0.017 (0.642)	0.030 (1.105)		
Number of domesticable big mammals	0.554 (8.349)***	0.258 (3.129)***		
Years since agricultural transition			0.426 (6.694)***	0.584 (6.887)***
Constant	4.657 (9.069)***	–0.164 (0.379)	–2.159 (4.421)***	–2.814 (5.463)***
Observations	100	100	98	98
Adjusted R^2	0.707	0.439	0.393	—

Notes: Robust *t* statistics in parentheses.
***Significant at the 1 percent level.
**Significant at the 5 percent level.
*Significant at the 10 percent level.

deviation change in years of agriculture is associated with 63 percent of a standard deviation change in log population density in 1500 (OLS). The corresponding standardized beta coefficient using IV is 88 percent. All of the other regressors feature much smaller standardized effects.

In addition to providing strong support in favor of the Malthusian view that technological improvements impact population density but not per capita income in preindustrial societies, the results in Ashraf and Galor (2011a), as summarized in table 2, add an important qualifier to the Olsson and Hibbs (2005) results. They show, not only that an earlier onset of the Neolithic transition contributed to the level of technological sophistication in the preindustrial world, but also that the effect of Diamond's biogeographic factors may well operate through the legacy of an early exposure to agriculture.

2.3 *Reversal of Fortune and the Role of Institutions*

Diamond's book, as well as the empirical work by Olsson and Hibbs and Ashraf and Galor, suggests an important role for geography and biogeography in the onset and diffusion of economic development over the past millennia. However, these analyses leave open the question of whether the effects of geography operate only through their historical legacy, or also affect contemporaneous income and productivity directly. Nunn (2009) makes a closely related point when discussing Nunn and Puga (2007), an attempt to estimate the magnitude of direct and indirect (historical) effects of a specific geographic characteristic: terrain ruggedness, measured by the average absolute slope of a region's surface area. Nunn and Puga (2007) argue that ruggedness has a negative direct effect on agriculture, construction, and trade, but a positive historical effect within Africa because it allowed protection from slave traders. They find that the historical (indirect) positive effect is twice as large as the negative (direct) contemporary effect.

A broader issue with Diamond's geographic explanation is that it denies a role for specific differences between populations, especially within Eurasia itself. For example, Appleby (2010) writes: "How deep are the roots of capitalism? [. . .] Jared Diamond wrote a best-selling study that emphasized the geographic and biological advantages the West enjoyed. Two central problems vex this interpretation: The advantages of the West were enjoyed by all of Europe, but only England experienced the breakthrough that others had to imitate to become capitalistic. Diamond's emphasis on physical factors also implies that they can account for the specific historical events that brought on Western modernity without reference to the individuals, ideas, and institutions that played so central a part in this historic development" (11). We return to these important questions below.

Acemoglu, Johnson, and Robinson (2002) address the issue of whether geography may have had a direct effect on development by documenting a "reversal of fortune" among former European colonies. This reversal of fortune suggests that the effect of geography was indirect. The simplest geography story states that some geographic features are conducive to development, but this story is inconsistent with the reversal of fortune since the same geographic features that made a society rich in 1500 should presumably make it rich today.[10] More sophisticated geography-centered arguments rely on the idea that geographic features conducive to development vary depending on the time period. A reversal of fortune would be consistent with nonpersistent direct effects of geography on productivity: features of geography that had positive effects on productivity in the past could have become a handicap in more recent times. However, such shifts would then have to be explained by specific changes in nongeographic factors (e.g., a technological revolution).

To proxy for levels of economic productivity and prosperity in a Malthusian world, Acemoglu, Johnson, and Robinson (2002) use data on urbanization patterns and population density. Contemporary income per capita is regressed on these measures of economic performance in 1500 to assess whether a reversal of fortune has occurred. The bottom panel of table 3 mirrors their main results: in various samples that all exclude European countries, the relationship between population density in 1500 and log

[10] Acemoglu, Johnson, and Robinson (2002) state that: "The simplest version of the geography hypothesis emphasizes the time-invariant effects of geographic variables, such as climate and disease, on work effort and productivity, and therefore predicts that nations and areas that were relatively rich in 1500 should also be relatively prosperous today" (1233).

per capita income in 2005 is negative. In the regression that corresponds to their baseline (column 3), looking only at former European colonies, the effect is large in magnitude and highly significant statistically: the standardized beta on 1500 density is 48 percent and the *t*-statistic is 7. Similar results hold for the whole World minus Europe (column 1), and also when restricting attention only to countries not currently populated by more than 50 percent of their indigenous population (columns 5 and 7).[11] These important findings suggest that the observed correlation between geographic variables and income per capita are unlikely to stem from direct effects of geography on productivity. In contrast, they point to indirect effects of geography operating through long-term changes in nongeographic variables.

Acemoglu, Johnson, and Robinson (2002) argue that the reversal reflects changes in the institutions resulting from European colonialism: Europeans were more likely to introduce institutions encouraging investment in regions with low population density and low urbanization, while they introduced extractive, investment-depressing institutions in richer regions. This interpretation is consistent with Acemoglu, Johnson, and Robinson (2001), where the focus is on an indirect biogeographic channel: European settlers introduced good (productivity-enhancing) institutions in regions where they faced favorable biogeographic conditions (low mortality rates), and bad institutions in regions where they faced unfavorable biogeographic conditions (high mortality rates).[12]

This line of research is part of a body of historical and empirical work emphasizing institutional differences across societies, including seminal contributions by North and Thomas (1973), North (1981, 1990), and Jones (1988), and more recently Engerman and Sokoloff (1997, 2002), Sokoloff and Engerman (2000), and Acemoglu, Johnson, and Robinson (2001, 2002, 2005). In particular, Engerman and Sokoloff (1997) provide a path-breaking investigation of the interplay between geographic and historical factors in explaining differential growth performance in the Americas (United States and Canada versus Latin America). They point out that Latin American societies also began with vast supplies of land and natural resources per capita, and "were among the most prosperous and coveted of the colonies in the seventeenth and eighteenth century. Indeed, so promising were these other regions, that Europeans of the time generally regarded the thirteen British colonies of the North American mainland and Canada as of relatively marginal economic interest—an opinion evidently shared by Native Americans who had concentrated disproportionally in the areas the Spanish eventually developed. Yet, despite their similar, if not less favorable, factor endowment, the U.S. and Canada ultimately proved to be far more successful than the other colonies in realizing sustained economic growth over time. This stark contrast in performance suggests that factor endowment alone cannot explain the diversity of outcomes" (Engerman and Sokoloff 1997, 260). Their central hypothesis was that differences in factor endowments across New World colonies played a key role in explaining different growth patterns after 1800, but that those effects were indirect. Different factor endowments created "substantial differences in the degree of inequality in wealth,

[11] To define whether a country's population today is composed of more than 50 percent of descendents of its 1500 population we rely on the World Migration Matrix of Putterman and Weil (2010), which we discuss in much greater detail in section 3.

[12] For a critical reassessment of the empirical strategy in Acemoglu, Johnson, and Robinson (2001), see Albouy (2012). See Acemoglu, Johnson, and Robinson (2012) for a reply.

TABLE 3
REVERSAL OF FORTUNE
(*Dependent variable: log per capita income, 2005; estimator: OLS*)

Sample:	Whole World	Europe Only	Former European Colony	Not Former European Colony	Non Indigenous	Indigenous	Former European colony, Non Indigenous	Former European Colony, Indigenous
	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)
	With European Countries							
Log of population density, year 1500	0.027 (0.389)	0.117 (1.276)	[b]	0.170 (2.045)**	[b]	0.193 (2.385)**	[b]	[b]
Beta coefficient on 1500 density	3.26%	22.76%		22.34%		20.00%		
Observations	171	35		73		138		
R^2	0.001	0.052		0.050		0.040		
	Without European Countries							
Log of population density, year 1500	–0.246 (3.304)***	[a]	–0.393 (7.093)***	–0.030 (0.184)	–0.232 (2.045)**	–0.117 (1.112)	–0.371 (4.027)***	–0.232 (2.740)**
Beta coefficient on 1500 density	–27.77%		–47.88%	–3.08%	–32.81%	–11.72%	–51.69%	–26.19%
Observations	136		98	38	33	103	28	70
R^2	0.077		0.229	0.001	0.108	0.014	0.267	0.069

Notes: All regressions include a constant term (estimates not reported). Robust *t* statistics in parentheses.
***Significant at the 1 percent level.
**Significant at the 5 percent level.
*Significant at the 10 percent level.
[a]Empty sample.
[b]No European countries in sample, regression results identical to those in the bottom panel.

human capital, and political power," which, in turn, were embodied in persistent societal traits and institutions. Societies that were endowed with climate and soil conditions well-suited for growing sugar, coffee, rice, tobacco, and other crops with high market value and economies of scale ended up with unequal slave economies in the hands of a small elite, implementing policies and institutions that perpetuated such inequality, lowering incentives for investment and innovation. In contrast, a more equal distribution

of wealth and power emerged in societies with small-scale crops (grain and livestock), with beneficial consequences for long-term economic performance.

An alternative to the institutional explanation for the reversal of fortune is rooted in the composition of world populations. For while Europeans may have left good institutions in former colonies that are rich today, they also brought themselves there. This point is stressed by Glaeser et al. (2004), who write: "[Acemoglu, Johnson, and Robinson's] results do not establish a role for institutions. Specifically, the Europeans who settled in the New World may have brought with them not so much their institutions, but themselves, that is, their human capital. This theoretical ambiguity is consistent with the empirical evidence as well" (274).

The top panel of table 3 shows that when Europe is included in the sample, any evidence for reversals of fortune disappears: the coefficient on 1500 population density is essentially zero for the broadest sample that includes the whole world (column 1). For countries that were not former European colonies, there is strong evidence of persistence, with a *positive* significant coefficient on 1500 density. The evidence of persistence is even stronger when looking at countries that are populated mostly by their indigenous populations (the evidence is yet stronger when defining "indigenous" countries more strictly, for instance requiring that more than 90 percent of the population be descended from those who inhabited the country in 1500).[13] In other words, the reversal of fortune is a feature of samples that exclude Europe and is driven largely by countries inhabited by populations that moved there after the discovery of the New World, and now constitute large portions of these countries' populations—either European colonizers (e.g., in North America and Oceania) or African slaves (e.g., in the Caribbean).

These regularities suggest that the broader features of a population, rather than institutions only, might account for the pattern of persistence and change in the relative economic performance of countries through history. Of course, the quality of institutions might be one of the features of a population (perhaps not the only feature) that makes it more or less susceptible to economic success, but the basic lesson from table 3 is that one cannot abstract from the ancestral structure of populations when trying to understand comparative development. This central idea is the subject of sections 3 and 4, so we will say little more for now.

Recent work casts additional doubt on the view that national institutions are paramount. In a paper on African development, Michalopoulos and Papaioannou (2010) find that national institutions have little effect when one looks at the economic performance of homogeneous ethnic groups divided by national borders. They examine the effects on comparative development of national contemporary institutions structures and ethnicity-specific precolonial societal traits, using a methodological approach that combines anthropological data on the spatial distribution of ethnicities before colonization, historical information on ethnic cultural and institutional traits, and contemporary light density image data from satellites as a proxy of regional development. Overall, their findings suggest that long-term features of populations, rather than institutions in isolation,

[13] The R^2 we obtain in the regressions of table 3 are commensurate in magnitude to those obtained from comparable specifications in Acemoglu, Johnson, and Robinson (2002). As expected, as the sample expands beyond former European colonies, the explanatory power of past development for current development falls, and correspondingly the R^2 falls. In general, R^2s are quite low because we are regressing two different measures of development on each other (per capita income and population density in 1500), and both variables (particularly historical population density) are measured with significant amounts of error.

play a central role in explaining comparative economic success.[14]

In sum, the evidence on reversal of fortune documented by Acemoglu, Johnson, and Robinson (2002) is consistent with an indirect rather than direct effect of geography on development, but is open to alternative interpretations about the mechanisms of transmission. A key issue is whether the differential settlement of Europeans across colonies after 1500 affect current income in former colonies exclusively through institutions, as argued by Acemoglu, Johnson, and Robinson (2001, 2002, 2005), or through other relevant factors and traits brought by Europeans, such as human capital (Glaeser et al. 2004) or culture (Landes 1998).

Disentangling the effects of specific societal characteristics, such as different aspects of institutions, values, norms, beliefs, other human traits, etc., is intrinsically difficult, because these variables are conceptually elusive to measure, deeply interlinked, and endogenous with respect to economic development. In spite of these intrinsic difficulties, a growing body of historical and empirical research, focusing on natural experiments, has attempted to provide insights on the complex relationships between geography and human history and their implications for comparative development (for example, see the contributions in Diamond and Robinson 2010).

As we discuss in the next two sections, recent contributions stress the importance of persistent characteristics transmitted intergenerationally over the long run. This literature is consistent with anthropological work, such as by Guglielmino et al. (1995), showing in the case of Africa that cultural traits are transmitted intergenerationally and bear only a weak correlation with environmental characteristics: "Most traits examined, in particular those affecting family structure and kinship, showed great conservation over generations. They are most probably transmitted by family members."

[14]The effects of ethnic/cultural differences on economic outcomes within a common national setting are also documented by Brügger, Lalive, and Zweimüller (2009), who compare different unemployment patterns across the language barrier in Switzerland, and find that job seekers living in Latin-speaking border communities take about 18 percent longer to leave unemployment than their neighbors in German-speaking communities.

3. *Development and the Long-Term History of Populations*

3.1 *Adjusting for Ancestry*

Historical population movements play a central role in the debate regarding the mechanism linking geography and economic development, as well as the interpretation of reversals of fortune. Recent research has focused on the measurement and estimation of the long-term effects of historical factors on contemporary income by explicitly taking into account the ancestral composition of current populations. We review some of these contributions in this section.

An important contribution within this line of research is Putterman and Weil (2010). They examine explicitly whether it is the historical legacy of geographic *locations* or the historical legacy of the *populations* currently inhabiting these locations that matters more for contemporary outcomes. To do so, they assemble a matrix showing the share of the contemporary population of each country descended from people in different source countries in the year 1500. The definition of ancestry is bound to have some degree of arbitrariness, since it refers to ancestral populations at a specific point in time. However, choosing 1500 is sensible since this date occurs prior to the massive population movements that followed the discovery of the New World, and data on population movements prior to that date are largely unavailable.

Building on previous work by Bockstette, Chanda, and Putterman (2002) and Chanda and Putterman (2007), they consider two indicators of early development: early state history and the number of years since the adoption of agriculture. They then construct two sets of historical variables, one set representing the history of the location, the other set weighted using the migration matrix, representing the same variables as they pertain not to the location but the contemporaneous population inhabiting this location. Inevitably, measuring these concepts is fraught with methodological issues. For instance, when it comes to state antiquity, experience with centralization that occurred in the distant past is discounted exponentially, while no discounting is applied to the measure of the years of agriculture. While these measurement choices will surely lead to future refinements, it is the comparison between the estimates obtained when looking at the history of locations rather than populations that leads to interesting inferences.

According to this approach, the United States has had a relatively short exposure to state centralization in terms of location, but once ancestry-adjusted it features a longer familiarity with state centralization, since the current inhabitants of the United States are mostly descended from Eurasian populations that have had a long history of centralized state institutions.[15] Clearly, in this work the New World plays a big role in identifying the difference in the coefficients between historical factors and their ancestry-adjusted counterparts, because outside the New World, everyone's ancestry is largely from their own location. Putterman and Weil explore how their two historical variables—each either ancestry adjusted or not—affect the level of income per capita and within-country income inequality in the world today.

Their key finding is that it is not as much the past history of locations that matters as it is the history of the ancestor populations. Tables 4 and 5 illustrate their approach in our unified empirical framework. Table 4 starts with simple correlations. The correlations between state history and years of agriculture, on the one hand, and per capita income in 2005, on the other hand, are of the expected positive signs, but are much larger when ancestry-adjusting—almost doubling in magnitude. These results are confirmed in the regressions of table 5. In these regressions, we start from the specification that controls for the baseline set of four geographic variables, and add the Putterman and Weil variables one by one, either ancestry-adjusted or not. The variables representing the history of the locations enter with an insignificant coefficient (columns 1 and 3), while the ancestry-adjusted variables enter with positive, statistically significant coefficients (columns 2 and 4). A one standard deviation change in ancestry-adjusted years of agriculture can account for 17 percent of a standard deviation of log per capita income,

[15] Germany and Italy, two countries from which many ancestors of current Americans originate, have fluctuated over their histories between fractured and unified states. For instance, Italy was a unified country under the Roman Empire, but a collection of city-states and local polities, partly under foreign control, prior to its unification in 1861. The index of state antiquity for such cases discounts periods that occurred in the distant past (see http://www.econ.brown.edu/fac/louis_putterman/Antiquity%20data%20page.htm for details on the computation of the index). Due to lengthy periods of unification or control of substantial parts of their territories by domestic regional states (such as the Republic of Venice and Prussia), however, Italy and Germany do not display state antiquity indices that are that different from other European countries. The United States overall has a state antiquity index roughly commensurate with that of European countries, despite the addition of populations, for instance descended from Native Americans or African slaves, that may have had limited exposure to centralized states. While the measurement of state antiquity can be questioned on several grounds, there is little doubt that ancestry adjustment implies that the United States had a longer experience with centralized states than the history of Native Americans would suggest.

TABLE 4
Historical Correlates of Development, with and without Ancestry Adjustment

	Log per capita income 2005	Years of agriculture	Ancestry adjusted years of agriculture	State history	Ancestry adjusted state history
Years of agriculture	0.228	1.000			
Ancestry-adjusted years of agriculture	0.457	0.817	1.000		
State history	0.257	0.618	0.457	1.000	
Ancestry-adjusted state history	0.481	0.424	0.613	0.783	1.000

Note: Observations: 139

while the corresponding figure is almost 22 percent for state history.

To summarize, a long history of centralized states as well as an early adoption of agriculture are positively associated with per capita income today, after ancestry adjustment.[16] Putterman and Weil also find that the variance of early development history across ancestor populations predicts within-country income inequality better than simple measures of ethnic and linguistic heterogeneity. For example, in Latin America, countries that are made up of a lot of Europeans along with a lot of Native Americans tend to display higher income inequality than countries that are made up mostly of European descendants. Finally, to further elucidate why correcting for ancestry matters, they also show that a variable capturing the extent of European ancestry accounts for 41 percent of the variation in per capita income, a topic to which we turn in the next subsection.

Putterman and Weil's results strongly suggest that the ultimate drivers of development cannot be fully disembodied from characteristics of human populations. When migrating to the New World, populations brought with them traits that carried the seeds of their economic performance. This stands in contrast to views emphasizing the direct effects of geography or the direct effects of institutions, for both of these characteristics could, in principle, operate irrespective of the population to which they apply. A population's long familiarity with certain types of institutions, human capital, norms of behavior or more broadly culture seems important to account for comparative development.

3.2 *The Role of Europeans*

Easterly and Levine (2012) confirm and expand upon Putterman and Weil's finding, showing that a large population of

[16] Interestingly, Paik (2010) documents that within Europe, an earlier onset of agriculture is negatively correlated with subsequent economic performance after the Industrial Revolution, contrary to the worldwide results of Putterman and Weil. Paik argues that the mechanism is cultural: a late adoption of agriculture is associated with individualist values that were conducive to economic success in the Industrial era.

TABLE 5
THE HISTORY OF POPULATIONS AND ECONOMIC DEVELOPMENT
(*Dependent variable: log per capita income, 2005; estimator: OLS*)

Main regressor:	Years of agriculture	Ancestry-adjusted years of agriculture	State history	Ancestry-adjusted state history
	(1)	(2)	(3)	(4)
Years of agriculture	**0.019**			
	(0.535)			
Ancestry-adjusted years of agriculture		**0.099**		
		(2.347)**		
State history			**0.074**	
			(0.245)	
Ancestry-adjusted state history				**1.217**
				(3.306)***
Absolute latitude	0.042	0.040	0.047	0.046
	(6.120)***	(6.168)***	(7.483)***	(7.313)***
Percent land area in the tropics	–0.188	–0.148	0.061	0.269
	(0.592)	(0.502)	(0.200)	(0.914)
Landlocked dummy	–0.753	–0.671	–0.697	–0.555
	(4.354)***	(3.847)***	(4.122)***	(3.201)***
Island dummy	0.681	0.562	0.531	0.503
	(2.550)**	(2.555)**	(2.216)**	(2.338)**
Constant	7.699	7.270	7.458	6.773
	(22.429)***	(21.455)***	(22.338)***	(19.539)***
Beta coefficients on the bold variable	3.75%	17.23%	1.50%	21.59%
Observations	150	148	136	135
R^2	0.475	0.523	0.558	0.588

Notes: Robust *t* statistics in parentheses.
***Significant at the 1 percent level.
**Significant at the 5 percent level.
*Significant at the 10 percent level.

European ancestry confers a strong advantage in development, using new data on European settlement during colonization and its historical determinants. They find that the share of the European population in colonial times has a large and significant impact on income per capita today, even when eliminating Neo-European countries and restricting the sample to countries where the European share is less than 15 percent—that is, in non-settler colonies, with crops and germs associated with bad institutions. The effect remains high and significant when controlling for the quality of institutions, while it weakens when controlling for measures of education.

TABLE 6
EUROPEANS AND DEVELOPMENT
(*Dependent variable: log per capita income, 2005; estimator: OLS*)

Main regressor:	Share of Europeans	Sample with less than 30% of Europeans	Control for years of agriculture	Control for state history	Control for genetic distance
	(1)	(2)	(3)	(4)	(5)
Share of descendants of Europeans, per Putterman and Weil	1.058 (4.743)***	2.892 (3.506)***	1.079 (4.782)***	1.108 (5.519)***	0.863 (3.601)***
Ancestry-adjusted years of agriculture, in thousands			0.105 (2.696)***		
Ancestry-adjusted state history				1.089 (3.108)***	
F_{ST} genetic distance to the United States, weighted					–4.576 (2.341)**
Constant	8.064 (24.338)***	7.853 (17.030)***	7.676 (21.984)***	7.195 (21.594)***	8.637 (20.941)***
Observations	150	92	147	134	149
R^2	0.526	0.340	0.580	0.656	0.545

Notes: All regressions include controls for the following geographic variables: absolute latitude; percent land area in the tropics; landlocked dummy; island dummy. Robust *t* statistics in parentheses.
***Significant at the 1 percent level.
**Significant at the 5 percent level.
*Significant at the 10 percent level.

Table 6 captures the essence of these results. Still controlling for our four baseline geographic variables, we introduce the share of Europeans (computed from the Putterman and Weil ancestry matrix) in a regression explaining log per capita income in 2005. The effect is large and statistically significant (column 1), and remains significant when confining attention to a sample of countries with fewer than 30 percent of Europeans. Introducing the Putterman and Weil ancestry-adjusted historical variables (columns 3 and 4), we find that years of agriculture and state history remain significant after controlling for the share of Europeans, suggesting that historical factors have an effect on contemporary development over and beyond the effect of European ancestry. In other words, while the traits characterizing European populations are correlated with development, the historical legacy of state centralization and early agricultural adoption matters independently.

Easterly and Levine (2012) interpret these findings as consistent with the human-capital argument by Glaeser et al. (2004) that Europeans brought their human capital, and the Galor and Weil (2000) and Galor, Moav, and Vollrath (2009) emphasis on the role of human capital in long-run development. However, Easterly and Levine (2012) also write: "Of course, there are many other things

that Europeans carried with them besides general education, scientific and technological knowledge, access to international markets, and human capital creating institutions. They also brought ideologies, values, social norms, and so on. It is difficult for us to evaluate which of these were crucial either alone or in combination" (27). This exemplifies the difficult issue of disentangling, with the imperfect data that must be used to study comparative development, the effects of different human characteristics. The bottom line, however, is that human traits are important to account for comparative development patterns, quite apart from the effects of geographic and institutional factors.

3.3 *The Persistence of Technological Advantages*

The deep historical roots of development are at the center of Comin, Easterly, and Gong (2010). They consider the adoption rates of various basic technologies in 1000 BC, 1 AD, and 1500 AD in a cross-section of countries defined by their current boundaries. They find that technology adoption in 1500, but also as far back as 1000 BC, is a significant predictor of income per capita and technology adoption today. The effects of past technology continue to hold when including continental dummies and other geographic controls. At the level of technologies, then, when examining a worldwide sample of countries (including European countries), there is no evidence of a reversal of fortune.

Interestingly, Comin, Easterly, and Gong (2010) also find that the effects of past technological adoption on current technological sophistication are much stronger when considering the past history of technology adoption of the ancestors of current populations, rather than technology adoption in current locations, using the migration matrix provided in Putterman and Weil (2010). Hence, Comin, Easterly, and Gong's results provide a message analogous to Putterman and Weil's: earlier historical development matters, and the mechanism is not through locations, but through ancestors—that is, intergenerational transmission.

The basic lesson from Putterman and Weil (2010), Easterly and Levine (2012), and Comin, Easterly, and Gong (2010) is that historical factors—experience with settled agriculture and with former political institutions, and past exposure to frontier technologies—predict current income per capita and income distribution within countries, and that these factors become more important when considering the history of populations rather than locations. These contributions point to a key role for persistent traits transmitted across generations within populations in explaining development outcomes over the very long run.

3.4 *Genetic Distance and Development*

Genealogical links among populations over time and space are at the center of Spolaore and Wacziarg (2009), where we emphasized intergenerationally transmitted human traits as important determinants of development. The main goal of this paper was to explore the pattern of diffusion of economic development since the onset of the Industrial Revolution in Northwestern Europe in the late eighteenth century and early nineteenth century. The idea is to identify barriers to the adoption of these new modes of production, with a specific focus on human barriers (while controlling for geographic barriers). The bottom line is, again, that human traits matter, but the paper emphasizes barrier effects stemming from differences in characteristics, rather than the direct effect of human characteristics on economic performance.

We compiled a data set, based on work by Cavalli-Sforza, Menozzi, and Piazza (1994), providing measures of genetic distance between pairs of countries, using

information about each population's ancestral composition.[17] Genetic distance is a summary measure of differences in allele frequencies between populations across a range of neutral genes (chromosomal loci). The measure we used, F_{ST} genetic distance, captures the length of time since two populations became separated from each other. When two populations split apart, random genetic mutations result in genetic differentiation over time. The longer the separation time, the greater the genetic distance computed from a set of neutral genes. Therefore, genetic distance captures the time since two populations have shared common ancestors (the time since they were parts of the same population), and can be viewed as a summary measure of relatedness between populations. An intuitive analogue is the concept of relatedness between individuals: two siblings are more closely related than two cousins because they share more recent common ancestors—their parents rather than their grandparents.

Figure 1 (from Cavalli-Sforza, Menozzi, and Piazza 1994, page 78) is a phylogenetic tree illustrating how different human populations have split apart over time. Such phylogenetic trees, constructed from genetic distance data, are the population analogs of family trees for individuals. In this tree, the greatest genetic distance observed is between Mbuti Pygmies and Papua New Guineans, where the F_{ST} distance is 0.4573, and the smallest is between the Danish and the English, where the genetic distance is 0.0021.[18]

To properly interpret the effect of genetic distance on differences in economic outcomes, two important clarifications are in order. First, since genetic distance is based on neutral change, it is not meant to capture differences in specific genetic traits that can directly matter for survival and fitness. Hence, we emphasize that empirical work using genetic distance provides *no evidence* for an effect of specific genes on income or productivity. Evidence of an "effect of genetic distance" is not evidence of a "genetic effect." Rather, it can serve as evidence for the importance of intergenerationally transmitted traits, including traits that are transmitted culturally from one generation to the next.

Second, the mechanism need not be a direct effect of those traits (whether culturally or genetically transmitted) on income and productivity. Rather, divergences in human traits, habits, norms, etc. have created barriers to communication and imitation across societies. While it is possible that intergenerationally transmitted traits have direct effects on productivity and economic performance (for example, if some parents transmit a stronger work ethic to their children), another possibility is that human traits also act to hinder development through a barrier effect: more closely related societies are more likely to learn from each other and adopt each other's innovations. It is easier for someone to learn from a sibling than from a cousin, and easier to learn from a cousin

[17] To accommodate the fact that some countries are composed of different genetic groups (e.g., the United States), we computed a measure of "weighted genetic distance," representing the *expected* genetic distance between two randomly chosen individuals, one from each country, using the genetic distances associated with their respective ancestor populations. That is, we do not consider the inhabitants of countries composed of different genetic groups as a new homogeneous "population" in the biological sense, but treat each of those countries as formed by distinct populations, to accurately capture the differences in ancestor-transmitted traits within and across countries. This is the measure used in the empirical work discussed below.

[18] Among the more disaggregated data for Europe, also used in Spolaore and Wacziarg (2009), the smallest genetic distance (equal to 0.0009) is between the Dutch and the Danish, and the largest (equal to 0.0667) is between the Lapps and the Sardinians. The mean genetic distance across European populations is 0.013. Genetic distances are roughly ten times smaller on average across populations of Europe than in the world data set.

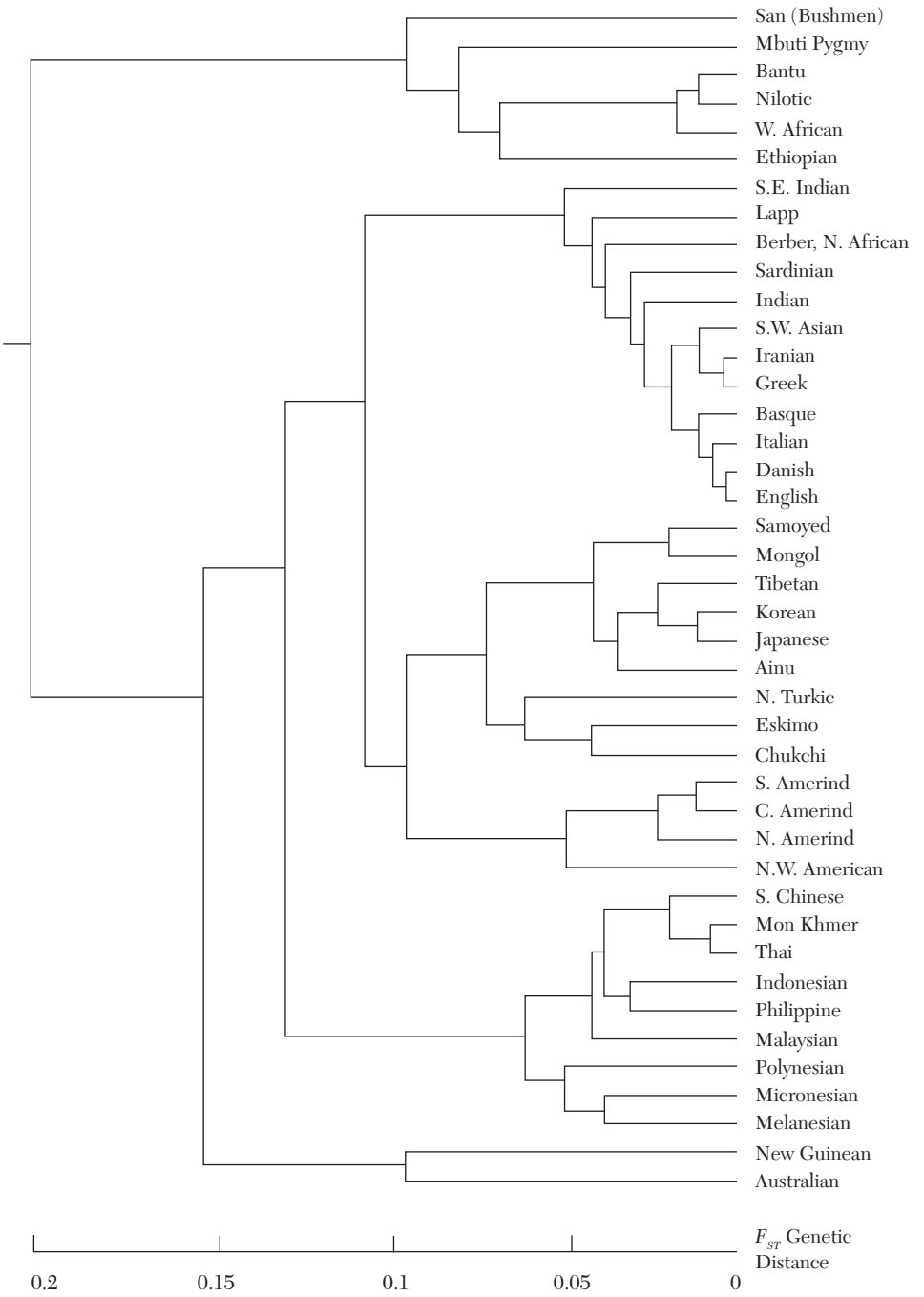

Figure 1. Genetic Distance among Forty-two Populations

Source: Cavalli-Sforza, Menozzi, and Piazza (1994).

than from a stranger. Populations that share more recent common ancestors have had less time to diverge in a wide range of traits and characteristics—many of them cultural rather than biological—that are transmitted from a generation to the next with variation. Similarity in such traits facilitates communication and learning, and hence the diffusion and adaptation of complex technological and institutional innovations.

Under this barriers interpretation, differences in traits across populations hinder the flow of technologies, goods and people, and in turn these barriers hurt development. For instance, historically rooted differences may generate mistrust, miscommunication, and even racial or ethnic bias and discrimination, hindering interactions between populations that could result in a quicker diffusion of productivity-enhancing innovations from the technological frontier to the rest of the world. The barriers framework in Spolaore and Wacziarg (2009) predicts that, ultimately, genetic distance should have no residual effect on income differences (unless another major innovation occurs), as more and more societies, farther from the frontier, come to imitate the frontier technology. This is consistent with the diffusion of economic development as emerging from the formation of a human web, gradually joined by different cultures and societies in function of their relative distance from the technological frontier (McNeill and McNeill 2003).

We test the idea that genealogical relatedness facilitates the diffusion of development in our unified empirical framework. Table 7, columns 1 and 2 introduce genetic distance to the United States in our basic income level regression, controlling for the baseline geographic variables.[19] Genetic distance as of 1500, reflecting the distance between indigenous populations, is negatively and significantly related to log income per capita in 2005. The effect rises in magnitude when considering genetic distance to the United States using the current genetic composition of countries. In other words, ancestry-adjusted genetic distance once more is a better predictor of current income than a variable based on indigenous characteristics, consistent with the results in table 5. Column 3 of table 7 introduces genetic distance alongside the share of Europeans, showing that genetic distance to the United States bears a significant partial correlation with current income that is not entirely attributable to the presence of Europeans.

While these simple regressions are informative, a better test of the hypothesis that genetic distance captures human barriers to the diffusion of development relies on a bilateral approach, whereby absolute log income differences are regressed on bilateral genetic distance, analogous to a gravity approach in international trade. This was the main approach in Spolaore and Wacziarg (2009), and is reflected in tables 8 and 9. The bilateral approach offers a test of the barriers story: if genetic distance acts as a barrier, it should not be the simple distance between countries that matters, but their genetic distance relative to the world technological frontier. In other words if genetic distance acts as a barrier, it should not be the genetic distance between, say, Ecuador and Brazil that should better explain their income difference, but their relative genetic distance to the United States, defined as the absolute

[19] Since several countries in our sample, especially the technological frontier (the United States) are composed of several distinct genetic groups, we used a weighted measure of genetic distance, capturing the expected genetic distance between two individuals, randomly selected from each of the two countries in a pair. Formally, the weighted F_{ST} genetic distance between countries 1 and 2 is defined as:

$$FST_{12}^{W} = \sum_{i=1}^{I} \sum_{j=1}^{J} (s_{1i} \times s_{2j} \times d_{ij})$$

where s_{ki} is the share of group i in country k, d_{ij} is the F_{ST} genetic distance between groups i and j.

TABLE 7
GENETIC DISTANCE AND ECONOMIC DEVELOPMENT, CROSS-SECTIONAL REGRESSIONS
(*Dependent variable: log per capita income, 2005*)

Main regressor:	Indigenous genetic distance	Ancestry-adjusted genetic distance	Control for the share of Europeans
	(1)	(2)	(3)
F_{ST} genetic distance to the United States, 1500 match	**–4.038**		
	(3.846)* **		
F_{ST} genetic distance to the United States, weighted, current match		**–6.440**	**–4.576**
		(3.392)* **	**(2.341)** **
Absolute latitude	0.034	0.030	0.015
	(5.068)***	(4.216)***	(1.838)*
Percent land area in the tropics	–0.182	–0.041	–0.384
	(0.582)	(0.135)	(1.189)
Landlocked dummy	–0.637	–0.537	–0.521
	(3.686)***	(2.971)***	(3.051)***
Island dummy	0.584	0.607	0.557
	(2.389)**	(2.392)**	(2.262)**
Share of descendants of Europeans, per Putterman and Weil			0.863
			(3.601)***
Constant	8.451	8.618	8.637
	(23.577)***	(21.563)***	(20.941)***
Beta coefficients on the bold variable	–23.85%	–27.11%	–20.30%
Observations	155	154	149
R^2	0.499	0.496	0.545

Notes: Robust t statistics in parentheses.
*** Significant at the 1 percent level.
** Significant at the 5 percent level.
* Significant at the 10 percent level.

difference between the Ecuador–U.S. genetic distance and the Brazil–U.S. genetic distance.

The specifications we use are as follows:

First, we estimate the effect of simple weighted genetic distance, denoted FST_{ij}^{W}, between country i and country j, on the absolute difference in log per capita income between the two countries, controlling for a vector X_{ij} of additional bilateral variables of a geographic nature:

$$(1) \quad |\log Y_i - \log Y_j| = \beta_0 + \beta_1 FST_{ij}^{W} + \beta_2' X_{ij} + \varepsilon_{ij}.$$

Second, we estimate the same specification, but using as a regressor relative genetic

TABLE 8
INCOME DIFFERENCE REGRESSIONS WITH GENETIC DISTANCE
(*Dependent variable: absolute value of difference in log per capita income, 2005*)

Specification includes:	Simple GD	Relative GD	Horserace	Control for Europeans	Relative GD
Estimator:	OLS	OLS	OLS	OLS	2SLS with 1500 GD
	(1)	(2)	(3)	(4)	(5)
F_{ST} genetic distance, weighted	**2.735 (0.687)****		**0.607 (0.683)**		
F_{ST} gen. dist. relative to the United States, weighted		**5.971 (1.085)****	**5.465 (1.174)****	**5.104 (1.038)****	**9.406 (1.887)****
Absolute difference in the shares of people of European descent				**0.620 (0.124)****	
Absolute difference in latitudes	0.562 (0.277)**	0.217 (0.242)	0.268 (0.250)	–0.369 (0.200)*	0.112 (0.294)
Absolute difference in longitudes	–0.117 (0.230)	–0.016 (0.214)	0.024 (0.205)	–0.308 (0.198)	0.245 (0.240)
Geodesic distance	–0.017 (0.030)	–0.018 (0.029)	–0.025 (0.028)	0.025 (0.027)	–0.049 (0.031)
=1 for contiguity	–0.536 (0.057)**	–0.475 (0.059)**	–0.469 (0.060)**	–0.351 (0.064)**	–0.395 (0.066)**
=1 if either country is an island	0.123 (0.097)	0.143 (0.093)	0.147 (0.094)	0.181 (0.095)*	0.180 (0.093)*
=1 if either country is landlocked	0.047 (0.089)	0.040 (0.085)	0.034 (0.087)	0.076 (0.085)	0.011 (0.085)
Difference in percent land area in KG tropical climates	0.156 (0.095)*	0.124 (0.096)	0.113 (0.093)	0.182 (0.092)**	0.050 (0.100)
=1 if pair shares at least one sea or ocean	–0.000 (0.076)	–0.027 (0.067)	–0.027 (0.068)	–0.008 (0.066)	–0.050 (0.079)
Freight rate (surface transport)	–0.506 (0.748)	–0.127 (0.835)	–0.162 (0.835)	–0.550 (0.783)	0.078 (0.674)
Constant	1.211 (0.161)**	1.083 (0.169)**	1.078 (0.171)**	0.984 (0.170)**	0.941 (0.169)**
Standardized Beta, absolute GD (percent)	19.47		4.32		
Standardized Beta, relative GD (percent)		28.57	26.16	24.43	45.01
Standardized Beta, difference in Europeans (percent)				24.95	
R^2	0.08	0.11	0.11	0.16	0.10

Notes: All regressions are based on 10,878 observations from 148 countries. Two-way clustered standard errors in parentheses.

**Significant at the 5 percent level.

*Significant at the 10 percent level.

distance rather than simple genetic distance. Genetic distance relative to the frontier (the United States) between countries i and j is defined as: $FST^R_{ij} = |FST^{\mathrm{W}}_{i,US} - FST^W_{j,US}|$:

$$(2) \quad |\log Y_i - \log Y_j| = \gamma_0 + \gamma_1 FST^R_{ij} + \gamma_3' X_{ij} + \nu_{ij}.$$

Third, we conduct a horse race between FST^W_{ij} and FST^R_{ij}:

$$(3) \quad |\log Y_i - \log Y_j| = \delta_0 + \delta_1 FST^R_{ij} + \delta_2 FST^W_{ij} + \delta_3' X_{ij} + \zeta_{ij}.$$

The prediction of the barrier model is that the effect of FST^R_{ij} should be larger in magnitude than the effect of FST^W_{ij} ($\gamma_1 > \beta_1$), and that FST^R_{ij} should "win out" in a horse race ($\delta_1 > \delta_2$).

Consistent with this prediction, in table 8, columns 1 and 2 show that relative genetic distance enters with a larger magnitude than simple genetic distance, and column 3 demonstrates that, when both measures are entered together, relative genetic distance trumps simple genetic distance. The magnitude of the effect is substantial, with a one standard deviation increase in genetic distance increasing economic distance by between 25 percent and 30 percent of a standard deviation in the absolute difference in log per capita income, depending on the specification. Column 4 shows once again that the effect of genetic distance is robust to including the absolute difference in the share of Europeans. In other words, genetic distance accounts for comparative development over and above the role played by the historical advantage of European populations. Finally, column 5 attempts to control for the possible endogeneity of post-1500 migrations (as well as possible measurement error in contemporary genetic distance) by using genetic distance in 1500 as an instrument for contemporary genetic distance. The magnitude of the beta coefficient increases to 45 percent.

Table 9 examines the relationship between genetic and economic distances through history, providing further evidence for the barriers interpretation. Here, we consider the relative genetic distance to the English population in a sample going back to 1820, using Maddison's data on per capita income. We continue to control for a large number of measures of geographic distance, climatic differences and transportation costs. Since the availability of data changes through time, we report both standardized betas for the full samples and for the sample common to all dates. Focusing on the latter for comparability across time, we see that the magnitude of the effect of genetic distance is maximal in 1870, in the wake of the Industrial Revolution. The effect then declines steadily from the peak of 16 percent in 1870 to 7.8 percent in 2005. This pattern provides a further suggestive test of the barriers model: in the wake of a big innovation occurring in Northwestern Europe, relative genetic distance to the frontier strongly predicts income differences, but as more and more countries join the ranks of industrialized countries, the effect declines. As already mentioned, this is consistent with a barrier model, which predicts that, ultimately, unless another major innovation occurs, relative genetic distance should have no residual effect on income differences, as more and more societies, increasingly distant from the frontier society, imitate the frontier technology. Thus, these findings are consistent with our interpretation of genetic distance as capturing barriers to the long-term diffusion of development.

What traits are captured by genetic distance? By its very definition, genetic distance

TABLE 9
Historical Regressions
(*Dependent variable: Absolute difference in log per capita income, 1820 to 2005; estimator: OLS*)

Income measured as of:	Income 1820	Income 1870	Income 1913	Income 1960	Income 2005
	(1)	(2)	(3)	(4)	(5)
Relative F_{ST} genetic distance to the English population, weighted	0.793 (0.291)**	1.885 (0.933)**	1.918 (0.955)**	4.197 (0.822)**	4.842 (0.877)**
Observations	990	1,431	1,596	4,005	10,878
Standardized Beta (percent)	14.31	23.06	20.93	31.56	28.50
Standardized Beta (percent), common sample[a]	10.98	16.37	15.53	9.00	7.77
R^2	0.36	0.30	0.29	0.22	0.23

Notes: All regressions include an intercept term as well as the following geographic control variables: Absolute difference in latitudes, absolute difference in longitudes, geodesic distance (1000s of km), dummy for contiguity, dummy if either country is an island, difference in percent land area in KG tropical climates, dummy if either country is landlocked, dummy if pair shares at least one sea or ocean, freight rate. Two-way clustered standard errors in parentheses.

[a]Common sample of 780 observations based on 40 countries for which data is available across all periods.

** Significant at the 5 percent level.

* Significant at the 10 percent level.

is a measure of genealogical relatedness between human populations. It is important to stress again that while effects of genetic distance point to the importance of intergenerational links, they are not evidence of direct effects of specific genes or genetically transmitted traits on income or productivity. Rather, genetic distance captures genealogical relations between populations, and hence differences in traits that are transmitted vertically from one generation to the next through a variety of mechanisms, biologically but also culturally, as well as through the interactions of the two inheritance systems (gene-culture coevolution). We detail these different mechanisms in the next section.

4. *The Intergenerational Transmission of Development*

4.1 *Mechanisms of Intergenerational Transmission*

The empirical literature on geography and the reversal of fortune and the more recent contributions on the role of ancestor populations suggest that, while there is significant persistence in development, this persistence is a characteristic of human populations and not of geographic locations. The work discussed so far points to a key role for traits transmitted from one generation to the next within populations over the long run. In this section, we provide a general taxonomy

of the different channels and mechanisms through which these traits can be transmitted across generations and affect economic development. We then use this framework to discuss recent contributions to the economics literature.

The starting point for our discussion is a classification of different mechanisms of intergenerational transmission. The more recent literature on heredity and evolution stresses that inheritance mechanisms are diverse and cannot be reduced to the old nature versus nurture dichotomy. On the contrary, people and societies inherit traits from their ancestors through a complex interaction of biological and cultural mechanisms, with an essential role played by environmental factors. Following Jablonka and Lamb (2005), we consider four inheritance dimensions: genetic, epigenetic, behavioral, and symbolic. For convenience and to keep the taxonomy relatively simple, we refer to the first two dimensions (genetic and epigenetic) as "biological" and the remaining two dimensions (behavioral and symbolic) as "cultural."

The genetic dimension has its molecular basis in DNA and its replication. Modern genetics stresses that the genome is a complex and dynamic system, and that genes alone do not determine individual characteristics. For example, Jablonka and Lamb (2005) write: "The stretch of DNA that is a 'gene' has meaning only within the system as a whole. And because the effect of a gene depends on its context, very often a change in a single gene does not have a consistent effect on the trait that it influences" (7). In general, it is useful to view genetic transmission as part of a broader system, interacting with other factors, including our second dimension: epigenetics.

The epigenetic dimension, even though important in biology and medicine, is not as well known among nonspecialists. Epigenetic inheritance systems refer to the ways cells with identical genetic information can acquire different phenotypes and transmit them to their daughter cells through the inheritance of epigenetic markers (for example, methylation patterns). The epigenetic dimension is vital for the biological development of individual organisms. In addition, some scholars argue that it may play an important role in evolution over time. An insightful and entertaining discussion of this view is provided in Jablonka and Lamb (2005, chapter 4). As they explain, "A person's liver cells, skin cells, and kidney cells, look different, behave differently, and function differently, yet they all contain the same genetic information. With very few exceptions, the differences between specialized cells are epigenetic, not genetic. They are the consequences of events that occurred during the developmental history of each type of cell and determined which genes are turned on, and how their products act and interact (. . .). Although their DNA sequences remain unchanged during development, cells nevertheless acquire information that they can pass to their progeny. This information is transmitted through what are known as epigenetic inheritance systems" (113). Even though the extent and relevance of heritable epigenetic effects is debated in the biological literature, there is increasing evidence that changes in the epigenome can be inherited across generations ("paramutation"). Reviews of the evidence are provided, for instance, in Chandler and Alleman (2008) and, for humans, in Morgan and Whitelaw (2008).[20] This mechanism could provide an explanation for rapid changes in populations that could not be brought about by genetic selection. In general, it is conceptually

[20] Morgan and Whitelaw (2008) mention the well-known Dutch Famine Birth Cohort Study (Lumey 1992), which reported that children born during famine in World War II were smaller than average and that the effects could last two generations. However, they also point out that a subsequent report by Stein and Lumey (2000) failed to reproduce some of the findings.

appropriate to consider both genetic and epigenetic transmission, and their interactions, when discussing biological inheritance systems.[21]

Clearly, humans do not inherit traits only biologically from their ancestors. Typically, people acquire all sorts of traits through cultural transmission (for example their mother tongue and all kinds of views and beliefs about the world). We can distinguish between behavioral transmission, which is also common among some animals (for instance, monkeys), and symbolic transmission, which some scholars view as uniquely human—the philosopher Cassirer (1944) famously defined man as "the symbolic animal." Both mechanisms involve social learning. Behavioral transmission refers to learning by direct observation and imitation: I learned how to cook spaghetti by watching my dad in the kitchen. In contrast, symbolic transmission allows learning via systems of symbols: I learned how to cook goulash from a cookbook. Human norms, habits, values, etc. tend to be passed across generations both behaviorally (by example) and symbolically (using language, art, writing, and so on). In general, culture can be defined as "information capable of affecting individuals' behavior that they acquire from other members of their species through teaching, imitation, and other forms of social transmission" (Richerson and Boyd 2005, 5).[22] In their insightful discussion of the "evolution of cultural evolution," Henrich and McElreath (2003) write: "While a variety of local genetic adaptations exist within our species, it seems certain that the same basic genetic endowment produces arctic foraging, tropical horticulture, and desert pastoralism [. . .]. The behavioral adaptations that explain the immense success of our species are cultural in the sense that they are transmitted among individuals by social learning and have accumulated over generations. Understanding how and when such culturally evolved adaptations arise requires understanding of both the evolution of the psychological mechanisms that underlie human social learning and the evolutionary (population) dynamics of cultural systems" (123).[23]

While it is conceptually useful to distinguish between biological and cultural transmission, we must keep in mind that in reality those dimensions are interconnected in complex ways. An increasingly influential literature within population genetics has emphasized that human outcomes often stem from the interaction of biological and cultural factors. Both genes and culture are informational entities that are transmitted at different rates across generations with variations, and can be studied within a unified framework that focuses on the interaction between biological and cultural inheritance systems. This approach is known as dual inheritance theory or gene–culture coevolution (Cavalli-Sforza and Feldman 1981; Boyd and Richerson 1985; Richerson and Boyd 2005). In such a framework, individual outcomes (phenotypes) are a mix of genetically and culturally transmitted traits, affecting the transmission rates of different genetic and cultural information. As Richerson and Boyd (2005) point out, genes and culture can

[21] In a different context, the relevance of epigenetics for the study of economic outcomes has been emphasized in the microeconomic literature on human capital formation. For instance, Cunha and Heckman (2007) write: "the nature versus nurture distinction is obsolete. The modern literature on epigenetic expression teaches us that the sharp distinction between acquired skills and ability featured in the early human capital literature is not tenable" (32).

[22] Of course, this is one among many possible definitions of culture. It is well known that the word "culture" has multiple meanings. In a widely cited study, Kroeber and Kluckhohn (1952) provided 164 definitions of culture.

[23] An interesting example of analysis of cultural evolution with long-term implications for economic development is Shariff, Norenzayan, and Henrich (2010).

be seen as "obligate mutualists, like two species that synergistically combine their specialized capacities to do things that neither can do alone. [. . .] Genes, by themselves can't readily adapt to rapidly changing environments. Cultural variants, by themselves, can't do anything without brains and bodies. Genes and culture are tightly coupled but subject to evolutionary forces that tug behavior in different directions" (194).

Proponents of dual inheritance theory believe that gene–culture evolution has played an important role in the evolution of human social psychology, including the evolution of social norms and institutions (e.g., Richerson and Boyd, chapter 6). This view informs a broad literature on the coevolution of preferences, institutions and behavior, such as the analyses of the evolution of altruistic behavior by Boyd et al. (2003) and Gintis et al. (2003). General discussions of the emergence of prosperity-generating behavior from an evolutionary perspective are provided by Seabright (2010) and Ridley (2010).

A famous example of gene–culture coevolution is the evolution of adult tolerance for milk in some, but not all, human populations (Simoons 1969, 1970).[24] Most people, like most other mammals, can digest milk as infants but not as adults, because they lack the enzyme to digest lactose. However, there are several populations where most adults can indeed digest milk. The largest concentration of lactose absorbers can be found in Northwestern Europe, where less than 10–15 percent of the population is lactose intolerant. Low levels of lactose intolerance are also found among Indians and some African populations (Tutsi and Fulani). In contrast, few Far Easterners, Bantu Africans, Pacific Islanders, and Native Americans can digest milk as adults.

It is now well understood that the adult ability to digest milk evolved in response to a cultural innovation: dairying. The (dominant) gene controlling lactose absorption spread rapidly among populations that kept cows, sheep or goats, making those practices even more valuable from an evolutionary perspective. It also spread, but to a lesser extent, among Mediterranean people who consume milk in the form of cheese and yogurt, from which the lactose has been removed, but it did not spread among populations without a dairying tradition. To predict whether a current population would have a high or low tolerance for milk, one must look at the history of dairying among the population's ancestors, no matter where they lived, rather than to the history of dairying in that population's current territory. For instance, within the United States, it has been observed that the percentage of lactose intolerant adults is almost 100 percent among Native Americans, 90 percent among Asian Americans, 75 percent among African Americans, and only 12 percent among European Americans (Kretchmer 1972; Enattah et al. 2002). This is consistent with the intergenerational transmission of the lactose absorption trait over an extended historical span, through genetic and cultural interaction.[25]

In general, the economic effects of human characteristics are likely to result from interactions of biological and cultural factors, with the effects of genetic or epigenetic characteristics on economic outcomes changing over space and time depending on cultural characteristics, and vice versa. Consider, for example, differences across individuals within a given population (say, the United States) with respect to a clearly genetic feature, such as having two X chromosomes, the purely genetic characteristic associated

[24] See also Durham (1991, chapter 5) and Richerson and Boyd (2005, chapter 6).

[25] More examples of gene–culture interaction, and a taxonomy, are provided by Durham (1991).

with the female gender. This characteristic is likely to have had very different effects on a person's income, life expectancy, and other outcomes in the year 1900 and in the year 2000, because of changes in culturally transmitted characteristics over the century. This is a case where the impact of genes on outcomes varies with a change in cultural characteristics.[26] Conversely, we can think of the differential impact of a given cultural characteristic—for example, the habit of drinking alcohol—on individuals with different genetic traits, such as variation in alcohol dehydrogenase, the alcohol-metabolizing enzyme.

In sum, we can aggregate inheritance dimensions and their complex interactions in three broad sets: (a) biological transmission (genetic and epigenetic, and their interaction), (b) cultural transmission (behavioral and symbolic, and their interaction), and (c) dual, capturing the interactions between biological and cultural transmission.

4.2 *Direct and Barrier Effects*

When considering how traits transmitted along these different channels may have affected development, we must introduce an additional distinction, orthogonal to the categories discussed up to this point. No matter how traits are transmitted, their effects on economic performance might operate either directly or as barriers to the diffusion of development.

One possibility is that intergenerationally transmitted traits have direct effects on productivity and economic performance. A slow-changing cultural trait developed in early history could be conducive directly to high incomes in modern times if it is transmitted from parents to kids within populations, either behaviorally or through complex symbolic systems (e.g., by religious teaching). For example, a direct effect stemming from cultural transmission would be Weber's (1905) argument that the Protestant ethic was a causal factor in industrialization (a recent critical reassessment of this hypothesis has been provided by Becker and Woessmann 2009).

As we discussed in the previous section, another possibility is that human traits act to hinder development through a barrier effect. In this case, it is not the trait itself that directly affects economic performance. Rather, it is differences in inherited characteristics across populations that create barriers to the flow of technological and institutional innovations, ideas, etc., and, consequently, hurt development. Historically rooted differences may generate barriers—e.g., via cultural, racial, and ethnic bias, discrimination, mistrust, and miscommunication—hindering interactions between populations that could result in a quicker diffusion of productivity-enhancing innovations across populations, as in Spolaore and Wacziarg (2009). A focus on barriers can explain why differences in inherited traits may matter, even though many new ideas and innovations are learned "horizontally" from individuals and populations that are not directly related, rather than "vertically" from one's close relatives and ancestors. The fact is that, when barrier effects exist, vertically transmitted traits also affect horizontal learning and diffusion. People are more likely to learn new ideas and adopt new technologies from other people who, while not directly related to them, share more recent common ancestors and, consequently, on average, a larger set of inherited traits and characteristics.

The microeconomic literature on the diffusion of innovations (Rogers 2003) is consistent with a major role for subjective barriers between groups and populations. As Rogers

[26] This is a variation on an example by Alison Gopnik in her comment to debate between Steven Pinker and Elizabeth Spelke at http://www.edge.org/discourse/science-gender.html#ag. Steven Pinker's response is also available at http://www.edge.org/discourse/sciencegender.html.

points out, summarizing the lessons from decades of research, most people depend upon a subjective evaluation of an innovation that is conveyed to them from other individuals like themselves, who have previously adopted the innovation. This dependence on the experience of near peers suggests that, at the heart of the diffusion process, we can often find potential adopters' imitation of their network partners.

4.3 *A General Taxonomy*

The distinction between barrier effects and direct effects on the one hand, and the different forms of intergenerational transmission on the other hand, can be conveniently captured in the following matrix:

	Direct Effect	Barrier Effect
Biological Transmission (genetic and/or epigenetic)	Quadrant I	Quadrant IV
Cultural Transmission (behavioral and/or symbolic)	Quadrant II	Quadrant V
Dual Transmission (biological-cultural interaction)	Quadrant III	Quadrant VI

In what follows, we provide examples of each of these quadrants from contributions to the social sciences, with a particular focus on research that stresses the role of intergenerationally transmitted traits on economic development. As we will see, mechanisms from all six of the quadrants in the figure above have been studied in the economic literature. However, so far there have been no systematic attempt to quantify the respective power of each of the major explanations, nor has there been enough work on the precise traits that can account for either direct or barrier effects on development. These are the major avenues for promising future research in this emerging field.

In light of the advances in the scientific literature that we have mentioned above, which have emphasized the interconnection and coevolution of biological and cultural traits, it may be very hard, or even meaningless, to separate biological and cultural effects in the long run. Therefore, while the rows in our taxonomy matrix provide useful ideal benchmarks from a theoretical perspective, a more productive empirical approach might be to focus on whether such intergenerational mechanisms—whether biological or cultural (or dual)—operate directly or as barriers to the diffusion of technological and institutional innovations—i.e., to identify the respective roles of each column rather than each row in the matrix that summarizes our proposed taxonomy. We return to these points below, as we discuss specific contributions to the economic literature.

4.3.1 *Quadrants I, II, and III*

A theory of development centered on a direct effect of biologically transmitted characteristics (Quadrant I) is provided in Galor and Moav (2002). These authors suggest that there may exist an intergenerationally transmitted trait affecting humans' fertility strategies, with some individuals inheriting traits that induce them to follow a quantity-biased strategy (having a high number of children), while others would lean toward quality-biased strategies (high parental investment in a smaller number of children).[27] Galor and Moav (2002) then argue that the evolutionary dynamics of these traits had important implications for the onset of the Industrial Revolution and the following demographic transition. Their starting point is the preindustrial world, where everybody was

[27] The authors are careful to notice that such differences do not imply that one strategy is "better" than the other, in the same way as we cannot say that giant sequoias (which follow an extreme quality-biased strategy) are "better" than humans.

caught in a Malthusian trap: technological improvements just led to larger populations but not an increase in income per capita and standards of living.[28] In such a world, a positive shock to productivity is associated with an expansion of the population, and hence selective pressure in favor of productivity-enhancing traits, such as a focus on parental investment. As the genetic predilection to having fewer children spread as a result of these selective pressures, a transition out of the Malthusian regime endogenously occurred. In sum, Galor and Moav (2002) provide a theoretical argument for a direct effect of intergenerationally transmitted traits on the onset of the Industrial Revolution. While the focus of their paper is on genetic transmission, Galor (2005) also points out that "the theory is applicable for either social or genetic intergenerational transmission of traits. A cultural transmission is likely to be more rapid and may govern some of the observed differences in fertility rates across regions" (250). With this broader interpretation, the theory in Galor and Moav (2002) spans Quadrants I, II, and III.

Another contribution that allows for a direct effect of inherited characteristics on development is Clark's (2007) book on the advent of the Industrial Revolution in England. As in Galor and Moav (2002), Clark's starting point is the preindustrial world caught in a Malthusian trap. In such a world, unlike in modern industrialized societies, economic success translated into reproductive success: the richer individuals had more surviving children, while the poorer individuals had so few surviving children that their families were often dying out. Therefore, over time the children of the richest individuals tended to replace the children of the poorest. Through this form of selection, traits that would "ensure later economic dynamism," such as patience, hard work, and innovativeness, spread "biologically throughout the population" (Clark 2007, 8). In Clark's view, this long-term process worked through all preindustrial agrarian societies caught in a Malthusian trap, but was especially powerful in England because of "accidents of institutional stability and demography: in particular the extraordinary stability of England back to at least 1200, the low growth of English population between 1300 and 1760, and the extraordinary fecundity of the rich and economically successful" (Clark 2007, 11). According to Clark, this process played an essential role in allowing England to break out of the Malthusian trap after 1800. Clark's argument, which is based on a detailed analysis of the historical record, is related to Galor and Moav's theoretical contribution, insofar as selection of traits in the Malthusian era sets the stage for future intensive economic growth. However, the specific inherited traits stressed by Clark are different from those at the center of Galor and Moav's story—Clark's focus is mainly on attitudes towards work.[29] Clark tends to emphasize biological mechanisms, but he does not take a definitive stance as to whether the human traits that caused the English to experience the Industrial Revolution were primarily biological or cultural. Hence, in a

[28] Empirical evidence on these effects is provided by Ashraf and Galor (2011a)—see our discussion in section 2 above.

[29] It is also worth noting that Clark, like Galor and Moav, is not making any claim that inherited traits made some populations generally "superior" to others: "This is not in any sense to say that people in settled agrarian economies on the eve of the Industrial Revolution had become 'smarter' than their counterparts in hunter–gatherer societies. . . . For the average person the division of labor . . . made work simpler and more repetitive. The argument is instead that it rewarded with economic and hence reproductive success a certain repertoire of skills and dispositions that were very different from those of the pre-agrarian world, such as the ability to perform simple repetitive tasks hour after hour, day after day. There is nothing natural or harmonic, for example, in having a disposition to work even when all basic needs of survival have been achieved" (Clark 2007, 187–88).

more general sense, Clark's suggested mechanisms also belong to Quadrants I, II, and III.

A different set of channels through which genetic forces may affect economic development is explored by Ashraf and Galor (2013). In that study, the authors focus on genetic diversity within populations. Genetic diversity is a different concept from genetic distance, as it was used in Spolaore and Wacziarg (2009). Genetic distance refers to genetic differences between populations, while genetic diversity is defined in terms of heterogeneity within populations. Because of the serial-founder effect, genetic diversity tended to decline as human populations moved from the ancestral lands where Homo sapiens originally emerged (East Africa) to the rest of the World (Eurasia, Oceania and the Americas).[30] Hence, genetic diversity is highest among African populations and lowest among Amerindian populations. Ashraf and Galor (2013) show that genetic diversity bears a nonmonotonic relationship with development outcomes between years 1 and 1500 AD, and that this effect extends to 2000 AD. They argue that this relation is causal, because of a trade-off between the beneficial and the detrimental effects of diversity of traits on productivity. In their view, a high level of genetic heterogeneity within populations comes with both costs and benefits for economic development. Heterogeneity can be costly because it may reduce trust and coordination among individuals that are less similar and less closely related. However, diversity also comes with advantages: "in an economy where the labor force is characterized by heterogeneity in a wide array of traits, to the extent that some of these traits lead to specialization in task-oriented activities, higher diversity will increase productivity for society as a whole, given complementarities across different tasks" (Ashraf and Galor 2013, 2, footnote 1). Given such conflicting effects of heterogeneity, Ashraf and Galor argue that intermediate levels of genetic diversity are most conducive to the accumulation of wealth. These can be interpreted as direct effects of inherited traits working through the biological channel (Quadrant I), and possibly its interaction with the cultural channel (Quadrant III). While the focus of Ashraf and Galor (2013) is on genetic diversity and biological mechanisms, a similar trade-off between costs and benefits could emerge with respect to diversity in culturally transmitted traits. Ashraf and Galor (2011b) explicitly focus on the costs and benefits of cultural diversity (Quadrant II) when providing a framework to understand the effects of prehistoric measures of geographic isolation on economic development.[31]

While there are relatively few contributions in the social sciences that focus on biological transmission, there is a much larger literature on culturally transmitted traits and development (Quadrant II). Among recent contributions, Tabellini (2008, 2010) argues that specific cultural traits, such as

[30] As explained in Ashraf and Galor (2013), subsets of populations left to establish new settlements, they carried with them only part of the overall genetic diversity of their parental populations, therefore reducing the heterogeneity of populations that settled farther from the original cradle of humankind.

[31] Regarding the mechanisms in Quadrant I, there is also a literature in political science, discussed by Fowler and Schreiber (2008), arguing that direct biological effects are relevant in the study of political attitudes and behavior. Fowler and Schreiber (2008) write "The new science of human nature demands that we recognize that genes are the institutions of the human body. [. . .] we cannot fully appreciate their function in humans without understanding their role in the very complex political and social interactions that characterize our species" (914). Among the biological evidence cited in their survey is the involvement of neuroreceptors in specific political behavior, such as the link between the DRD2 gene, which codes for a dopamine receptor, and voter turnout (Dawes and Fowler 2009). These claims are controversial among political scientists, and have been criticized, for example, by Charney and English (2012). For a recent contribution on the molecular-genetic-based heritability of economic and political preferences, see Benjamin et al. (2012).

generalized trust and individualism, can account causally for variation in institutional development across regions of Europe, and hence indirectly for variation in the level of economic development there. An extensive comparative and historical analysis of the role of culture, institutions, and development is provided in Greif (1994, 2006), who offers a unified conceptual framework for analyzing the persistence of institutions, their endogenous change, and the impact of past institutions on subsequent development. As Greif (2006, chapter 1) points out, culturally transmitted traits, such as beliefs and norms, play a key role in determining which formal rules are followed and what is the actual economic impact of an institutional organization. Guiso, Sapienza, and Zingales (2008) explain the persistence of differences in culturally transmitted beliefs regarding collective action and cooperation across Italian cities by successfully testing Putnam's (1993) hypothesis that those differences reflect the impact of historical variables on local civic values.[32]

Cultural transmission plays a key role in the analysis of divergent paths by China and Europe in Greif and Tabellini (2010), who argue that China's and Europe's distinct cultural and institutional trajectories during the last millennium reflect the impact of different initial moral systems and kinship organizations. According to Greif and Tabellini (2010): "The Chinese clan is a kinship-based hierarchical organization in which strong moral ties and reputation among clan's members are particularly important in sustaining cooperation. In Medieval Europe, by contrast, the main example of a cooperative organization is the city. Here cooperation is across kinship lines and external enforcement plays a bigger role. But morality and reputation, although weaker, also matter and extend beyond one's kin." This analysis sheds light on why China and other advanced societies in East Asia have taken so long to catch up with the Industrial Revolution, in spite of positive historical preconditions and a significant technological lead in early periods, as documented in the aforementioned studies by Comin, Easterly, and Gong (2010) and Putterman and Weil (2010).[33]

Direct cultural mechanisms are also at the heart of the already cited study by Ashraf and Galor (2011b), who argue that the interplay between the forces of cultural assimilation and cultural diffusion contributed to the long-term patterns of relative development in Europe and Asia. According to these authors, cultural rigidity was an advantage in earlier phases of development but a hindrance at later stages.[34] Along similar lines, Gorodnichenko and Roland (2010) study the interplay between culture, institutions, and economic development. In their analysis, individualism leads to more innovation while collectivism is associated with static efficiency gains. Consistent with the view that cultural traits are intergenerationally transmitted, Gorodnichenko and Roland use genetic variables as instruments to study the effects of culture on productivity. An issue for this empirical strategy is whether one can exclude additional channels (other intergenerationally transmitted traits, in addition to

[32] Evidence on the long-term persistence of pernicious cultural traits is provided by Voigtländer and Voth (2012), who use data on anti-Semitism in Germany and find continuity at the local level over six centuries: anti-Semitic pogroms during the Black Death in 1348–50 are a strong and robust predictor of violence against Jews in the 1920s and of the vote share of the Nazi Party.

[33] This is an issue that Diamond also had to face in his book (1997, chapter 16). Classic references on this topic are Rosenberg and Birdzell (1987) and Mokyr (1990).

[34] While Ashraf and Galor's (2011b) model is specified in terms of direct effects of inherited cultural traits on development (Quadrant II), some of their mechanisms could be interpreted in terms of barrier effects (Quadrant VI)—e.g., the gains from what they call "cultural diffusion" could include the benefits from openness to innovations from other cultures. We discuss barrier effects below.

individualism versus collectivism), which may also affect productivity and development.

Cultural transmission is also at the center of the contribution by Doepke and Zilibotti (2008), who provide a theory of preference formation to explain the emergence of industrial capitalists as the economically dominant group following the British Industrial Revolution. In this paper, altruistic parents shape their children's preferences in response to economic incentives, resulting in the transmission of values across generations. In their framework, middle-class families worked in occupations that required effort, skill, and experience, and developed patience and work ethic, whereas landowning aristocratic families relied on rents, and cultivated a taste for leisure. Those class-specific attitudes, rooted in preindustrial professions, became determinants of economic success after the British Industrial Revolution transformed the economic environment.

The long-term effects of culturally transmitted traits and attitudes have been studied in several important studies at a more microeconomic level. For instance, Fernandez and Fogli (2009) study the economic impact of culture by examining the work and fertility behavior of second-generation American women (women born and raised in the United States from immigrant families), and find a significant effect of intergenerationally transmitted traits, proxied by outcomes in a woman's country of ancestry. Alesina and Giuliano (2010) study the relation between family ties and a series of economic outcomes in production and labor markets. They define a measure of family ties using individual responses from the World Value Survey regarding family role and children's love and respect for their parents, looking at the behavior of second-generation immigrants to assess causality and isolate the effect of culture. Identification is obtained by regressing individual-level economic outcomes on the average extent of family ties in the country of origin of second-generation immigrants. Reverse causality is not an issue in this context because the socioeconomic behavior of second-generation immigrants cannot affect the extent of family ties in their country of origin. They find that the strength of family ties significantly increases home production, reduces female and youth labor force participation and reduces geographic mobility. These results are consistent with a direct effect on economic outcomes of traits transmitted across generations. Alesina, Giuliano, and Nunn (2013) study the evolution and persistence of cultural norms about gender roles and division of labor. They find that the contemporary rates of female participation in labor, entrepreneurial, and political activities are significantly lower for the descendants of societies that traditionally practiced plough agriculture. Traditional plough agriculture is also associated with cultural attitudes disfavoring gender equality. A key role of cultural transmission as the relevant mechanism is confirmed by their analysis of female labor force participation of second-generation immigrants living in the United States.

These contributions are part of a growing economic literature that studies the determination and dynamics of intergenerationally transmitted preferences, beliefs, habits, norms, and attitudes. In pioneering work, Bisin and Verdier (2000, 2001) provide an economic framework for the study of the intergenerational transmission of cultural traits. Building on the population genetics approach of Cavalli-Sforza and Feldman (1981), Bisin and Verdier go beyond mechanical models of transmission. They explicitly introduce parents' decisions regarding their children's cultural socialization, assuming that parents are altruistic toward their children, but can evaluate the effects of different cultural norms only through the filter of their own culturally determined evaluation of their children's utility. In these economic models, cultural transmission is the outcome

of purposeful socialization decisions inside the family (vertical socialization) as well as of indirect socialization processes, such as social imitation and learning (horizontal and oblique socialization). The persistence of cultural traits of minorities or cultural assimilation are the outcomes of different costs and benefits associated with the socialization of children in various environments, which affect the children's opportunities for social imitation (what we call "behavioral transmission" in our taxonomy) and learning. An important assumption in Bisin and Verdier's approach is "imperfect empathy" by parents towards their children. In Bisin and Verdier's framework, parents know the different traits that children can adopt, and anticipate the choices that a child with a given trait will make, but, as already mentioned, they evaluate those choices only through their own subjective evaluations, not their children's own evaluations. Hence, parents, while altruistic, cannot "perfectly empathize" with their children, and tend to prefer children with their own cultural traits. As Bisin and Verdier (2001) write, such "cultural transmission mechanisms have very different implications than evolutionary selection mechanisms with respect to the dynamics of the distribution of the traits in the population" (298). For instance, unlike more mechanical noneconomic models of cultural transmission, Bisin and Verdier's approach does not predict complete assimilation of minorities and faster assimilation for smaller minorities. On the contrary, their model can shed light on the persistence of "ethnic capital" in immigrants' descendants, documented by Borjas (1992). The cultural transmission model of Bisin and Verdier has been applied to several cultural traits and norms (for a review of this literature, see Bisin and Verdier 2010). For instance, Bisin, Topa, and Verdier (2004) estimate the structural parameters of the model of marriage and child socialization in Bisin and Verdier (2000) for religious traits in the United States. They find that observed intermarriage and socialization rates are consistent with Protestants, Catholics, and Jews having a strong preference for children who identify with their own religious beliefs, and taking costly decisions to influence their children's beliefs. The framework can therefore explain long-term persistence of traits and lack of cultural assimilation.

The Bisin–Verdier approach has been used by François (2002) and François and Zabojnik (2005) to study social capital and comparative economic development. François and Zabojnik (2005) use the framework to study the cultural transmission of social capital, defined in terms of "trustworthiness." Their results point to long-term persistence, and "provide an explanation for why late developing countries may not easily be able to transplant the modes of production that have proved useful in the West" (François and Zabojnik 2005, 51). Such contributions are part of a much larger literature on the evolution of cooperation and trust, which has a distinguished pedigree in economics. As Zak and Knack (2001, 295) point out, cross-country differences in trust were observed by Smith (1766) and Mill (1848), who wrote "There are countries in Europe ... where the most serious impediment to conducting business concerns on a large scale, is the rarity of persons who are supposed fit to be trusted with the receipt and expenditure of large sums of money" (Mill 1848, 132). A recent example of the fast-expanding literature on trust and development is the empirical contribution by Algan and Cahuc (2010), who explicitly exploit transmission across generations. Algan and Cahuc estimate the effect of trust on economic growth by using the inherited component of trust and its time variation. They show that inherited trust of descendants of immigrants in the United States is influenced by the country of origin and the timing of arrival of their ancestors, and use inherited trust of those descendants

as a time-varying measure of inherited trust in their country of origin. They find a sizable causal impact of inherited trust on worldwide growth during the twentieth century, controlling for country fixed effects.

While most economic contributions on cooperation and trust tend to focus on purely cultural transmission (Quadrant II), an interdisciplinary literature on the evolution of altruistic behavior has also stressed gene–culture interactions (Quadrant III), which includes Boyd et al. (2003), and Gintis et al. (2003). A recent book on this important topic is Bowles and Gintis (2011). Building on extensive empirical research, Bowles and Gintis calibrate models of the coevolution of genes and culture using genetic, archaeological, ethnographic, and experimental data. According to these authors, cooperation with fellow group members has been essential to human survival for thousands of generations, and groups that created social institutions to protect the altruistic from exploitation by the selfish have been able to flourish and prevail in conflicts with less cooperative groups. In particular, this research suggests that the emergence of social emotions, such as shame and guilt, and the internalization of social norms have been essential to the process of genetic and cultural coevolution (Quadrant III).

4.3.2 *Quadrants IV, V, and VI*

Other accounts of the development process over the long run rely on barrier effects. The basic hypothesis is that the intergenerational transmission of human traits—biologically and/or culturally—generates long-term persistence in income levels because, over time, genetic and cultural drift leads to greater distance between populations, and thus higher barriers to the adoption of major innovations when a given population is distant from the innovator population.

One example of how genetically transmitted traits can create barriers between populations (Quadrant IV) is the argument in Guiso, Sapienza, and Zingales (2009) that somatic distance between European populations is a negative correlate of bilateral trust, and in turn of bilateral trade. Cultural barriers to trade exemplify the effects in Quadrant V. For instance, Felbermayr and Toubal (2010) provide a creative empirical analysis of the relation between cultural proximity and international trade, using bilateral score data from the Eurovision Song Contest, a popular pan-European television show. Viewers in Cyprus award Greek singers 7.41 more points on average than the Greeks receive from viewers in other countries, and Greek viewers award Cypriot singers an extra 6.26 points on average. The scores also reveal a lack of affinity between some countries—for example, Cyprus and Turkey viewers award each other below-average grades. The relation need not be reciprocal. French viewers grade British singers 0.86 points below average, while British viewers are neutral about French singers. Felbermayr and Toubal exploit the variation of these scores across time and within-pair to study the effects of cultural proximity on bilateral trade, separating a preference channel from a trade-cost channel.[35] They find that one-third of the total effect of cultural proximity on bilateral trade is due to the preference effect.

A theoretical study of the interactions between trade and long-term cultural and institutional diversity across societies is provided by Belloc and Bowles (2012). Their paper is motivated by the persistence of cultural and institutional differences in a

[35] Felbermayr and Toubal (2010) use two empirical strategies. The first strategy assumes that trade costs are not affected by swings in bilateral attitudes but depend on the deep time-invariant components of cultural proximity, while the preference channel depends on more short-lived fads. The second strategy assumes that trade costs depend only on the symmetric component of cultural proximity. The two strategies provide similar results.

globally integrated world economy. In their framework, the decentralized updating of both preferences and contractual choices support durable cultural and institutional differences, which provide a basis for specialization, comparative advantage, and trade. In Belloc and Bowles (2012), international economic integration, by making experimentation more costly, paradoxically increases the barriers to cultural–institutional transitions.

As already described in section 3, in Spolaore and Wacziarg (2009) we emphasize the types of long-run effects captured by Quadrants IV, V, and VI. In that paper, we place the genealogical history of populations at the center of our analysis. The central hypothesis is that distance in human traits (rather than distance in geographic space) created barriers to the diffusion of fundamental innovations—most importantly, in recent centuries, to the spread of the Industrial Revolution. We use relative genetic distance from the frontier to capture those long-term barriers. As already discussed in the previous section, genetic distance is a measure of general genealogical relatedness, i.e., of similarity of slow-moving traits, genetic, epigenetic, and cultural. Hence, the "effects of genetic distance" studied by Spolaore and Wacziarg (2009) are not synonymous with "effects of genetic transmission," but capture the effects of all kinds of intergenerationally transmitted traits. In particular, the barrier effects emphasized in that contribution can operate through any combination of inheritance mechanisms (Quadrants IV, V, and VI).

As discussed above, the most recent scientific literature suggests that it may be conceptually very difficult, or even meaningless, to separate biological and cultural mechanisms, given the coevolution of biological and cultural traits. Consequently, a more productive approach, from an empirical perspective, is to focus on whether intergenerationally transmitted traits—whether biological or cultural—operate directly or as barriers to the diffusion of innovations. In other words, while the rows in our taxonomy matrix may be useful to sketch ideal types of inheritance mechanisms, empirically it may be more fruitful to focus on the columns. Consistent with this view, Spolaore and Wacziarg (2009) use genetic distance relative to the technological frontier to provide evidence on *barrier* effects associated with long-term historical relatedness between populations, while remaining agnostic about whether the inheritance mechanisms behind those barriers are biological, cultural, or a combination of both. However, indirect evidence about the timing of the effects and the fact that they operate even among populations that are genetically very close (e.g., within Europe) suggest that a significant part of these barrier effects, while measured by genetic distance, are likely to have been transmitted culturally rather than biologically across generations.

In Spolaore and Wacziarg (2012a), we pursue these ideas by studying the effects of human relatedness on the adoption of specific technologies across countries. To do so, we use the Comin, Easterly, and Gong (2010) historical data set and the data set for post-1800 technologies from Comin and Hobijn (2009). We compare the empirical effects of the simple genetic distance between populations to that of genetic distance relative to the technological frontier, finding that the latter trumps the former as a determinant of bilateral differences in technological adoption rates. This empirical test is consistent with a barrier effect of long-term historical distance, whereby societies that are more distant from the technological frontier tend to face higher imitation costs—for example, because people may respond to differences with distrust and unwillingness to interact and learn from each other. We find large and statistically significant effects of genetic distance relative to the frontier on technology use differences. These large effects at the level of individual technologies can help

explain current differences in total factor productivity and income per capita across countries.[36]

Desmet et al. (2011) document the close relationship between genetic distance and cultural differences. They show a strong and robust correlation between answers to the World Values Survey (WVS) and genetic distance, finding that European populations that are genetically closer give more similar answers to a set of 430 questions about norms, values, and cultural characteristics, included in the 2005 WVS sections on perceptions of life, family, religion, and morals. They also find that the correlation between genetic distance and cultural values remains positive and significant after controlling for linguistic and geographic distances. Their empirical analysis supports Spolaore and Wacziarg's (2009, 2012a) interpretation of genetic distance, *not* as a purely genetic measure capturing exclusively biological effects and mechanisms, but as a broad genealogical measure of historical links between populations, capturing the intergenerational transmission of traits along the three dimensions, including the cultural channel and the gene-culture interaction channel (Quadrant IV, V, VI).

A focus on barrier effects is especially promising when the goal is to study the diffusion of development and innovations from the technological frontier. In contrast, it is much harder to assess the effects of intergenerationally transmitted traits on the onset of major technological changes. For instance, while barrier effects can explain how the Industrial Revolution spread across different societies over time and space, it is much harder to identify which intergenerationally transmitted traits, if any, are responsible for the original onset of such a major technological and institutional change. This difficulty is due to at least two reasons. Firstly, phenomena such as the Industrial Revolution are, almost by definition, unique and exceptional, and therefore one cannot build a data set of different and independent Industrial Revolutions to test alternative theories of onset. Secondly, such a complex phenomenon is likely to be the outcome of a vast set of forces and causes, including historical accidents and contingencies. For example, it has been argued that the Industrial Revolution may not have occurred where and when it did, were it not for a series of historical contingencies, such as the events leading to the signing of the Magna Carta, the failure of the Spanish armies to subjugate Protestant societies, the Glorious Revolution, and, at a deeper level, the emergence of a transnational market for ideas during the Enlightenment. An extensive discussion of these important issues appears in Mokyr (2005, 2010). As Mokyr (2005) points out: "underneath its surface the European soil in 1500 already contained the seeds of future divergence in 1750. There was, however, nothing inexorable about what happened after: the seeds need not have sprouted, they could have been washed away by the flood of wars, or the young sprouts of future growth might have been pulled out by rapacious tax collectors or burned by intolerant religious authorities. There could have been a Great Convergence after 1800 instead of what actually took place, in which Europe would have reverted back to the kind of economic performance prevalent in 1500. In the end, the economic history of technology—like all evolutionary sequences—contains a deep and irreducible element of contingency. Not all that was had to be" (1171).

In general, a fuller understanding of the process of economic development will emerge from the study of the interactions

[36]While long-term historical barriers captured by genetic distance tend to prevent productivity-enhancing interactions, such as the spread of new technologies, they may also reduce destructive interactions between populations, such as international conflict, as we show in Spolaore and Wacziarg (2012b).

between persistent traits, transmitted from one generation to the next over the long run, and contingent shocks and changes, whose effects across societies may partly depend on persistent traits—for example, when the diffusion of brand-new technological and institutional innovations in modern times depends on long-term genealogical relatedness.

5. *Conclusion*

The recent literature on economic growth and development has increasingly focused on very long-run effects of geographic, historical, and cultural factors on productivity and income per capita. In this article we have reviewed this line of research, and presented empirical evidence documenting such effects. In conclusion, what have we learned from this new literature?

A first message from this research is that technology and productivity tend to be highly persistent even at very long horizons. A major finding is the indirect and persistent effect of prehistorical biogeographic conditions. According to Olsson and Hibbs (2005), Neolithic advantages continue to have effects on contemporary income per capita, consistently with Diamond's hypothesis. The effects of favorable Neolithic conditions on productivity in more recent times is also documented by Ashraf and Galor (2011a). Long-term persistence is at the heart of Comin, Easterly, and Gong's (2010) findings that countries using the most advanced technologies in the year 1000 B.C. tend to remain the users of the most advanced technologies in 1500 and today, particularly if we correct for their populations' changing ancestry.

The importance of controlling for populations' ancestry highlights the second message from this literature: long-term persistence holds at the level of populations rather than locations. A focus on populations rather than locations helps us understand both persistence and reversal of fortune, and sheds light on the spread of economic development. The need to adjust for population ancestry is at the core of Putterman and Weil's (2010) contribution, showing that current economic development is correlated with historical characteristics of a population's ancestors, including ancestors' years of experience with agriculture, going back, again, to the Neolithic transition. The overall message from Comin, Easterly, and Gong (2010), Putterman and Weil (2010), and several other contributions covered in this article is that long-term historical factors predict current income per capita, and that these factors become much more important when considering the history of populations rather than locations.

Spolaore and Wacziarg (2009, 2012a) take this insight a step further, studying the diffusion of development and innovations with an explicit focus on measures of long-term genealogical relatedness between populations (genetic distance). The third message from this literature, then, is that long-term genealogical links across populations play an important role in explaining the transmission of technological and institutional knowledge and the diffusion of economic development.

Much research remains to be done on the specific mechanisms at work, and the specific intergenerationally transmitted traits that hinder development either directly or by creating barriers. Conceptually, one can distinguish among different transmission mechanisms (biological and cultural). However, current scientific advances have increasingly blurred and made obsolete the old distinction between nature and nurture, and emphasized the complex interactions among different inheritance systems (genetic, epigenetic, behavioral, and symbolic: Jablonka and Lamb 2005) and the coevolution of genes and culture (Richerson and Boyd 2005). In this article, we argue that, when studying the economic

impact of intergenerational transmission, a more promising approach can proceed from the distinction between direct and barrier effects. The hypothesis behind barriers effects of genealogical relatedness is that populations which happen to be historically and culturally farther from the innovators tend to face higher costs to imitate and adopt new technologies, because of differences in values and norms, mistrust, miscommunication, discrimination, etc. Our findings (Spolaore and Wacziarg 2009, 2012a) on the effects of genetic distance relative to the technological frontier are consistent with an important role for barrier effects, but the respective quantitative contribution of direct versus barrier effects remains a subject for future research.

Taking the recent literature seriously implies acknowledging the limits faced by policymakers in significantly altering the wealth of nations when history casts a very long shadow. A realistic understanding of the role of historical factors is essential for policy assessment. One could obtain misleading conclusions about the effects of specific policies and institutions when not taking into account the role of long-term variables. For example, one may erroneously infer a major role for specific national institutions in Africa, even though, as shown by Michalopoulos and Papaioannou (2010), national institutions have little effect when looking at the economic performance of homogeneous ethnic groups divided by national borders. In general, a richer understanding of the mechanisms through which long-term variables affect current outcomes will improve our ability to assess the impact of current and future policies.

If current development is a function of very long-term historical factors, are development policies hopeless? Not necessarily. The evidence is consistent with cautious optimism about our ability to overcome long-term constraints, for three major reasons:

Firstly, long-term history, while very important, is not a deterministic straightjacket. Historical variables do not explain all of the variation in income per capita. In Putterman and Weil (2010), the R^2 on state history, agriculture adoption and the fraction of European descent jointly does not exceed 60 percent. In Comin, Easterly, and Gong (2010), the R^2 in regressions of current income or technological sophistication on lagged technologies is never greater than 40 percent, depending on the exact time frame (see their table 8B). In Spolaore and Wacziarg (2009), a standard deviation change in genetic distance relative to the world technological frontier accounts for about 35 percent of the variation in income differences. That leaves a large fraction of variation to be explained by other factors and forces, suggesting that many societies can escape the straightjacket of history. Persistence does not mean perfect, deterministic persistence. While there is significant persistence in the use of advanced technologies over time and space, there have also been significant shifts in the technological frontier, with populations at the periphery becoming major innovators, and former frontier societies falling behind. In a nutshell, while long-term history matters, there is much scope for variations, exceptions and contingencies.

Secondly, such variations, exceptions and contingencies are unlikely to take place in a purely random fashion, but are affected by human actions. The intergenerational transmission of traits and characteristics happens with variation, and the diffusion of knowledge takes place not only vertically (from one generation to the next within populations) but also horizontally (across populations). Major changes can sometime take place relatively quickly, sidestepping historical constraints. Still, they are more likely to be successful and persistent if rooted in a fuller understanding of long-term forces and traditions. To paraphrase the Churchill quote with which we

opened this article, the further backward you look, the further forward you may be able to produce positive change. Cultures and societies are persistent but dynamic, and can change over time, as stressed in a famous quote attributed to Senator Daniel Patrick Moynihan: "The central conservative truth is that it is culture, not politics, that determines the success of a society. The central liberal truth is that politics can change a culture and save it from itself."[37]

Thirdly, a cautiously optimistic outlook can emerge if we interpret the effects of history and relatedness in terms of barriers to the diffusion of development and innovations. Barriers do matter and can explain long delays in the diffusion of prosperity across societies. Barriers can also be overcome and have indeed been overcome historically. In our work, the estimated effect of relative genetic distance on income differences peaked in the second half of the nineteenth century, and has been declining in the second half of the twentieth century. This suggests that the degree to which differences in intergenerationally transmitted traits constitute barriers has changed in the era of globalization, through greater exchanges of human capital, ideas, blueprints, and greater convergence of norms and values, facilitating the horizontal diffusion of technological and institutional innovations.[38]

The diffusion of modern development to East Asia, which started in Japan and spread to nearby societies, is an example of successfully overcoming long-term barriers. Japan is geographically, historically, and genetically distant from the European innovators, but it got the Industrial Revolution relatively early. This is not inconsistent with the existence of historical and cultural barriers across populations, because such barriers operate on average, and it is always possible for some society to develop traits and characteristics that make it closer to the innovator, or to sidestep cultural and historical barriers altogether through historical contingencies. When Japan got the Industrial Revolution, it became a cultural beachhead. South Korea followed, and then industrialization and modernization spread across several societies in East Asia. North Korea, in contrast, is a sad example that very bad policies and institutions can kill growth and development in a society irrespectively of any long-term historical and cultural variables. One can hope that North Koreans will be able to benefit from their historical, cultural, and geographic proximity to South Koreans when those artificial constraints to development are finally removed. An example of how more recent institutional shocks may interact with longer-term variables is provided by Bai and Kung (2011), who use the ending of the severance of ties between the Chinese mainland and Taiwan as a natural experiment. They find that relative but not absolute genetic distance from Taiwan has increased the income difference between pairs of Chinese provinces. While one must be cautious about the interpretation of this specific case study, these barrier effects are consistent with the mechanisms suggested in our own research (Spolaore and Wacziarg 2009 and 2012a). In general, these examples illustrate the complex interplay between more recent political and institutional shocks and long-term historical forces.

Another interesting example is the role of Hong Kong in China's development, recently stressed by Romer (2009). Romer argues that the fast rate of economic growth in China has a lot to do with the demonstration effect of Hong Kong—that is, Hong Kong was a beachhead in China from which

[37] This quote inspired a book by Harrison (2006).

[38] Fruitful links may exist between this important area for future research and the growing literature on education and human-capital externalities in neighborhoods and cities (e.g., see Moretti 2004) and on the economics of social interactions (e.g., see Durlauf and Ioannides 2010; Ioannides 2012).

modernity was able to spread. Under this view, when Britain gave back Hong Kong to China in 1997, it was not so much the reintegration of Hong Kong into China but rather the reintegration of China into Hong Kong. According to Romer, Southern Chinese cities or special economic zones developed largely as the result of having generalized what had worked in Hong Kong. This progressively led to the spread of more free-market oriented rules, as Romer calls them, to the rest of China. Romer advocates generalizing this example by ways of charter cities that could act as beachheads in order to accelerate the diffusion of development. While we do not know whether this specific idea may actually work in practice, we present it as an interesting example of the kind of policies reflecting an understanding of long-term historical forces and barriers to the diffusion of development. In a way, this can be interpreted as an example of a more general approach to development policies: if you want to develop, build on historical precedent but try to generalize exceptions to the persistence of economic fortunes.

In conclusion, there is still room for development policies to reduce barrier effects and to accelerate the spread of ideas and innovations across populations, especially in the context of an increasingly globalized world where barriers to the diffusion of development can be brought down more rapidly. The research surveyed in this article can help us assess both the potential and limits of these policies.

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