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Abstract

This paper suggests a theoretical framework and provides empirical evidence for a hump-shaped relationship between the fraction of novelty-seeking traits in society and current levels of per capita income. The hypothesis is that novelty-seeking traits produce two countervailing effects on aggregate productivity and hence economic development. The beneficial effect consists in explorative knowledge acquisition, which contributes significantly to the process of economic development. The detrimental effect results from a certain amount of this knowledge not being used reliably for capital accumulation due to the high fraction of individuals engaged in exploration rather than in production. One main conclusion of the empirical analysis is that the high fraction of novelty-seeking individuals in society engaged in short-run explorative knowledge acquisition prevent permanent settlement and therefore act as an obstacle to the development of centralized states, which are a precursor to modern industrial production.

Keywords: Novelty-Seeking Behavior, Entrepreneurial Traits, Economic Development, Natural Selection, Genetic Diversity

JEL Classification Numbers: N50, O10, O50, Z10

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1 Introduction

There exist major disparities in the standard of living across countries in the world today. Identifying the main factors that contribute to the process of economic development is one of the key challenges of economic research. Although the theories proposed to explain this process remain inconclusive so far, there is broad consensus that historical factors emerging hundreds, even thousands of years ago matter for a country's contemporary economic development.[1] Gallup et al. (1999), for example, show that geographic location and climate have large and persistent impacts on economic development through their effects on agricultural productivity, transports costs, disease burdens, population growth, and economic policy choices. Acemoglu et al. (2001, 2002) stressed the importance of geography for European colonization strategies after 1500 AD, when colonial powers began implementing extractive, investment-reducing political institutions in dense, resource-rich areas with high settler mortality rates and growth-enhancing institutions in areas where European settlement was encouraged by favorable geographic conditions. Olsson and Hibbs (2005) found that initial biogeographical endowments influenced the location and timing of the transition from hunter-gatherer economies to agricultural production, contributing significantly to the development of complex social organizations and the emergence of centralized states. Moreover, as discussed in Bockstette et al. (2002) and further analyzed by Chanda and Putterman (2007), a longer history of statehood experience for the period 1 to 1950 AD is conducive to various measures of institutional quality, the level of per capita income, and economic growth in the post-World War II period. The main conclusion that can be drawn from the previous studies is that populations that formed state institutions relatively early are in the favorable position of being able to adjust their institutional capacities and cultures to the specific needs of modern economic conditions.

Recent research has demonstrated the importance of historical factors underlying disparities in the standard of living across countries. Nevertheless, this kind of historical analysis often neglects an important issue pertaining to the large migration flows during the post-Columbian era: the history of state development by a particular population. During the period since 1500 AD, high migration to areas of the New World–countries located on the American landmass and Neo-European countries such as Australia and New Zealand–has blurred the influence of geographic location on income inequality across countries, raising the question of whether the economic history of a particular geographic area can be analyzed separately from the history of

[1] See Spolaore and Wacziarg (2013) for a literature overview.

the populations that live there. This argument was put forward by Putterman and Weil (2010), who argue that not the location of a population but rather its history of state development is the crucial factor affecting its standard of living today. Although the concrete mechanism behind this result is still not fully explained, evidence suggests that the human capital people brought with them (e.g., institutions, social norms, beliefs, and cultural attitudes) when they moved to new and unpopulated areas of the world may play a key role. In particular, Hall and Jones (1999) found that countries with significant populations of immigrants from Western Europe are now better off in terms of output per worker because they adopted European-influenced policies that are conducive to physical and human capital accumulation. Easterly and Levine (2013) devote special attention to the role of European populations in economic development during the early stages of colonization. The authors found a positive role of European settlement during colonization on the level of per capita income today. Interestingly, the effect vanishes when controlling for the quality of political institutions or the level of educational attainment. This result is consistent with the findings in Glaeser et al. (2004), who argue that Europeans, when colonizing areas of the New World, brought with them (European) human capital and political institutions that were favorable to economic development. Moreover, Comin et al. (2010) found a strong and robust relationship between past levels of population-adjusted technology adoption in 1000 BC, 0 AD, and 1500 AD with per capita income and technology adoption today. Their results strongly confirm the findings in Putterman and Weil (2010) that the history of populations rather than their locations directly affect current levels of per capita income.

These studies raise the general question of which human traits are actually transmitted, either genetically or culturally, from generation to generation and thereby affect economic development today.[2] Genetic relatedness among populations is at the forefront in an intriguing study by Spolaore and Wacziarg (2009). The authors hypothesize and empirically establish a positive association between relative genetic distance and the technological frontier of contemporary

[2]Economic models of intergenerationally transmitted cultural traits (e.g., values, norms, beliefs, and preferences) have been studied in detail by Bisin and Verdier (2000, 2001) (see also Bisin and Verdier (2005) for an overview). These models are related to theoretical contributions from the field of evolutionary biology applied to the intergenerational transmission of cultural traits, as outlined by Cavalli-Sforza and Feldman (1981) and Boyd and Richerson (1985). For example, Bisin and Verdier (2001) studied how altruistic parents socialize their children to their specific preferences in various social environments. The authors argue that parents prefer that their children adopt their own cultural preferences, and therefore socialize their children in accordance with their own traits. The main conclusion of their study is that society displays heterogenous preferences that may interact with genetic traits (gene-culture co-evolution processes) that emerge from various socioeconomic systems.

income differences between countries. They interpret their findings as evidence that genetic distance captures the notion of barriers to technological diffusion across countries. They do not claim that specific genetic traits spur economic development while others not. Rather, they assert that genetic relatedness between populations facilitates technological diffusion and access to international markets because of similar values, norms, and beliefs–that is, cultures–that are persistently transmitted within populations. More recently, Ashraf and Galor (2013) found a non-monotonic, hump-shaped relationship between genetic diversity *within* a country in general and comparative economic development. The authors stress that genetic diversity has two conflicting effects on aggregate productivity and hence on comparative economic development. First, higher genetic diversity produces beneficial effects by expanding a society's production possibility frontier. Second, higher genetic diversity is associated with lower coordination, trust, and social cooperation, which inhibits the ability of a society to efficiently employ its production possibility frontier. These two countervailing effects imply a level of genetic diversity at which the two effects precisely offset each other and which maximizes income per capita. Other studies highlight additional mechanisms by which traits transmitted over generations have affected recent economic development. Cook (2011), for example, found that the frequent contact of humans with domesticated animals since the transition to agricultural production promoted the expression of disease-related genes, contributing significantly to higher life expectancy today. In addition, as analyzed in Cook (2013), the ability to digest milk gave certain populations an evolutionary advantage in historical times. Milk, as an additional food source, improved fertility rates in these populations, thus enabling them to escape from the Malthusian economy.

This paper builds on past results showing that the traits transmitted from one generation to the next in a population–rather than the population's geographic location over the course of history–are responsible for income differences across countries. Specifically, the present study explores, both theoretically and empirically, the significant role of the human trait associated with novelty-seeking behavior and its implications for current levels of per capita income. Previous theoretical work by Galor and Michalopoulos (2012) suggests the importance of novelty-seeking traits–which they interpret as entrepreneurial traits–for the pace of technological progress and process of economic development in a society. They emphasize the Darwinian selection of entrepreneurial traits by virtue of differences in the degree of risk aversion with respect to consumption choices. The hereditary component of entrepreneurial activity has been analyzed empirically by White et al. (2006). Their results suggest that increased testosterone levels in MBA students are significantly correlated with new venture creation. They explain this based on the argument that increased testosterone levels increase risk-taking behavior. Regarding the parental transmission of entrepreneurial preferences, Doepke and Zilibotti (2014) also established a link between the growth rate of the economy and the fraction of the population becoming entrepreneurs. Their theoretical model suggests that the fraction of entrepreneurs in a population depends on parental efforts to shape their children's patience and risk behavior. Taken together, the aforementioned studies stress the importance of entrepreneurial or novelty-seeking activities for a society's comparative economic development. The theoretical model considered in this paper assumes that novelty-seeking traits in society have two countervailing effects on aggregate productivity and, therefore, on economic development. The beneficial effect of these traits lies in explorative knowledge creation–e.g., ideas, views, and enhanced technology that increase the production possibility frontier in society, thus contributing significantly to the process of economic development. The negative effect consists in society's failure to use a certain amount of this knowledge reliably for physical capital accumulation due to the high fraction of individuals engaged in exploration rather than in production. Therefore, the model predicts that populations with intermediate levels of novelty-seeking traits perform better economically because they allocate an optimal percentage of the population to explorative knowledge acquisition, whereas the remaining portion of the population employs this knowledge effectively in the production process. In summary, the social benefits of a heterogeneous society consisting of 'normal' and novelty-seeking individuals include the expansion of the production possibility frontier through the creation of new knowledge, whereas the individual or physical costs are borne by a small minority group.

The theoretical model suggests that differences in per capita income across countries stem, to some extent, from differences in the prevalence of novelty-seeking traits in society and, additionally, that these traits affect economic development in a non-linear, hump-shaped fashion. To examine this hypothesis empirically, I construct a new data set on the prevalence of novelty-seeking traits in society in a number of different countries. In doing so, I borrow from the approach of Gören (2014), who provides genetic data on the human DRD4 exon III locus, a particular gene variant known to be associated with the human personality trait of novelty-seeking behavior, on a large number of populations across the world. He utilizes high-resolution geospatial data on the population level to uncover the biogeographical origins of novelty-seeking traits in a large number of populations worldwide. The revealed association between biogeographical indicators (e.g., land suitability for agriculture, the fraction of land allocated to pasture, and terrain ruggedness) with novelty-seeking traits is quite useful for the current empirical analysis.

Because genetic data on DRD4 exon III are only available at the population level, countries generally consist of various populations partly due to high post-1500 migration flows. To resolve this difficulty, I rely on two strategies in the construction of DRD4 exon III expected heterozygosity measures on the country level. First, using observed DRD4 exon III allele frequencies, I construct genetic measures of *expected heterozygosity* for the subset of indigenous populations across the globe. Then, given these observations, I employ the predictive power of biogeographical indicators to overcome data limitations and potential endogeneity bias. Second, given the explanatory power of biogeographical indicators, I focus in the subsequent empirical analysis on constructing *country-specific* DRD4 exon III expected heterozygosity measures based on *country-specific* biogeographical indicators. Furthermore, to account for large migration flows since the year 1500 AD, I construct ancestry-adjusted DRD4 exon III expected heterozygosity measures on the country level by employing migration data from Putterman and Weil (2010). It is precisely this ancestry-adjusted index that I utilize in the empirical analysis to determine the impact of novelty-seeking traits in society on current per capita income levels in a large sample of countries.

The baseline results demonstrate that DRD4 exon III diversity has a statistically significant, hump-shaped impact on current levels of per capita income. This hump-shaped effect is in line with the proposed theory and robust to a wide range of controls for continent fixed effects, the health environment, climatic factors, biogeographical endowments, Neolithic transition timing, ethnic diversity, population density, state history, institutional quality, population structure (e.g., the share of a country's population that is descended from populations on the European continent in the year 1500 AD), and a set of variables for geographical, legal origin, and major religion effects.

The unconditional direct impact of DRD4 exon III diversity on log per capita income in the year 2000 is positive and highly statistically significant. The estimate suggests that a one standard deviation increase in DRD4 exon III diversity would, ceteris paribus, lead to a 67% increase in the level of GDP per capita in the year 2000. In other words, the result suggests a beneficial effect of diverse personality traits in society on current levels of per capita income. This result is in line with the hypothesis that a wider spectrum of diverse, novelty-seeking personality traits is positively associated with explorative knowledge creation, thus contributing significantly to higher current levels of per capita income. Turning to the analysis with respect to the proposed hump-shaped relationship between log GDP per capita and novelty-seeking traits in society, the empirical results reveal that, once the geographical, disease-related, and biogeographical factors have been controlled for, a 1% change in DRD4 exon III diversity evaluated at the median diverse country (Papua New Guinea) would raise per capita income in the year 2000 by roughly 1.3%. This hump-shaped relationship is further confirmed when controlling for cultural, population-related, institutional, and religious factors. Moreover, the results are not prone to possible endogeneity bias arising from large migration flows since the year 1500 AD. Potential endogeneity bias could arise from the fact that novelty-seeking, risk-taking individuals migrated into highly developed or resource-rich countries, thus creating an empirical artifact between novelty-seeking traits in society and current levels of per capita income. Fortunately, the empirical results are not sensitive to the exclusion of OECD countries, Neo-European countries (e.g., USA, Canada, Australia, and New Zealand), Latin American countries, Sub-Saharan African countries, and to the restriction of countries whose indigenous populations can trace more than 85% of their ancestry to populations living in the country in 1500 AD. In addition, consistent with the proposed theory that novelty-seeking traits are a cultural attitude prevalent in populations with nomadic lifestyles, resulting in lower levels of physical capital accumulation, the empirical analysis provides further evidence that DRD4 exon III diversity is indeed negatively associated with physical capital accumulation, as measured by the investment share of GDP per capita in 2000.

The remainder of the paper is organized as follows. Section 2 provides a theoretical model of the relationship between novelty-seeking traits in society and the level of per capita income. Section 3 discusses the data and estimation methodology in more detail. Section 4 presents the empirical results for contemporary economic development. Section 5 checks the robustness of the results and provides empirical evidence for a possible transmission channel through which novelty-seeking traits may affect current levels of living standards across countries. Finally, Section 6 concludes by summarizing the main results.

2 Model Building

This section presents a theoretical framework for the proposed association between the prevalence of novelty-seeking and the country's process of economic development. The goal is to provide a testable econometric hypothesis for the prevalence of novelty-seeking traits and current levels of per capita income. The heritable component of novelty-seeking traits in society and its implications for the pace of technological progress and the process of economic development is the subject of analysis in Galor and Michalopoulos (2012). The authors considered a Darwinian evolutionary growth model with overlapping generations, establishing a significant role of novelty-seeking, entrepreneurial traits in the process of economic development. Their model predicts that in the course of economic development, the evolutionary advantage of novelty-seeking traits reversed and risk-averse traits gained an evolutionary advantage, which reduced technological progress and thus contributed to a convergence in economic growth across countries. In contrast, the main focus in this paper is to provide a theoretical framework that can explain differences in long-run economic performance by analyzing the predictive power of novelty-seeking traits in society for the cross-country variation in *levels* of per capita income. For this reason, the current paper develops a neoclassical growth model with consumer optimization and physical capital accumulation. The main feature of the model is that differences in biogeographical endowments and the prevalence of novelty-seeking traits in society explain differences in the level of technology and the accumulation of physical capital across countries. These differences in ultimate factors underlying the key determinants of economic development (e.g., technology and the accumulation of physical capital) provide further insights into the large and pervasive differences in income per capita across countries today. Since the distribution of novelty-seeking traits across populations is the result of human exposure to existing biogeographical conditions, it enters exogenously into the framework of neoclassical growth. This assumption is sufficient because the main purpose of the paper is to investigate the impact of novelty-seeking traits on comparative economic development. In addition, given the temporal framework of neoclassical growth models explaining the recent phenomenon of sustained economic development, it is not believed that the genetic composition of novelty-seeking traits in society will change substantially over this relatively short time horizon.

Suppose that the distribution of individuals allocated to production and explorative activities depends on the prevalence of novelty-seeking traits in society, $\omega \in [0, 1]$, and biogeographical factors, $\gamma \in [0, 1]$. The parameter γ indicates the type of environmental conditions and their influence on the fraction of individuals engaged in explorative knowledge acquisition, where larger values for this parameter correspond to environmental conditions less suitable for human settlements. Specifically, the fraction of individuals engaged in explorative knowledge creation equals

$$v = v(\gamma, \omega), \tag{1}$$

where $0 < v(\gamma, \omega) < 1, v_\tau(\gamma, \omega) > 0$, $v_{\tau\tau}(\gamma, \omega) < 0$, $\lim\limits_{\tau \to 0} v_\tau(\gamma, \omega) = \infty$, and $\lim\limits_{\tau \to 1} v_\tau(\gamma, \omega) < \infty$, for all $\omega, \gamma \in [0, 1]$, and $\tau = (\gamma, \omega)$, respectively, and $v_\tau(\bullet)$ is the partial derivative of v with respect to τ. Therefore, the fraction of individuals engaged in explorative behavior (v) increases with the prevalence of novelty-seeking traits (ω) in society, but at a diminishing rate. In addition, biogeographical conditions unsuitable for sedentary life (e.g., this would correspond to a higher value for the parameter γ) increases the fraction of total population engaged in exploration. This is the result of past human exposure to frequently changing environments, forcing populations to develop certain production modes, that is, knowledge or cultures, that would enable them to increase their reproductive success in otherwise resource-depleted areas. For example, Eisenberg et al. (2008) found that explorative behavior is a cultural attitude predominant in populations with a long history of nomadic lifestyles. Their result provides evidence that historical differences in biogeographical endowments explain the emergence of nomadic lifestyles. These societies, which were mainly egalitarian in nature, did not produce bureaucrats and chiefs for the development of complex political organizations (e.g., centralized states) to redistribute wealth from sedentary production, thus preventing their transition to modern industrial production.

Furthermore, assume that the state of technology or knowledge, A, is a function of institutional, human capital and biogeographical factors, the share of individuals allocated to knowledge creation, as well as the prevalence of novelty-seeking traits in society. In particular, the level of technology is determined by a spectrum of novelty-seeking traits, such that:[3]

$$A(z,\gamma,\omega) = zv(\gamma,\omega)\int_{i=0}^{\omega} x(i)^{\theta}di, \tag{2}$$

where $x(i)$ is the quantity of novelty-seeking trait i in society, uniformly distributed over the interval $[0,\omega]$, $\theta \in (0,1)$ is the knowledge elasticity of novelty-seeking traits, and z refers to institutional and human capital factors. The functional form suggests that technological knowledge inherent in novelty-seeking individuals can be used only if a certain percentage of individuals are allocated to explorative activities and if society as a whole benefits from this experimentation in terms of an increased production possibility frontier. Although societies with a lower prevalence of novelty-seeking traits allocate more resources to the production process, their level of knowledge will be relatively low due to a lower level of explorative activity.

Output is therefore determined by the level of technology, $A(z,\gamma,\omega)$, the level of capital inputs used in the production process, and the fraction of total population engaged in production. In particular, the amount of output produced in the economy corresponds to:

$$Y(t) = A(z,\gamma,\omega)K(t)^{\alpha}\left[(1-v(\gamma,\omega))L(t)\right]^{(1-\alpha)}, \tag{3}$$

[3]The functional form for the level of technology is similar to that analyzed in Ashraf and Galor (2013).

where $K(t)$ reflects the upper bound to a continuum of capital inputs used in production at time t, $L(t)$ is total population, and $\alpha \in (0,1)$ is the output elasticity with respect to capital inputs. The different types of intermediate goods can be expressed according to the product-variety definition, as introduced in Romer (1990) in continuous form, such that $K(t) = \left[\int_{s=0}^{K(t)} m(s)^{\alpha} ds \right]^{\frac{1}{\alpha}}$, where $m(s)$ is the quantity of intermediate good s, α is the elasticity of intermediate goods, and $m(s) = 1$ for all s and t. Then, output per capita is given by the following expression:

$$y(t) = A(z,\gamma,\omega)\left[1 - v(\gamma,\omega)\right]^{1-\alpha}\left[k(t)\right]^{\alpha} \equiv f\left[k(t)\right], \tag{4}$$

where $k(t)$ now refers to the capital-labor ratio.

As a specific example, consider the following functional form for the fraction of individuals engaged in explorative knowledge creation:

$$v(\gamma,\omega) = \gamma^{\beta}\omega^{1-\beta}, \tag{5}$$

where β measures the prevalence of biogeographical factors in the allocation of individuals to experimentation. Specifically, a lower biogeographical elasticity, β, increases the relative importance of novelty-seeking traits in explorative knowledge creation. The functional form further suggests that populations residing in areas unsuitable to sedentary practices or consisting of a higher prevalence of novelty-seeking traits will allocate more individuals to explorative knowledge creation and less to the production process. In addition, as mentioned by Williams and Taylor (2006), before populations begin to explore new ideas and technologies, humans also need the tools that make knowledge creation possible. For example, as extensively analyzed in Diamond (1997), explorative behavior will quickly reach its limits in areas lacking mineral resources (e.g., iron, gold, and coal) or plants and animals suitable for domestication. This would correspond to a higher value for the parameter γ, preventing the accumulation of physical capital and leading in turn to lower levels of per capita income today. Interestingly, the social benefits of novelty-seeking traits for aggregate productivity is the highest in harsh and frequently changing environments unsuitable for sedentary life, because $\frac{\partial^2 v}{\partial\gamma\partial\omega} = \beta(1-\beta)\gamma^{\beta-1}\omega^{-\beta} > 0$.

In addition, assume for the sake of simplicity that the quantity of novelty-seeking traits in society is equally distributed, such that $x(i) = 1/\omega$ for all i. Then, equation (2) can be written as $A(z,\gamma,\omega) = z\gamma^{\beta}\omega^{(1-\theta)+(1-\beta)}$, where $(1-\theta)+(1-\beta)$ now refers to the composite knowledge elasticity of novelty-seeking traits. It follows that an increase in the spectrum of novelty-seeking traits in turn leads to an increase in the level of aggregate technology at a diminishing rate, if $(\theta+\beta)$ is strictly greater than 1. Thus, if most individuals in society are endowed with novelty-seeking traits, the technological benefit of an additional increase in ω is small because of the high explorative behavior in society overall. In contrast, when most members of society are engaged in the production process, a small increase in novelty-seeking traits will generate high social benefits because of the increase in the production possibility frontier. This result stems from the fact that the marginal product of an increase in ω on aggregate productivity outperforms the reduction triggered by the decrease in the fraction of individuals employed in the production process.

Because the prevalence of novelty-seeking traits in society has been the result of former human exposure to biogeographical factors, it enters exogenously into the framework of neoclassical growth. Again, this model framework is particularly convenient for analyzing the recent phenomenon in economic development.[4] Therefore, the social planner maximizes utility subject to technology and resource constraints:

$$\max_{[k(t),c(t)]_{t=0}^{\infty}} \int_{0}^{\infty} \frac{c(t)^{1-\sigma}-1}{1-\sigma} e^{-(\rho-n)t} dt, \tag{6}$$

with respect to

$$\dot{k}(t) = f\left[k(t)\right] - (n+\delta)k(t) - c(t), \tag{7}$$

where $c(t)$ refers to consumption per capita, ρ is the discount rate, σ is the reciprocal of the intertemporal elasticity of substitution, and n denotes the population growth rate. The accumulation of factor inputs decline partly due to depreciation, because over time, some intermediate factor inputs become obsolete and therefore can no longer be used for production. Moreover, the accumulation of factor inputs over time is useless in populations characterized by high explorative behavior. In these cases, individuals are engaged mainly in short-run knowledge acquisition to uncover certain production modes, responding effectively to frequently changing environments in order to maintain their reproductive success in otherwise resource-depleted areas.

Without loss of generality, the following part dispenses with the time subscript. Setting up the current value Hamiltonian yields:

$$\mathbf{H}(k,c,\mu) = \frac{c^{1-\sigma}-1}{1-\sigma} + \mu\left[f(k) - (n+\delta)k - c\right]. \tag{8}$$

[4] This assumption is also in line with Galor and Michalopoulos (2012) who argue that '[...] genes appear to have been reshaped by natural selection within the last 5,000 to 15,000 years.' Given the short time period which produced the recent discrepancies in living standards across countries, it is not believed that the composition of novelty-seeking traits in society has been subject to major changes during the analyzed time horizon.

The optimality conditions for this dynamic model are given by the following expressions:

$$\frac{\partial H}{\partial c} = c^{-\sigma} - \mu = 0$$

$$\Leftrightarrow \mu = c^{-\sigma} \tag{9}$$

$$\dot{\mu} = (\rho - n)\mu - \frac{\partial H}{\partial k} \tag{10}$$

$$\dot{\mu} = (\rho - n)\mu - \mu\left[f_k(k) - (n+\delta)\right]$$

$$\Leftrightarrow \frac{\dot{\mu}}{\mu} = (\rho - n) - \left[z\gamma^{\beta}\omega^{(1-\theta)+(1-\beta)}\left(1-\gamma^{\beta}\omega^{1-\beta}\right)^{(1-\alpha)}\alpha k^{(\alpha-1)} - (n+\delta)\right]$$

$$\lim_{t\to\infty}\left(\mu k e^{-(\rho-n)t}\right) = 0 \tag{11}$$

The interpretation of the equations are standard: equation (9) is the optimality condition with respect to the control variable c. It says that the marginal return of per capita consumption must equal its shadow price over time. Equation (10) requires that at the optimum, the marginal rate of return to capital must equal the rate of consumption.[5] Moreover, equation (11) is the well-known transversality condition.

It is a matter of algebra to show that the steady state level of the capital-labor ratio is given by:

$$k^* = \left[\frac{z\gamma^{\beta}\omega^{(1-\theta)+(1-\beta)}\left(1-\gamma^{\beta}\omega^{1-\beta}\right)^{(1-\alpha)}\alpha}{\delta+\rho}\right]^{\frac{1}{[1-\alpha]}}. \tag{12}$$

Inserting this expression into equation (4) gives the solution for per capita income:

$$y^* = \left(z\gamma^{\beta}\omega^{(1-\theta)+(1-\beta)}\right)^{\frac{1}{[1-\alpha]}}\left(1-\gamma^{\beta}\omega^{1-\beta}\right)\left[\frac{\alpha}{\delta+\rho}\right]^{\frac{\alpha}{[1-\alpha]}}. \tag{13}$$

It is worth mentioning that populations with unfavorable biogeographical endowments or a high representation of novelty-seeking traits could never reach a high level of economic development. Although the level of knowledge or technology is high in these populations, the accumulation of physical capital was hampered in the past, resulting in lower levels of income per capita today. Moreover, to study the impact of novelty-seeking traits in society on income per capita, a log-transformation of equation (13) is considered:

$$\ln(y^*) = \frac{1}{[1-\alpha]}\ln\left(z\gamma^{\beta}\omega^{(1-\theta)+(1-\beta)}\right) + \ln\left(1-\gamma^{\beta}\omega^{1-\beta}\right) + \frac{\alpha}{[1-\alpha]}\left[\ln(\alpha) - \ln(\delta+\rho)\right]. \tag{14}$$

Thus, there exists an intermediate, reduced-form level of novelty-seeking traits in society that maximizes the level of income per capita, such that:

$$\frac{\partial \ln(y^*)}{\partial \omega} = \begin{cases} > 0, & if \quad \omega < \left[\frac{(1-\theta)+(1-\beta)}{\gamma^{\beta}[(1-\theta)+(2-\alpha)(1-\beta)]}\right]^{\frac{1}{[1-\beta]}}, \\ < 0, & if \quad \omega > \left[\frac{(1-\theta)+(1-\beta)}{\gamma^{\beta}[(1-\theta)+(2-\alpha)(1-\beta)]}\right]^{\frac{1}{[1-\beta]}}. \end{cases} \tag{15}$$

[5] According to Barro and Sala-i-Martin (2004) the term μ is the price of capital expressed in current utility, $\frac{\partial H}{\partial k}$ refers to the marginal contribution of capital to utility, and $\dot{\mu}$ is the capital gain over time. Hence, at the optimum the rate of return to capital, $\left(\frac{\partial H}{\partial k} + \dot{\mu}\right)/\mu$, must equal the return to consumption, $(\rho - n)$.

The impact of novelty-seeking traits in society on income per capita is positive as long as these traits are sufficiently small. As already shown based on the previous results, an increase in the elasticity of novelty-seeking traits θ, indicating the relative importance of these traits in society for knowledge acquisition, negatively affects the optimal turning point for income per capita. In a similar vein, populations residing in biogeographical areas unfavorable for sedentary life allocate more individuals to explorative knowledge creation and less to production, again negatively affecting the optimal turning point for income per capita.

3 Data and Estimation Methodology

In evaluating the impact of novelty-seeking traits in society on comparative economic development, this study employs DRD4 exon III genetic data on the population level. Population geneticists rely on a measure called *expected heterozygosity* to measure the level of diversity of a single gene within a particular population. The measure of DRD4 exon III expected heterozygosity used on the set of populations in this study is constructed as follows:[6]

$$H_k^{DRD4} = 1 - \sum_{a \in S_{DRD4}} p_{ak}^2, \tag{16}$$

where H_k^{DRD4} is the expected heterozygosity measure of population k with respect to the DRD4 exon III locus, S_{DRD4} refers to the set of observed DRD4 exon III alleles in population k, and p_{ak} is the frequency for the ath DRD4 exon III allele for this particular population. This measure corresponds to the probability that two randomly selected individuals from the *same* population will have different DRD4 exon III allele variants. Furthermore, this measure precisely captures the prevalence of novelty-seeking traits in society, because higher values of this measure inevitably correspond to more diverse personality traits in the population.

Although it is widely accepted that preferences for specific economic attitudes in areas such as economic risk-taking and trust are transmitted from parents to their offspring (Dohmen et al., 2012), suggesting an important role of children's socialization. These studies cannot, however, distinguish between theories of genetic and cultural transmission of preferences. Indeed, within the economics literature, studies using behavioral genetic analysis argue that human behavior is to some extent heritable. For example, Cesarini et al. (2009), using a twin design laboratory experiment, found that preferences for giving and risk-taking are explained by genetic differences.

[6]Further details regarding the sampled populations with respect to the DRD4 exon III gene along with bibliographical sources are available from the author upon request.

In addition, Zhong et al. (2009), also using a classical twin design, argue that roughly 57% of individual economic risk-taking behavior is broadly heritable. Other studies from the field of molecular genetics have uncovered specific genes or gene variants that help to explain individual financial risk-taking behavior. For instance, Dreber et al. (2009) and Kuhnen and Chiao (2009) established an association between financial risk-taking and the presence of the 7-repeat allele of DRD4 exon III in laboratory experiments. In a related study, Apicella et al. (2008) found that financial risk preferences in men can be explained by increased testosterone levels in an investment game. These studies suggest that carefully collected data from molecular genetic studies can aid in our understanding of causal relationships between individual preferences and economic outcomes, where genetic data can provide possible proxy variables related to certain individual preferences or as instrumental variables in regression analysis to control for reverse causality.[7] The measures of the prevalence of novelty-seeking traits considered in this paper have some advantages over survey-based or self-reported individual preferences. For example, Brosig et al. (2007) showed that individual behavior is inconsistent across time in the same experiment, therefore casting some doubt on the economic validity of laboratory experiments. This issue is particularly important when performing cross-country analysis using survey-based measures of economic attitudes from laboratory experiments subject to different environmental conditions and experimental methods.[8] In contrast, compiled data on DRD4 exon III from molecular genetic studies on the different sampled populations meet rigorous standards for data reliability and are therefore less susceptible to measurement errors. In particular, the constructed index based on DRD4 exon allele frequencies is regarded as a possible proxy for the latent variable associated with novelty-seeking behavior in society.

The biogeographical origins of novelty-seeking traits in a large sample of populations across the world are the subject of analysis in Gören (2014). The author found that migratory distance from East Africa and various measures of land suitability (e.g., land suitability for agriculture, the fraction of land allocated to pasture, and elevation) are significantly related to specific novelty-seeking traits. These findings have a clear advantage for empirical analysis when investigating the relationship between novelty-seeking traits and income per capita today. First,

[7] The interested reader is referred to Beauchamp et al. (2011) for an excellent discussion on this topic.

[8] Furthermore, another source of measurement error in the relationship between survey-based indicators and cross-country variation in standards of living is the lack of representativeness of the sampled individuals in terms of demographic, social, and economic outcomes. Overall, measurement error in one independent variable has the negative side-effect of biasing the coefficient estimate toward zero, thus making it difficult to detect a significant impact on the dependent variable.

biogeographical factors serve as qualified instrumental variables for DRD4 exon III expected heterozygosity and therefore reduce potential endogeneity bias with levels of per capita income that have emerged in the wake of post-1500 migration flows. Second, the predictive power of biogeographical variables and migratory distance from East Africa for DRD4 exon III expected heterozygosity permits the actual analysis to be unrestricted to a limited number of countries for which observed DRD4 exon III allele frequencies from various populations have been compiled from molecular genetic studies. Because economic data are available for a large number of countries, DRD4 exon III expected heterozygosity predicted by biogeographical characteristics and migratory distance from East Africa will considerably enhance the empirical analysis. Specifically, a logistic regression for DRD4 exon III expected heterozygosity in the subset of indigenous populations across the world is estimated based on migratory distance from East Africa and various measures of population-specific biogeographical indicators. Based on the coefficient estimates from this first-stage regression, the second step in the regression analysis deals with the construction of DRD4 exon III expected heterozygosity measures on the *country* level by replacing the biogeographical characteristics on the population level with those on the country level. This procedure provides DRD4 exon III expected heterozygosity measures *predicted* by biogeographical indicators for each country.[9] Because countries in the post-Columbian era have experienced large migration flows from other countries, an ancestry-adjusted DRD4 exon III expected heterozygosity measure for each country is constructed based on post-1500 population flows data from Putterman and Weil (2010).[10] It is precisely this predicted variable and its squared value that will be used in the empirical analysis of comparative economic development. Since this instrumental variable strategy yields consistent estimates for the estimated regressors, it fails to account for the presence of generated regressors. Standard errors for the generated regressors are inconsistently estimated and this would lead to erroneously rejecting the null hy-

[9]Similar strategies were employed in Hall and Jones (1999), Chanda and Putterman (2007) and Ashraf and Galor (2013) to obtain generated regressors on the macro level. Detailed information in the construction of country-specific DRD4 exon III expected heterozygosity measures can be found in the Appendix.

[10]Indeed, an alternative approach would be to assign populations to ethnic groups within countries. For example, Spolaore and Wacziarg (2009) matched the set of 42 world populations from Cavalli-Sforza et al. (1994) to the classification of ethnic groups from Alesina et al. (2003). However, errors in matching populations to ethnic groups are inevitable given the relative small number of populations. However, based on genetic data from 92 indigenous populations around the world, this research utilizes the predictive power of biogeographical indicators in the construction of DRD4 exon III expected heterozygosity measures on the country level. This approach solves to some extent the arbitrary assignment of populations to ethnic groups.

pothesis too often.[11] This study therefore adopts the two-step bootstrapping method outlined in the empirical study in Ashraf and Galor (2013). The standard errors for the explanatory variables were constructed in the following way: First, a random population sample with replacement from each country is drawn from the list of compiled DRD4 exon III genetic studies. Based on this random population sample, predicted DRD4 exon III expected heterozygosity measures for each country were constructed applying the regression coefficients from the logistic model on country-specific biogeographical indicators and migratory distance from East Africa. Then, ancestry-adjusted DRD4 exon III expected heterozygosity measures for each country were constructed applying data from the *World Migration Matrix*, as reported by Putterman and Weil (2010), to the country-specific predicted DRD4 exon III expected heterozygosity measures. Second, these population-weighted measures were used to estimate the impact of DRD4 exon III expected heterozygosity on current levels of per capita income on a random sample from the extended list of countries. The estimated coefficients on this second regression step were noted accordingly. This procedure was repeated 1,000 times to get bootstrapped standard errors, which are the standard errors of the estimated coefficients for the regressors used.

Maintaining the robustness of the non-linear, hump-shaped relationship of DRD4 exon III expected heterozygosity on comparative economic development, this study further controls for a broad set of geographical, climatic, institutional, and cultural factors. Specifically, the following level regression for the empirical analysis is adopted:

$$\text{Ln } Y_c^{2000} = \alpha + \lambda_1 W\widehat{H_c^{DRD4}} + \lambda_2 \left(W\widehat{H_c^{DRD4}}\right)^2 + \mathbf{R_c'}\beta_1 + \mathbf{\Gamma_i'}\beta_2 + \mathbf{\Delta_c'}\beta_3 + \mathbf{\Theta_c'}\beta_4 + \mathbf{X_c'}\beta_5 + \varepsilon_c, \quad (17)$$

where Ln Y_c^{2000} is the natural logarithm of real GDP per capita in 2000 for country c, $W\widehat{H_c^{DRD4}}$ and $\left(W\widehat{H_c^{DRD4}}\right)^2$ is the ancestry-adjusted DRD4 exon III expected heterozygosity measure and its squared value, respectively, $\mathbf{R}$ is a vector of regional variables (e.g., continent fixed effects, island dummy), $\mathbf{\Gamma}$ refers to a vector of institutional factors (e.g., legal origin dummies, a measure of institutional quality), $\mathbf{\Delta}$ incorporates cultural variables (e.g., major religion shares, a measure of ethnic diversity, the share of the country's current population descended from the European continent in 1500 AD), $\mathbf{\Theta}$ is a vector of climatic and health conditions (e.g., the share of a country's land area in tropical zones, absolute latitude, the percentage of population at risk of contracting malaria in the year 1995, and the mean distance to nearest waterway or sea-navigable river). Finally, $\mathbf{X}$ is a vector of agricultural conditions (e.g., arable land area, the time elapsed between when the country began practicing sedentary agriculture and the year 2000), and ε_c is

[11] For a detailed discussion of this issue, see Pagan (1984) and Murphy and Topel (1985).

a country-specific error term.[12]

A positive sign for λ_1 and a negative one for λ_2 would be consistent with the theoretical hump-shaped relationship between the prevalence of novelty-seeking traits and the level of per capita income in a country in the year 2000. This reduced-form result is taken as evidence of the complementary effects of diverse novelty-seeking traits in society and their implications for current standards of living. The beneficial effect would correspond to the role of novelty-seeking individuals in enhancing a society's knowledge frontier.[13] In contrast, a society consisting of a high fraction of novelty-seeking individuals would act as a barrier to economic development. The reason is that these societies, whose main activity is short-run knowledge acquisition, failed to accumulate physical capital in the past, a factor crucial in the development of modern statehood and the transition to modern industrial production. Thus, only societies with intermediate levels of novelty-seeking traits have performed optimally because they effectively exploit the knowledge created by explorative individuals in the production process, whereas the individual or physical costs are borne by a small minority group.

Overall, this paper advances and empirically confirms the hypothesis that the high fraction of novelty-seeking traits in some societies has acted as an obstacle to permanent settlement, leading in turn to reduced capital accumulation. This offers an additional explanation for the high inequalities in income per capita across countries today.

4 Empirical Results

Table 1 presents the results of the extended country sample explaining log GDP per capita in 2000. Column (1) displays the simple bivariate relationship between log GDP per capita in 2000 and the ancestry-adjusted predicted DRD4 exon III expected heterozygosity measure.

< − Table 1 about here − >

The explanatory variable has a positive coefficient that is significant at the 1% level and explains roughly 14% of the variation in log GDP per capita in 2000. Specifically, a one standard

[12] A full description of the variables employed in this study along with bibliographical sources is given in the Appendix.

[13] For example, novelty-seeking, explorative individuals expanded the knowledge frontier of different societies significantly in the pre-industrialized era due to the prevalence of migratory lifestyles. In particular, Khazanov (2003) discusses in depth how nomadic cultures facilitated the transcontinental diffusion of goods, ideas, and technology on the Eurasian landmass by maintaining long-distance trade relationships between sedentary civilizations.

deviation increase in $WH_c^{\widehat{DRD4}}$ (0.0464) is associated with a roughly 67% increase in the level of GDP per capita in 2000.[14] For Iraq, the country with the median GDP per capita level in the 136-country sample (4,138$), this corresponds to an increase of 2,782$ in GDP per capita in the year 2000. Qualitatively, the results suggest a beneficial effect of diverse personality traits on comparative economic development.

In column (2), $WH_c^{\widehat{DRD4}}$ squared is included in the regression in column (1). Interestingly, the estimates suggest no unconditional hump-shaped relationship between log GDP per capita in 2000 and the DRD4 exon III expected heterozygosity measure. This result suggests that the hump-shaped impact of DRD4 exon III expected heterozygosity on economic development might be conditional on other country-specific characteristics, as analyzed in columns (3) to (7).

Column (3) confirms the proposed hump-shaped relationship of DRD4 exon III expected heterozygosity on GDP per capita to the inclusion of controls for the health environment (e.g., the percentage of a country's population in 1995 at risk of contracting malaria and the percentage of a country's land area in tropical zones), and distance to the nearest coastline or sea-navigable river. As expected, distance to the coast or sea-navigable rivers considerably reduces current standards of living due to weaker trade relationships with other countries. Notice that the distance to the coast also captures the vulnerability to colonial powers and thus should be interpreted with caution.[15] For example, as examined by Nunn and Puga (2007) and further analyzed by Nunn (2009), terrain ruggedness in Africa has two countervailing effects on economic development: The negative impact of terrain ruggedness pertains to lower agricultural productivity and goods trade, while the positive effect within African countries is associated with higher protection against colonial powers conducting slave trade. Furthermore, the percentage of tropical land area and the risk of contracting malaria are negatively associated with economic development. Consistent with previous findings in Gallup et al. (1999), this provides evidence of the heavy burden of disease on environments and the resulting limitations on agricultural productivity. More importantly, the hump-shaped effect of DRD4 exon III expected heterozygosity on log GDP per capita in 2000 now becomes statistically significant. The estimated coefficients suggest that increasing DRD4 exon III expected heterozygosity by 1% of the median DRD4 exon III diverse country in the 136-country sample (this corresponds to a 0.00429 change, from the

[14] For example, given the coefficient estimate of $\widehat{\lambda}_1$, the estimated impact on income per capita of a one standard deviation increase in DRD4 exon III expected heterozygosity, $SD\left(WH^{\widehat{DRD4}}\right)$, is calculated according to $\Delta Y/Y = \exp\left[\lambda_1 SD\left(WH^{\widehat{DRD4}}\right)\right] - 1 = \exp(11.082 \times 0.0464) - 1 = 67\%$.

[15] Nunn (2008) empirically examined the detrimental impact of post-Columbian slave trading on the development of African countries.

level of Papua New Guinea where DRD4 exon III expected heterozygosity is 0.429 to the level of Israel where DRD4 exon III expected heterozygosity equals 0.434) would, ceteris paribus, raise its GDP per capita in 2000 by roughly 2%.[16]

The regression analysis examined in column (4) demonstrates the robustness of the hump-shaped result to the inclusion of controls for variables such as climatic factors, distance-based trade costs, and a country's endowments of high-value natural resources. The log of absolute latitude, as a rough measure of climatic characteristics, enters insignificantly into the regression. Given that distance to major markets, measured as the minimum log distance to New York, Rotterdam, or Tokyo have been found to be an important predictor for economic development, its inclusion, as expected, enters with a negative coefficient into the regression. A country's endowment with natural resources (deposits of petroleum and natural gas) displays a positive association with GDP per capita.[17] Moreover, the estimated hump-shaped relationship of DRD4 exon III expected heterozygosity remains relatively unaffected, with a considerable increase in the significance level. The estimated coefficients associated with DRD4 exon III expected heterozygosity evaluated at its median level (0.429) suggest that a 1% increase in this measure (0.00429) would raise GDP per capita in 2000 by roughly 1%.[18]

In column (5), various measures of land productivity are included in the regression. Because land suitability for agriculture and the amount of arable land increases population density, its association with GDP per capita in 2000 is, as expected, negative. This result indicates that a 10% increase in the index for land suitability for agriculture decreases GDP per capita in 2000 by roughly 2%. In other words, if India had the same index of land suitability (an index of 0.5) as in Sweden (an index of 0.08) then its GDP per capita in 2000 would be, ceteris paribus, about 38% ($0.38 \times 1,922\$ = 730\$$) higher. This increase in GDP per capita causes India to move up the income ranking from position 92 to 83 in the 136-country sample. Furthermore, the estimated coefficients on DRD4 exon III diversity remain highly statistically significant and of the expected signs. The findings provide evidence that a 1% increase at the median DRD4 exon III expected heterozygosity measure increases GDP per capita in 2000 by about 1.7%.

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[16]Given the coefficient estimates of $\widehat{\lambda}_1$ and $\widehat{\lambda}_2$, the estimated impact on income per capita of a $\Delta W\widehat{H^{DRD4}}$ change in DRD4 exon III expected heterozygosity at the specified level $\overline{W\widehat{H^{DRD4}}}$ is obtained according to $\Delta Y/Y = \exp\left[\left(\widehat{\lambda}_1 + 2\widehat{\lambda}_2\overline{W\widehat{H^{DRD4}}} + \widehat{\lambda}_2\Delta W\widehat{H^{DRD4}}\right)\Delta W\widehat{H^{DRD4}}\right] - 1$.

[17]However, as discussed by Sachs and Warner (1995b), countries rich in hydrocarbons per capita do not necessarily have higher economic growth rates. Indeed, the authors found a negative impact of natural resources on subsequent economic growth rates.

[18]For example, $\exp\left[(37.964 - 2 \times 41.252 \times 0.429 - 41.252 \times 0.00429) \times 0.00429\right] - 1 = 1.017\%$.

To test and control for the hypothesis of Diamond, who argues that populations residing on the Eurasian landmass experienced the agricultural transition earlier because of their favorable biogeographical situation, the log of the ancestry-adjusted transition to agriculture until the year 2000 across countries is included in the regression as shown in column (6). The estimated coefficient enters negatively into the regression, but is not statistically significant. The negative coefficient is in line with the Malthusian model, since an early transition to agricultural production gave rise to higher population density.[19] The results pertaining to the hump-shaped relationship between log GDP per capita in 2000 and DRD4 exon III expected heterozygosity is maintained further. The estimated coefficients indicate that a 1% change in DRD4 exon III expected heterozygosity around its median value would raise GDP per capita in 2000 by about 1.7%.

< − Table 2 about here − >

Finally, the estimated results are not sensitive to the inclusion of region fixed effects or to the inclusion of an island and OPEC dummy, as reported in column (7). The last column indicates that a 1% change in DRD4 exon III expected heterozygosity around its median value would, once again, increase GDP per capita in 2000 by roughly 1.3%.

Table 2 establishes the hump-shaped relationship between DRD4 exon III expected heterozygosity and comparative economic development to the inclusion of various socioeconomic determinants. Column (1) shows the base specification for the socioeconomic sample. The statistical significance of the estimated coefficients associated with the hump-shaped impact of DRD4 exon III expected heterozygosity on current levels of per capita income is, again, maintained.

The regression analysis in column (2) further confirms the robustness of the hypothesized hump-shaped result to the inclusion of legal origin and major religion shares effects, as proposed by La Porta et al. (1999).

The regression in column (3) is designed to test the robustness of the reduced-form, hump-shaped relationship to the inclusion of an ethnic diversity measure. The statistical significance of the linear and quadratic coefficient associated with DRD4 exon III expected heterozygosity is relatively stable and of the expected signs. Although previous empirical results found an inverse relationship between ethnic diversity and per capita GDP growth, the estimated impact of ethnic diversity on the level of log GDP per capita is statistically insignificant.

[19] Olsson and Paik (2012) go one step further and point to a western reversal since the Neolithic transition. Their main argument was that countries that made the transition to agriculture earlier also tended to develop autocratic, non-egalitarian systems with high social inequality and pervasive rent-seeking behavior.

In order to test the robustness of the results to the reversal of fortune hypothesis proposed by Acemoglu et al. (2001, 2002), column (4) includes the log of population density in 1500 AD in the regression equation. The argument is that countries that were rich in 1500 AD (measured by population density) are now at a disadvantage in terms of economic development. This result would be consistent with European colonization strategies of introducing extractive institutions in densely populated and resource-rich areas, while introducing innovation-enhancing institutions in areas with low population density and biogeographical conditions favorable to European settlement. Indeed, the coefficient associated with log population density in 1500 AD is negative and statistically significant at the 5% level.

Column (5) demonstrates the robustness of the results to the inclusion of a measure of state history. Specifically, log state history refers to a discounted ancestry-adjusted measure of early state development until the year 1500 AD. This measure is primarily intended to measure historical experiences of populations with state formation and centralization. The impact of state history on log GDP per capita in 2000 is positive, but statistically insignificant.

Column (6) illustrates the robustness of the non-linear impact of DRD4 exon III expected heterozygosity on log GDP per capita in 2000 to the inclusion of a measure of institutional quality, as suggested by Acemoglu and Johnson (2005). As expected, the coefficient associated with institutional quality is positive and statistically significant at the 5% level. Higher institutional quality is, therefore, positively associated with the log of GDP per capita in 2000.

The regression analysis shown in column (7) further maintains the hump-shaped relationship of DRD4 exon III expected heterozygosity with economic development, even when controlling for the share of European populations. The positive sign associated with the variable for the share of Europeans is consistent with the notion that not locations but rather populations have had large and persistent impacts on log GDP per capita measured in the year 2000. Interestingly, the coefficients associated with DRD4 exon III expected heterozygosity are affected substantially after including the share of European populations in the regression equation but still remain highly statistically significant.

As shown in column (8), even after including region fixed effects for Sub-Saharan Africa, America, Asia, and Europe in the regression analysis, the hump-shaped relationship between DRD4 exon III expected heterozygosity and log GDP per capita in 2000 remains consistent and relatively stable.

5 Robustness Analysis

The empirical relationship between the ancestry-adjusted DRD4 exon III expected heterozygosity measure and log GDP per capita in the year 2000 may be prone to endogeneity bias arising from large immigration flows into some countries beginning in 1500 AD. Potential endogeneity bias could arise in cases where populations migrated into highly developed or resource-rich countries to engage in explorative activities, therefore creating an empirical artifact in the relationship between novelty-seeking traits in society and current levels of per capita income.

To control for this possibility, the analysis conducted in Table 3 truncates the final specification in Table 2 by regional coverage and the fraction of the current population that can trace its ancestry back to the population of the country in 1500 AD. The specification in column (1) corresponds to that analyzed in specification (8) in Table 2 and is shown for comparison purposes.

< − Table 3 about here − >

Column (2) excludes OECD countries from the analysis, therefore restricting the estimation sample to those countries that were potentially less attractive for immigration. This results in the exclusion of 26 countries from the base sample. The coefficients associated with the DRD4 exon III expected heterozygosity measure remain rather stable.

Column (3) excludes Neo-European countries from the estimation sample (e.g., USA, Canada, Australia, and New Zealand). Again, the estimated coefficients of DRD4 exon III expected heterozygosity remain consistent and precisely estimated.

To further assess the robustness of the results, columns (4) and (5) restrict the analysis to non-Latin American and non-Sub-Saharan African countries, respectively. The exclusion of Latin American countries from the estimation sample is of special interest, because this region experienced a large inflow of immigrants from other regions (especially from the European continent) around the world and therefore may bias the results disproportionately. However, the coefficients associated with the hump-shaped effect of DRD4 exon III expected heterozygosity on current levels of per capita income is further maintained in both cases.

Column (6) only utilizes those countries whose indigenous population is larger than 50% of the current population. This procedure results in the exclusion of 22 countries from the baseline sample. The estimates, however, remain of the expected signs and are precisely estimated. Restricting the analysis to the fraction of indigenous population exceeding 75% of the current population, as shown in column (7), does not affect the main results substantially. Finally, column (8) considers those countries whose indigenous populations exceed 85% of the entire current population. This results in the exclusion of 44 countries from the baseline sample. The coefficients associated with DRD4 exon III expected heterozygosity are of the expected signs and statistically significant at the 5% level.

The theoretical model suggests that increased explorative behavior in society may hamper the accumulation of physical capital and therefore act as an obstacle to permanent settlement, a precursor to modern industrial production. The following Table 4 therefore explores a possible transmission channel of novelty-seeking traits in society to current levels of per capita income. As stated above, the explorative nature of novelty-seeking individuals is a cultural attitude specific to populations with nomadic lifestyles.

< − Table 4 about here − >

These populations, mostly egalitarian in nature, failed to develop advanced political organizations ruled by bureaucrats or chiefs, thus inhibiting the accumulation of physical capital, an important proximate factor for the emergence of modern statehood. The analysis shown in Table 4, column (1), thus investigates the impact of DRD4 exon III expected heterozygosity on the investment share of GDP per capita in 2000 (as a measure of physical capital accumulation) along with other control variables. The results show that the prevalence of novelty-seeking traits in society indeed lowers the accumulation of physical capital. The estimated coefficient states that, ceteris paribus, a one standard deviation change in the 95-country sample under consideration (0.0413) would lower the investment share of GDP per capita in 2000 by about 1.615 percentage points. This impact is precisely estimated and significant at the 1% level. Column (2) establishes the robustness of the results to the inclusion of a measure of ethnic diversity. The negative sign, although imprecisely estimated, provides evidence for pervasive rent-seeking activities in ethnically diverse countries (Easterly and Levine, 1997) leading to lower physical capital accumulation. The estimate in column (3) accounts for the inclusion of a measure of the quality of social infrastructure. Hall and Jones (1999) found that institutional quality and the existence of government policies (which they summarize as social infrastructure) are driving forces in explaining differences in capital accumulation across countries. As expected, the coefficient associated with the social infrastructure variable has a positive sign and is statistically significant at the 10% level. The estimated magnitude associated with DRD4 exon III expected heterozygosity measure remains precisely estimated. Again, a one standard deviation change in this variable (0.0413) would, ceteris paribus, result in a decrease of the investment share to GDP per capita in 2000 by approximately 1.974 percentage points. The estimates in columns (4) and

(5) are designed to control for the log of average years of schooling in the population aged 25 and above during the time period 1960 to 2000, legal origin, and major religion effects. The statistically significant negative sign of DRD4 exon III expected heterozygosity on the investment share is once again maintained. Finally, as shown in column (6), even including region fixed effects in the regression analysis, the negative sign of DRD4 exon III expected heterozygosity remains statistically significant at the 10% level. The corresponding estimate suggests that a one standard deviation change of DRD4 exon III expected heterozygosity (0.0413) would, ceteris paribus, result in a lower investment share of GDP per capita in 2000 by about 1.195 percentage points.

6 Conclusion

This paper contributes to the existing literature on the role of some deep-rooted factors in income inequality across countries today. It provides a theoretical model and empirical evidence on the role of novelty-seeking traits in explorative knowledge acquisition and the implications thereof for current levels of per capita income. The empirical results suggest a hump-shaped relationship between DRD4 exon III expected heterozygosity, a particular gene variant associated with the human personality trait of novelty-seeking behavior, and the level of per capita income in 2000, as proposed by the theoretical model. This result is robust to a broad range of institutional, cultural, and biogeographical factors and across different specifications. The main conclusion is that historical differences in biogeographical endowments across populations exposed humans to strong selective pressure, initiating the rise of location-specific cultural values. Past research has argued that novelty-seeking traits are a cultural attitude mainly observed in populations with a long history of nomadic lifestyles. These populations developed certain production modes in order to enhance reproductive success in otherwise resource-depleted environments. However, the high fraction of novelty-seeking traits in these societies may have acted as an obstacle to permanent settlement, which is a precursor to early state development and modern industrial production. Although, from an evolutionary perspective, novelty-seeking individuals can be seen as extending a population's knowledge frontier, the accumulation of physical capital in these societies may be low due to the higher fraction of individuals engaged in short-run knowledge acquisition than in production. Indeed, in addition to the previous results, the estimates presented here show that the prevalence of novelty-seeking traits in society is negatively correlated with the investment share of GDP per capita in 2000. The findings from this study therefore confirm the existence of an indirect mechanism by which biogeography affects differences in standards of living across countries via the distribution of specific human traits. This highlights the important role of population characteristics-rather than a direct role of locations-in a country's economic development.

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A Regression Tables

Table 1: DRD4 Exon III Expected Heterozygosity and Log GDP per Capita in 2000 (Baseline Results).

	(1)	(2)	(3)	(4)	(5)	(6)	(7)
	Dependent Variable: Log GDP per Capita in 2000						
$W\widehat{H_c^{DRD4}}$	11.082***	-7.334	34.929**	37.964***	47.360***	47.799***	46.059***
	(2.523)	(18.256)	(13.739)	(11.932)	(10.928)	(10.980)	(11.154)
$W\widehat{H_c^{DRD4}}$ squared		21.886	-34.799**	-41.252***	-50.263***	-50.850***	-49.864***
		(21.998)	(15.199)	(13.104)	(12.016)	(12.086)	(12.375)
Distance to Coast or River			-0.560**	-0.533***	-0.438**	-0.440**	-0.173
			(0.218)	(0.183)	(0.201)	(0.200)	(0.216)
Tropical Land Area			-0.682***	-0.485*	-0.234	-0.230	-0.500
			(0.222)	(0.265)	(0.274)	(0.275)	(0.311)
Malaria Index			-1.773***	-1.400***	-1.509***	-1.542***	-1.314***
			(0.209)	(0.184)	(0.179)	(0.225)	(0.354)
Log Absolute Latitude				-0.097	-0.072	-0.070	-0.104
				(0.138)	(0.129)	(0.129)	(0.139)
Log Distance to Major Markets				-0.500***	-0.548***	-0.551***	-0.413***
				(0.087)	(0.094)	(0.095)	(0.111)
Log Hydrocarbons per Person				0.068***	0.054***	0.055***	0.041**
				(0.017)	(0.018)	(0.017)	(0.017)
Log Arable Land Area					-0.083	-0.083	-0.098*
					(0.052)	(0.052)	(0.053)
Log Agricultural Suitability					-0.209***	-0.209**	-0.196**
					(0.081)	(0.082)	(0.084)
Log Transition Timing						-0.053	0.009
						(0.216)	(0.297)
Constant	3.580***	7.406**	0.822	4.769	3.218	3.616	2.452
	(1.137)	(3.744)	(3.079)	(2.986)	(2.777)	(3.308)	(3.606)
Number of Countries	136	136	136	136	136	136	136
R^2	0.139	0.141	0.609	0.723	0.763	0.763	0.786
Continent Effects	No	No	No	No	No	No	Yes
Island Dummy	No	No	No	No	No	No	Yes
OPEC Dummy	No	No	No	No	No	No	Yes

Notes: The dependent variable is the log of real GDP per capita (in constant 2005 international dollars) in the year 2000. ***Independent variables***: $W\widehat{H_c^{DRD4}}$ refers to the ancestry-adjusted DRD4 exon III expected heterozygosity measure for each country applying data from the *World Migration Matrix* since 1500 AD, as reported by Putterman and Weil (2010), to the country-specific predicted DRD4 exon III expected heterozygosity measures. *Distance to Coast or River* is the mean distance (in 1,000 km) to the nearest ice-free coastline or sea-navigable river. *Tropical Land Area* refers to the percentage of a country's land area that is located in the tropics. *Malaria Index* is the fraction of a country's population in 1995 residing in areas contracting with malaria falciparum. *Log Absolute Latitude* is the log absolute value of a country's approximate centroid latitude in decimal degrees. *Log Distance to Major Markets* is the log of the minimum great-circle distance in kilometers from the country's capital city to New York, Rotterdam, or Tokyo. *Log Hydrocarbons per Person* is the log of British thermal units per person of proven crude oil and natural gas reserves in 1993. *Log Arable Land Area* is the log of a country's arable land area, in square kilometers. *Log Agricultural Suitability* is the log of a geospatial indicator, ranging from 0 to 1, of a country's land suitability for agriculture across 5-degree grid cells. *Log Transition Timing* is the log of the time elapsed between when the country began practicing sedentary agriculture and the year 2000 (ancestry-adjusted). *Continent Effects* refer to region dummies for Sub-Saharan Africa, America, Asia and Europe. *OPEC Dummy* takes value 1 for member countries belonging to the Organization of the Petroleum Exporting Countries (OPEC).
Bootstrapped standard errors based on 1,000 replications are reported between parenthesis.
*: Significant at the 10% level. **: Significant at the 5% level. ***: Significant at the 1% level.

Table 2: DRD4 Exon III Expected Heterozygosity and Log GDP per Capita in 2000 (Socioeconomic Sample).

	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)
	Dependent Variable: Log GDP per Capita in 2000							
$W\widehat{H_c^{DRD4}}$	37.098***	41.734***	41.727***	42.906***	43.828***	43.431***	35.952***	36.414***
	(11.290)	(12.292)	(12.351)	(11.911)	(12.014)	(11.339)	(11.479)	(10.010)
$W\widehat{H_c^{DRD4}}$ squared	-38.758***	-46.765***	-46.757***	-48.605***	-49.717***	-50.087***	-42.110***	-41.664***
	(12.360)	(13.511)	(13.579)	(13.186)	(13.324)	(12.659)	(12.640)	(11.060)
Distance to Coast or River	-0.361**	-0.210	-0.210	-0.341**	-0.321*	-0.295*	-0.236	-0.122
	(0.168)	(0.151)	(0.155)	(0.167)	(0.178)	(0.178)	(0.165)	(0.191)
Tropical Land Area	-0.355	-0.372	-0.372	-0.370	-0.352	-0.280	-0.115	-0.075
	(0.248)	(0.243)	(0.244)	(0.232)	(0.234)	(0.243)	(0.240)	(0.267)
Malaria Index	-1.495***	-1.335***	-1.334***	-1.205***	-1.162***	-0.992***	-0.869***	-0.997***
	(0.169)	(0.205)	(0.205)	(0.214)	(0.220)	(0.227)	(0.232)	(0.327)
Log Absolute Latitude	-0.116	0.035	0.034	-0.005	-0.005	-0.048	-0.088	-0.063
	(0.137)	(0.147)	(0.150)	(0.151)	(0.153)	(0.151)	(0.150)	(0.148)
Log Distance to Major Markets	-0.550***	-0.477***	-0.477***	-0.583***	-0.574***	-0.573***	-0.478***	-0.491***
	(0.098)	(0.085)	(0.086)	(0.113)	(0.115)	(0.119)	(0.110)	(0.106)
Log Hydrocarbons per Person	0.049***	0.062***	0.062***	0.062***	0.060***	0.067***	0.065***	0.034**
	(0.017)	(0.016)	(0.016)	(0.015)	(0.016)	(0.017)	(0.016)	(0.016)
Ethnic Diversity			-0.006	-0.139	-0.131	-0.110	-0.234	-0.119
			(0.335)	(0.322)	(0.325)	(0.329)	(0.305)	(0.334)
Log Population Density 1500				-0.136**	-0.139**	-0.144**	-0.138**	-0.179**
				(0.057)	(0.058)	(0.060)	(0.056)	(0.080)
Log State History 1500					0.470	0.436	0.550	0.654
					(0.875)	(0.855)	(0.857)	(0.851)
Institutions						0.111**	0.094**	0.089*
						(0.046)	(0.046)	(0.052)
European Population							0.765***	1.294**
							(0.284)	(0.584)
Constant	5.042*	4.339	4.341	5.585*	5.144*	4.918*	5.516**	5.311**
	(2.858)	(2.970)	(2.978)	(2.997)	(3.046)	(2.878)	(2.744)	(2.488)
Number of Countries	127	127	127	127	127	127	127	127
R^2	0.736	0.800	0.800	0.813	0.814	0.823	0.837	0.869
Continent Effects	No	No	No	No	No	No	No	Yes
Island Dummy	No	No	No	No	No	No	No	Yes
OPEC Dummy	No	No	No	No	No	No	No	Yes
Legal Origin Effects	No	Yes	Yes	Yes	Yes	Yes	Yes	Yes
Major Religion Effects	No	Yes	Yes	Yes	Yes	Yes	Yes	Yes

Notes: The dependent variable is the log of real GDP per capita (in constant 2005 international dollars) in the year 2000.

Independent variables: $W\widehat{H_c^{DRD4}}$ refers to the ancestry-adjusted DRD4 exon III expected heterozygosity measure for each country applying data from the *World Migration Matrix* since 1500 AD, as reported by Putterman and Weil (2010), to the country-specific predicted DRD4 exon III expected heterozygosity measures. *Distance to Coast or River* is the mean distance (in 1,000 km) to the nearest ice-free coastline or sea-navigable river. *Tropical Land Area* refers to the percentage of a country's land area that is located in the tropics. *Malaria Index* is the fraction of a country's population in 1995 residing in areas contracting with malaria falciparum. *Log Absolute Latitude* is the log absolute value of a country's approximate centroid latitude in decimal degrees. *Log Distance to Major Markets* is the log of the minimum great-circle distance in kilometers from the country's capital city to New York, Rotterdam, or Tokyo. *Log Hydrocarbons per Person* is the log of British thermal units per person of proven crude oil and natural gas reserves in 1993. *Ethnic Diversity* is the probability that two randomly chosen individuals from the same country will belong to different ethnic groups. *Log Population Density 1500* is the log of population density in 1500 AD, expressed in persons per square kilometer. *Log State History 1500* measures the experience of present day countries with early state formation from 1 AD to 1500 AD (ancestry-adjusted). *Institutions* is a seven-category scale, indicating the constraint on executive power, ranging from 1 to 7, with higher scores indicating better institutional quality (average values from 1900 to 2000). *European Population* is the share of a country's current population in the year 2000 descended from the European continent in the year 1500 AD. *Continent Effects* refer to region dummies for Sub-Saharan Africa, America, Asia and Europe. *OPEC Dummy* takes value 1 for member countries belonging to the Organization of the Petroleum Exporting Countries (OPEC). *Legal Origin Effects* refer to dummy variables for British, French, German or Socialist legal origin. *Major Religion Shares*, measured in percent, for Muslim, Catholic, and Protestant religions.

Bootstrapped standard errors based on 1,000 replications are reported between parenthesis.

*: Significant at the 10% level. **: Significant at the 5% level. ***: Significant at the 1% level.

Table 3: DRD4 Exon III Expected Heterozygosity and Log GDP per Capita in 2000 (Robustness to Regional Coverage and Population Structure).

	(1) Full Sample	(2) Non OECD	(3) Without New World	(4) Without Latin America	(5) Without Sub-Saharan Africa	(6) Indigenous > 50%	(7) Indigenous > 75%	(8) Indigenous > 85%
	Dependent Variable: Log GDP per Capita in 2000							
$WH_c^{\widehat{DRD4}}$	36.414***	43.501***	40.824***	36.448***	36.182***	36.469***	32.501***	28.405**
	(10.010)	(11.407)	(10.538)	(10.326)	(13.549)	(10.589)	(12.184)	(12.608)
$WH_c^{\widehat{DRD4}}$ squared	-41.664***	-51.238***	-47.378***	-41.844***	-40.802***	-41.658***	-35.793***	-30.192**
	(11.060)	(12.991)	(11.708)	(11.850)	(14.792)	(12.028)	(13.589)	(14.124)
Distance to Coast or River	-0.122	-0.173	-0.115	-0.108	-0.052	-0.149	-0.066	-0.097
	(0.191)	(0.277)	(0.211)	(0.227)	(0.244)	(0.258)	(0.271)	(0.269)
Tropical Land Area	-0.075	-0.031	-0.052	-0.073	-0.279	0.006	-0.117	-0.165
	(0.267)	(0.331)	(0.283)	(0.358)	(0.446)	(0.333)	(0.517)	(0.542)
Malaria Index	-0.997***	-0.889**	-0.911***	-0.867**	-1.062**	-0.760*	-0.536	-0.523
	(0.327)	(0.358)	(0.331)	(0.390)	(0.494)	(0.405)	(0.461)	(0.467)
Log Absolute Latitude	-0.063	-0.121	-0.074	-0.185	-0.035	-0.115	-0.146	-0.163
	(0.148)	(0.154)	(0.147)	(0.168)	(0.234)	(0.165)	(0.262)	(0.267)
Log Distance to Major Markets	-0.491***	-0.867**	-0.660***	-0.664***	-0.389***	-0.665***	-0.644***	-0.620***
	(0.106)	(0.339)	(0.138)	(0.150)	(0.108)	(0.163)	(0.172)	(0.186)
Log Hydrocarbons per Person	0.034**	0.041	0.038**	0.033	0.029	0.042*	0.036	0.041
	(0.016)	(0.025)	(0.017)	(0.020)	(0.020)	(0.022)	(0.028)	(0.028)
Ethnic Diversity	-0.119	-0.104	-0.113	-0.194	-0.174	-0.002	-0.304	-0.193
	(0.334)	(0.465)	(0.371)	(0.432)	(0.394)	(0.433)	(0.473)	(0.492)
Log Population Density 1500	-0.179**	-0.252**	-0.225**	-0.237**	-0.159*	-0.259***	-0.260**	-0.260**
	(0.080)	(0.104)	(0.091)	(0.097)	(0.094)	(0.094)	(0.108)	(0.113)
Log State History 1500	0.654	0.301	0.662	0.547	0.991	0.910	0.907	0.451
	(0.851)	(0.942)	(0.899)	(0.916)	(1.174)	(1.031)	(1.111)	(1.111)
Institutions	0.089*	0.105	0.093*	0.141**	0.022	0.087	0.131*	0.121*
	(0.052)	(0.064)	(0.052)	(0.059)	(0.067)	(0.056)	(0.070)	(0.073)
European Population	1.294**	1.461	1.288*	2.071*	1.229*	2.262	3.328	1.542
	(0.584)	(0.916)	(0.718)	(1.187)	(0.717)	(2.011)	(3.535)	(4.760)
Constant	5.311**	6.046	5.643**	6.572**	3.953	6.479**	7.169**	8.213**
	(2.488)	(3.722)	(2.692)	(2.620)	(3.541)	(2.824)	(3.513)	(3.697)
Number of Countries	127	101	123	107	91	105	87	83
R^2	0.869	0.779	0.863	0.892	0.844	0.887	0.904	0.909
Continent Effects	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes
Island Dummy	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes
OPEC Dummy	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes
Legal Origin Effects	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes
Major Religion Effects	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes

Notes: The dependent variable is the log of real GDP per capita (in constant 2005 international dollars) in the year 2000.
Independent variables: $WH_c^{\widehat{DRD4}}$ refers to the ancestry-adjusted DRD4 exon III expected heterozygosity measure for each country applying data from the *World Migration Matrix* since 1500 AD, as reported by Putterman and Weil (2010), to the country-specific predicted DRD4 exon III expected heterozygosity measures. *Distance to Coast or River* is the mean distance (in 1,000 km) to the nearest ice-free coastline or sea-navigable river. *Tropical Land Area* refers to the percentage of a country's land area that is located in the tropics. *Malaria Index* is the fraction of a country's population in 1995 residing in areas contracting with malaria falciparum. *Log Absolute Latitude* is the log absolute value of a country's approximate centroid latitude in decimal degrees. *Log Distance to Major Markets* is the log of the minimum great-circle distance in kilometers from the country's capital city to New York, Rotterdam, or Tokyo. *Log Hydrocarbons per Person* is the log of British thermal units per person of proven crude oil and natural gas reserves in 1993. *Ethnic Diversity* is the probability that two randomly chosen individuals from the same country will belong to different ethnic groups. *Log Population Density 1500* is the log of population density in 1500 AD, expressed in persons per square kilometer. *Log State History 1500* measures the experience of present day countries with early state formation from 1 AD to 1500 AD (ancestry-adjusted). *Institutions* is a seven-category scale, indicating the constraint on executive power, ranging from 1 to 7, with higher scores indicating better institutional quality (average values from 1900 to 2000). *European Population* is the share of a country's current population in the year 2000 descended from the European continent in the year 1500 AD. *Continent Effects* refer to region dummies for Sub-Saharan Africa, America, Asia and Europe. *OPEC Dummy* takes value 1 for member countries belonging to the Organization of the Petroleum Exporting Countries (OPEC). *Legal Origin Effects* refer to dummy variables for British, French, German or Socialist legal origin. *Major Religion Shares*, measured in percent, for Muslim, Catholic, and Protestant religions.
Bootstrapped standard errors based on 1,000 replications are reported between parenthesis.
*: Significant at the 10% level. **: Significant at the 5% level. ***: Significant at the 1% level.

Table 4: DRD4 Exon III Expected Heterozygosity and Investment Share of GDP per Capita in 2000.

	(1)	(2)	(3)	(4)	(5)	(6)
	Dependent Variable: Investment Share of GDP per Capita in 2000					
$WH_c^{\widehat{DRD4}}$	-39.114***	-37.997***	-47.794***	-46.286***	-43.681***	-28.945*
	(12.817)	(12.832)	(14.511)	(14.329)	(15.432)	(16.469)
Distance to Coast or River	-2.218	-1.979	-1.782	-2.114	-1.511	-1.451
	(3.066)	(3.288)	(3.305)	(3.375)	(3.630)	(4.279)
Tropical Land Area	-3.763	-3.823	-2.829	-3.095	-2.557	-5.121
	(2.857)	(2.883)	(3.003)	(3.020)	(3.115)	(3.769)
Malaria Index	-10.536***	-10.080***	-8.497***	-9.131***	-9.083**	-10.576
	(2.865)	(2.813)	(2.953)	(3.253)	(3.816)	(6.488)
Log Absolute Latitude	-0.575	-0.741	-0.483	-0.604	-0.344	0.474
	(1.308)	(1.391)	(1.366)	(1.347)	(1.504)	(1.615)
Log Distance to Major Markets	-0.563	-0.487	0.525	0.542	0.775	0.134
	(0.690)	(0.699)	(0.919)	(0.900)	(1.017)	(1.238)
Log Hydrocarbons per Person	-0.078	-0.074	-0.079	-0.076	-0.055	-0.253
	(0.187)	(0.187)	(0.193)	(0.194)	(0.221)	(0.208)
Log Arable Land Area	-0.582	-0.549	-0.440	-0.433	-0.526	-0.674
	(0.569)	(0.576)	(0.550)	(0.552)	(0.681)	(0.715)
Ethnic Diversity		-1.967	-2.684	-2.812	-3.689	-3.808
		(3.471)	(3.585)	(3.634)	(3.909)	(4.147)
Social Infrastructure			8.696*	9.849**	10.683*	15.951**
			(4.774)	(4.939)	(6.168)	(7.673)
Log Years of Schooling				-0.975	-0.965	-2.721
				(1.669)	(2.381)	(2.564)
Constant	55.723***	55.406***	45.043***	45.701***	37.871**	35.633*
	(11.994)	(12.352)	(13.426)	(13.505)	(18.270)	(20.583)
Number of Countries	95	95	95	95	95	95
R^2	0.384	0.386	0.416	0.419	0.436	0.544
Continent Effects	No	No	No	No	No	Yes
Island Dummy	No	No	No	No	No	Yes
OPEC Dummy	No	No	No	No	No	Yes
Legal Origin Effects	No	No	No	No	Yes	Yes
Major Religion Effects	No	No	No	No	Yes	Yes

Notes: The dependent variable is the ratio of investment share of GDP per capita (in constant 2005 international dollars) in the year 2000, measured in %.
Independent variables: $WH_c^{\widehat{DRD4}}$ refers to the ancestry-adjusted DRD4 exon III expected heterozygosity measure for each country applying data from the *World Migration Matrix* since 1500 AD, as reported by Putterman and Weil (2010), to the country-specific predicted DRD4 exon III expected heterozygosity measures. *Distance to Coast or River* is the mean distance (in 1,000 km) to the nearest ice-free coastline or sea-navigable river. *Tropical Land Area* refers to the percentage of a country's land area that is located in the tropics. *Malaria Index* is the fraction of a country's population in 1995 residing in areas contracting with malaria falciparum. *Log Absolute Latitude* is the log absolute value of a country's approximate centroid latitude in decimal degrees. *Log Distance to Major Markets* is the log of the minimum great-circle distance in kilometers from the country's capital city to New York, Rotterdam, or Tokyo. *Log Hydrocarbons per Person* is the log of British thermal units per person of proven crude oil and natural gas reserves in 1993. *Log Arable Land Area* is the log of a country's arable land area, in square kilometers. *Ethnic Diversity* is the probability that two randomly chosen individuals from the same country will belong to different ethnic groups. *Social Infrastructure* is an index reflecting the quality of institutions and government policies that promotes the accumulation of physical and human capital. *Log Years of Schooling* is the log of average schooling years in the total population aged 25 and above, taken as mean value during the years 1960 to 2000 across five-years observations. *Continent Effects* refer to region dummies for Sub-Saharan Africa, America, Asia and Europe. *OPEC Dummy* takes value 1 for member countries belonging to the Organization of the Petroleum Exporting Countries (OPEC). *Legal Origin Effects* refer to dummy variables for British, French, German or Socialist legal origin. *Major Religion Shares*, measured in percent, for Muslim, Catholic, and Protestant religions.
Bootstrapped standard errors based on 1,000 replications are reported between parenthesis.
*: Significant at the 10% level. **: Significant at the 5% level. ***: Significant at the 1% level.

B Descriptive Statistics

Table 5: Summary Statistics for the 136-Country Sample.

	Obs.	Mean	S.D.	Min.	Max.
Log GDP per Capita in 2000	136	8.3303	1.3804	5.1918	11.0303
$WH_c^{\widehat{DRD4}}$	136	0.4286	0.0464	0.2722	0.5536
$WH_c^{\widehat{DRD4}}$ squared	136	0.1859	0.0392	0.0741	0.3065
Distance to Coast or River	136	0.3728	0.4704	0.0205	2.3856
Tropical Land Area	136	0.3018	0.4023	0.0000	1.0000
Malaria Index	136	0.3277	0.4321	0.0000	1.0000
Log Absolute Latitude	136	2.9851	0.9637	0.0000	4.1589
Log Distance to Major Markets	136	8.0313	0.9192	4.9416	9.1399
Log Hydrocarbons per Person	136	0.9096	4.5572	-4.6052	10.5947
Log Arable Land Area	136	10.1688	1.6128	4.6031	14.3813
Log Agricultural Suitability	136	-1.4016	1.2596	-5.8569	-0.0408
Log Transition Timing	136	8.4865	0.4511	7.2130	9.2496

Table 6: Pairwise Correlations for the 136-Country Sample.

	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)	(11)	(12)
(1) Log GDP per Capita in 2000	1.0000											
(2) $WH_c^{\widehat{DRD4}}$	0.3725	1.0000										
(3) $WH_c^{\widehat{DRD4}}$ squared	0.3754	0.9967	1.0000									
(4) Distance to Coast or River	-0.3272	-0.4511	-0.4469	1.0000								
(5) Tropical Land Area	-0.4247	0.1352	0.1206	-0.1418	1.0000							
(6) Malaria Index	-0.7133	-0.2226	-0.2371	0.1379	0.5270	1.0000						
(7) Log Absolute Latitude	0.5285	0.1533	0.1651	-0.0450	-0.7491	-0.6580	1.0000					
(8) Log Distance to Major Markets	-0.6349	-0.3872	-0.4009	0.2340	0.3639	0.4692	-0.5228	1.0000				
(9) Log Hydrocarbons per Person	0.3512	-0.0699	-0.0714	0.0978	-0.1725	-0.2546	0.0759	-0.0577	1.0000			
(10) Log Arable Land Area	-0.0427	0.0565	0.0525	0.2731	-0.1110	-0.0790	0.1105	-0.1028	0.2118	1.0000		
(11) Log Agricultural Suitability	-0.0968	0.4021	0.3955	-0.2625	0.2960	-0.0425	-0.0401	-0.1583	-0.3524	0.1826	1.0000	
(12) Log Transition Timing	0.5163	0.0888	0.0923	-0.0992	-0.3623	-0.6580	0.4482	-0.3594	0.3204	0.0910	-0.0418	1.0000

Table 7: Summary Statistics for the 127-Country Sample.

	Obs.	Mean	S.D.	Min.	Max.
Log GDP per Capita in 2000	127	8.2809	1.3571	5.1918	10.7221
$WH_c^{\widehat{DRD4}}$	127	0.4292	0.0465	0.2722	0.5536
$WH_c^{\widehat{DRD4}}$ squared	127	0.1864	0.0391	0.0741	0.3065
Distance to Coast or River	127	0.3892	0.4810	0.0205	2.3856
Tropical Land Area	127	0.3087	0.4027	0.0000	1.0000
Malaria Index	127	0.3234	0.4309	0.0000	1.0000
Log Absolute Latitude	127	2.9726	0.9808	0.0000	4.1589
Log Distance to Major Markets	127	8.0289	0.9083	4.9416	9.1399
Log Hydrocarbons per Person	127	0.7135	4.4320	-4.6052	9.1361
Ethnic Diversity	127	0.4617	0.2602	0.0020	0.9302
Log Population Density 1500	127	0.9179	1.4991	-3.8170	3.8424
Log State History 1500	127	0.2000	0.1184	0.0000	0.4305
Institutions	127	4.5718	2.0623	1.0000	7.0000
European Population	127	0.3415	0.4213	0.0000	1.0000

Table 8: Pairwise Correlations for the 127-Country Sample.

	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)	(11)	(12)	(13)	(14)
(1) Log GDP per Capita in 2000	1.0000													
(2) $WH_c^{\widehat{DRD4}}$	0.4252	1.0000												
(3) $WH_c^{\widehat{DRD4}}$ squared	0.4290	0.9965	1.0000											
(4) Distance to Coast or River	-0.3156	-0.4708	-0.4676	1.0000										
(5) Tropical Land Area	-0.3895	0.1298	0.1155	-0.1649	1.0000									
(6) Malaria Index	-0.7223	-0.2218	-0.2368	0.1369	0.5169	1.0000								
(7) Log Absolute Latitude	0.5212	0.1454	0.1569	-0.0295	-0.7479	-0.6555	1.0000							
(8) Log Distance to Major Markets	-0.6669	-0.3618	-0.3756	0.2364	0.3708	0.4626	-0.5190	1.0000						
(9) Log Hydrocarbons per Person	0.3094	-0.0268	-0.0283	0.1252	-0.1379	-0.2701	0.0681	-0.0843	1.0000					
(10) Ethnic Diversity	-0.5558	-0.2863	-0.2939	0.2746	0.3438	0.5918	-0.5414	0.4568	-0.0648	1.0000				
(11) Log Population Density 1500	0.0511	0.1272	0.1264	-0.3364	0.0117	-0.0008	0.0587	-0.3823	-0.0937	-0.2257	1.0000			
(12) Log State History 1500	0.4407	0.1007	0.1134	-0.2006	-0.4070	-0.5346	0.4435	-0.3961	0.2637	-0.3791	0.2524	1.0000		
(13) Institutions	0.6159	0.4529	0.4639	-0.3731	-0.2367	-0.4908	0.3874	-0.4162	-0.1308	-0.4526	0.0653	0.1839	1.0000	
(14) European Population	0.7248	0.4587	0.4651	-0.2763	-0.3596	-0.5930	0.5245	-0.5923	0.0521	-0.4712	0.0739	0.2120	0.6172	1.0000

Table 9: Summary Statistics for the 95-Country Investment Sample.

	Obs.	Mean	S.D.	Min.	Max.
Investment Share of GDP per Capita in 2000	95	20.9875	8.0513	1.4354	47.9185
$WH_c^{\widehat{DRD4}}$	95	0.4351	0.0413	0.3483	0.5536
Distance to Coast or River	95	0.3063	0.3301	0.0205	1.4667
Tropical Land Area	95	0.3478	0.4164	0.0000	1.0000
Malaria Index	95	0.3283	0.4249	0.0000	1.0000
Log Absolute Latitude	95	2.8480	1.0495	0.0000	4.1589
Log Distance to Major Markets	95	8.0060	1.0250	4.9416	9.1399
Log Hydrocarbons per Person	95	0.9382	4.3530	-4.6052	9.1361
Log Arable Land Area	95	10.3824	1.4880	7.6197	14.3813
Ethnic Diversity	95	0.4371	0.2661	0.0020	0.9302
Social Infrastructure	95	0.4666	0.2481	0.1127	1.0000
Log Years of Schooling	95	1.2995	0.7225	-0.7558	2.4370

Table 10: Pairwise Correlations for the 95-Country Investment Sample.

	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)	(11)	(12)
(1) Investment Share of GDP per Capita in 2000	1.0000											
(2) $WH_c^{\widehat{DRD4}}$	0.1070	1.0000										
(3) Distance to Coast or River	-0.2878	-0.4490	1.0000									
(4) Tropical Land Area	-0.4012	-0.0299	-0.0063	1.0000								
(5) Malaria Index	-0.5635	-0.4544	0.4791	0.4935	1.0000							
(6) Log Absolute Latitude	0.4103	0.2994	-0.3012	-0.7550	-0.6432	1.0000						
(7) Log Distance to Major Markets	-0.2866	-0.4249	0.2651	0.3968	0.4609	-0.5332	1.0000					
(8) Log Hydrocarbons per Person	0.0888	0.0466	-0.0428	-0.1470	-0.2507	0.0660	-0.1178	1.0000				
(9) Log Arable Land Area	-0.0199	-0.0197	0.2516	-0.2498	-0.1417	0.2057	-0.1167	0.3243	1.0000			
(10) Ethnic Diversity	-0.4317	-0.3093	0.4507	0.4123	0.6386	-0.6108	0.4650	-0.0609	0.0166	1.0000		
(11) Social Infrastructure	0.4432	0.4898	-0.3317	-0.3936	-0.5826	0.4730	-0.6728	0.1448	0.0409	-0.4103	1.0000	
(12) Log Years of Schooling	0.4253	0.4869	-0.4704	-0.3880	-0.7217	0.4712	-0.4965	0.1977	0.0493	-0.5010	0.7071	1.0000

C Data Description and Sources

Log GDP per Capita in 2000. PPP converted real GDP per capita, in constant 2005 international dollars, from the Penn World Tables, Version 7.1 (Heston et al., 2012). The data is available at https://pwt.sas.upenn.edu/.

DRD4 Exon III Expected Heterozygosity Measure. The expected heterozygosity measure from observed DRD4 exon III allele frequencies across populations. This measure corresponds to the probability that two randomly selected individuals from the same population will differ with respect to the DRD4 exon III gene. See also Gören (2014) for more details. The full list of sampled populations along with bibliographical sources is available from the author upon request.

Predicted DRD4 Exon III Expected Heterozygosity Measure (Ancestry-Adjusted). The ancestry-adjusted DRD4 exon III expected heterozygosity measure on the country level. This measure is constructed by applying the coefficient estimates in a logistic regression model between observed DRD4 exon III expected heterozygosity as the dependent variable and population-specific biogeographical indicators and migratory distance from East Africa as explanatory variables. Based on the coefficient estimates from this first-stage regression, the second step in the regression analysis deals with the construction of DRD4 exon III expected heterozygosity measures on the country level $\left(\widehat{H_c^{DRD4}}\right)$ by replacing the biogeographical characteristics on the population level with those on the country level. Since countries in the post-Columbian era have experienced large migration flows from other countries across the world, an ancestry-adjusted DRD4 exon III expected heterozygosity measure for each country is constructed based on post-1500 population flows data. This ancestry-adjusted measure then corresponds to $W\widehat{H_c^{DRD4}} = \sum_{m \in A} w_{cm} \widehat{H_m^{DRD4}}$, where w_{cm} refers to the share of a country's c population in the year 2000 that is descended from populations in country m due to migration since 1500 AD, and A is the set of countries from which data on immigration flows are available. The data source for the ancestral populations in each country is the *World Migration Matrix*, as reported by Putterman and Weil (2010). The interested reader is referred to Gören (2014) for more details in the relationship between novelty-seeking traits, biogeographical indicators, and migratory distance from East Africa.

Absolute Latitude. The absolute value of a country's approximate centroid latitude in decimal degrees. The data source for the country's representative latitude is from the CIA's *The World Factbook*, which is available at https://www.cia.gov/library/publications/the-world-factbook/.

Land Suitability for Agriculture. A geospatial indicator, ranging from 0 to 1, of land suitability for agriculture on the country level. The raw data are provided in high resolution gridded form of 0.5 decimal degrees latitude $\times$ longitude by Ramankutty et al. (2002). This index represents the probability that a particular grid cell will be cultivated. The measures of land suitability for agriculture are based on indicators of climatic suitability, S_{clim}, (e.g., growing degree days (GDD) and a moisture index (α), capturing the availability of water to plants) and soil suitability for cultivation, S_{soil}, (e.g., soil carbon density (C_{soil}) and an indicator (pH_{soil}) capturing the extent of acidic or alkaline soil characteristics). The land suitability index for agriculture is then constructed as $S = S_{clim} \times S_{soil}$, where the functional forms for S_{clim} and S_{soil} are derived from probability density functions of actual cropland area, A_{crop}, versus each component in GDD, α, C_{soil}, and pH_{soil}, respectively. Ramankutty et al. (2002) have chosen empirically fitted sigmoidal functions given by $S_{clim} = f_1(GDD) \times f_2(\alpha)$ and $S_{soil} = g_1(C_{soil}) \times g_2(pH_{soil})$, respectively. Specifically, $f_1(GDD) = \frac{1}{[1+e^{a(b-GDD)}]}$ and $f_2(\alpha) = \frac{1}{[1+e^{c(d-\alpha)}]}$, with $a = 0.0052$, $b = 1334$, $c = 14.705$, and $d = 0.3295$. The empirically fitted functions for $g_1(C_{soil})$ and $g_2(pH_{soil})$ are given by $g_1(C_{soil}) = \frac{a}{[1+e^{b(c-C_{soil})}]} \times \frac{a}{[1+e^{d(e-C_{soil})}]}$, with $a = 3.9157$, $b = 1.3766$, $c = 3.468$, $d = -0.0791$, $e = -27.33$, and

$$g_2(pH_{soil}) = \begin{cases} -2.085 + 0.475pH_{soil}, & if \quad pH_{soil} \leq 6.5, \\ 1.0, & if \quad 6.5 < pH_{soil} \leq 8, \\ 1.0 - 2.0pH_{soil}, & if \quad pH_{soil} \geq 8. \end{cases}$$

The raw data are available online at the Center for Sustainability and the Global Environment (SAGE), http://www.sage.wisc.edu, at the University of Wisconsin. The values for the cross-country analysis are constructed by intersecting the global grid cells with data on the location that are covered by each country. The variable is obtained from the data set of Michalopoulos (2012).

Distance to Coast or River. The mean distance (in 1,000 km) from a 1-degree grid cell to the nearest ice-free coastline or sea-navigable river, averaged across grid cells within each country. This variable was firstly discussed by Gallup et al. (1999) and is part of *The Center for International Development* at Harvard University. The variable is available at http://www.cid.harvard.edu/economic.htm.

Tropical Land Area. The percentage of a country's land area that is located in the tropics. This variable was firstly discussed by Gallup et al. (1999) and is part of *The Center for International Development* at Harvard University. The variable is available at http://www.cid.harvard.edu/economic.htm.

Malaria Index. The fraction of a country's population in 1995 residing in areas contracting with *malaria falciparum*. This variable is discussed, in depth, in the study of Gallup and Sachs (2001) and is part of *The Center for International Development* at Harvard University. The variable is available at http://www.cid.harvard.edu/economic.htm.

Log Distance to Major Markets. The log of the minimum great-circle distance in kilometers to one of the three capital-goods-supplying regions: the United States, Western Europe, or Japan, measured as distance from the country's capital city to New York, Rotterdam, or Tokyo. This variable is discussed in Gallup et al. (1999) and is part of *The Center for International Development* at Harvard University. The variable is available at http://www.cid.harvard.edu/economic.htm.

Log Hydrocarbons per Person. The log of British thermal units per person of proven crude oil and natural gas reserves in 1993, from the World Resources Institute (WRI 1996). This variable was originally discussed in Gallup et al. (1999) and is part of *The Center for International Development* at Harvard University. The variable is available at http://www.cid.harvard.edu/economic.htm.

Log Arable Land Area. The log of a country's arable land area, in square kilometers, as reported by the World Bank's *World Development Indicators*. This variable is adopted from Ashraf and Galor (2013).

Log Transition Timing (Ancestry-Adjusted). The log of the time elapsed between when the country began practicing sedentary agriculture and the year 2000. A correction for world migrations since 1500 AD is constructed from the Putterman and Weil (2010) *World Migration Matrix* data. See also Putterman (2008) for a detailed treatment of this more sophisticated measure, which is related to Diamond's hypothesis of early agricultural transition. This variable is adopted from Ashraf and Galor (2013).

Ethnic Diversity. A measure of ethnic diversity, capturing the probability that two randomly chosen individuals from the *same* country will belong to different ethnic groups. The measures are constructed by Alesina et al. (2003).

Log Population Density 1500. The log of population density in 1500 AD, expressed in persons per square kilometer. Population data is reported by McEvedy and Jones (1978), and data on total land area for the country's contemporary borders is reported by the World Bank's *World Development Indicators*. The interested reader is referred to Ashraf and Galor (2013) for further details in the construction of this variable.

Log State History 1500 (Ancestry-Adjusted). This variable measures the experience of present day countries with early state formation. The data for the ancestry-adjusted measure of state history from 1 to 1500 AD is constructed as follows: The data of state history, as discussed in Chanda and Putterman (2007), begin in 1 AD and continue in half-century intervals until the year 1500 AD. When constructing the index, more weights are assigned to most recent half-centuries of state experiences and earlier half-centuries are discounted by 5% $\left(\text{e.g.}, \frac{1}{[1.05]}, \frac{1}{[1.05]^2}, \text{etc.}\right)$. This measure is then normalized to be in the range of 0 (the lowest possible experience of early state formation) and 1 (the highest possible experience with early state formation) making it easier to interpret. Finally, an ancestry-adjusted measure of early state formation for each country is constructed based on post-1500 population flows data, as reported by Putterman and Weil (2010).

Institutions. A seven-category scale, indicating the constraint on executive power, ranging from 1 to 7, with higher scores indicating better institutional quality (average values from 1900 to 2000), as reported by the Polity IV data set. This measure is adopted from Acemoglu and Johnson (2005).

Social Infrastructure. An index constructed by Hall and Jones (1999), reflecting the quality of institutions and government policies within a socioeconomic system that promotes productive activities and the accumulation of physical and human capital. This index combines data from two, equally-weighted, main sources. The first is an index of government antidiversion policies (*GADP*) assembled by the *International Country Risk Guide* for the period 1986 to 1995, based on five categories: (i) law and order, (ii) bureaucratic quality, (iii) corruption, (iv) risk of expropriation, and (v) government repudiation of contracts. The average value of these five variables constitute the index *GADP*. This index is bounded between zero and one, where higher values indicate more effective policies for supporting production. The second is a trade openness index, compiled by Sachs and Warner (1995a), indicating the fraction of years that a particular country has been open for international trade during the years 1950 to 1994. The decision whether a country fulfills the requirement of free open trade in each year is based on the following five criteria: (i) non-tariff barriers cover less than 40%, (ii) average tariff rates are less than 40%, (iii) any black market premium was less than 20% during the 1970s and 1980s, (iv) the country is non-socialist, and (v) the government does not monopolize major exports.

Log Years of Schooling. The log of average schooling years in the total population aged 25 and above, taken as mean value during the years 1960 to 2000 across five-years observations. The data were taken from Barro and Lee (2013).

Share of European Population. The share of a country's current population in the year 2000 descended from the European continent in the year 1500 AD, as reported in the *World Migration Matrix* of Putterman and Weil (2010). This measure is adopted from Ashraf and Galor (2013).

Share of Indigenous Population. The share of a country's current population descended from the within country 1500 AD population, as reported in the *World Migration Matrix* of Putterman and Weil (2010). This measure is adopted from Ashraf and Galor (2013).

Legal Origin Dummies. Legal Origin Dummies for British, French, German or Socialist legal origin, as reported by La Porta et al. (1999).

Major Religion Shares. The major religion shares, measured in percent, for Muslim, Catholic, and Protestant religions, as reported by La Porta et al. (1999).

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