Geography, biogeography, and why some countries are rich and others are poor

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The most important event in human economic history before the industrial revolution was the Neolithic transition from a nomadic hunter-gatherer lifestyle to sedentary agriculture, beginning ≈10,000 years ago. The transition made possible the human population explosion, the rise of non-food-producing specialists, and the acceleration of technological progress that led eventually to the industrial revolution. But the transition occurred at different times in different regions of the world, with big consequences for the present-day economic conditions of populations indigenous to each region. In this article, we show that differences in biogeographic initial conditions and in geography largely account for the different timings of the Neolithic transition and, thereby, ultimately help account for the 100-fold differences among the prosperity of nations today. The effects of biogeography and geography on the wealth of nations are partly mediated by the quality of present-day institutions but also are partly independent of institutional quality.

The prosperity of nations varies enormously. If one ranks countries by their per capita incomes, those in the top 10% are on average ≈30 times richer than those in the bottom 10%. The richest country is >100 times more prosperous than the poorest (www.worldbank.org/data). How can this large variation in the wealth of nations be explained?

Traditionally, economists emphasize the accumulation of human and physical capital and successful adoption of state-of-the-art technologies as the main explanations of variation in economic productivity (1). Recently, however, economists have begun to regard those explanations as proximate ones and to appreciate the role of deeper institutional explanations of those proximate factors. Capital accumulation and technology adoption are now commonly viewed as proximate variables molded by the political institutions essential for the smooth functioning of markets, such as honest and efficient government based on the rule of law and promoting impartial enforcement of contracts, protection of private property from theft and government takeover, and related practices safeguarding the fruits of entrepreneurship, innovation, investment, and hard work (2). Empirical studies have established strong connections between such "good institutions" and national economic performance (3–5).

In this article, we demonstrate the importance of still deeper, more nearly ultimate sources of contemporary prosperity: biogeographic initial conditions 12,000 years ago, just before the origins of agriculture. Our model and empirical analyses are broadly consistent with the sweeping framework for explaining world socioeconomic and political history laid out by Jared Diamond (6) and, to various degrees, by other recent authors cited ahead. Diamond argues that the enormous size of the Eurasian continent, the large Mediterranean zone of western Eurasia, and the East-West orientation of the continent's major axis compared with that of other continents meant that Eurasia was prehistorically endowed with more numerous and more valuable wild plant and animal species suited for domestication and with natural corridors facilitating rapid dispersal of those species as well as of technologies, ideas, and people. Because of those geographic and biogeographic advantages, the original transition from the hunting-gathering lifestyle that had prevailed throughout the previous 5 million years of human history to agriculture and animal husbandry occurred earlier in Eurasia than anywhere else. The capacity of agriculture to yield far more food, feed far more people, and generate storable food surpluses permitted the development of specialized classes who were freed of the necessity of raising their own food and were crucial for the development of technology and of complex political institutions and, hence, for economic growth.

In this article we model this line of thinking, and we apply standard statistical methods to test the capacity of our model to explain the present-day economic development of nations. The most important hypothesis we investigate is that biogeographic initial conditions decisively affected the timing of transitions to agriculture, and through that route they affect contemporary levels of national prosperity. The empirical analyses reported ahead support the following specific conclusions. (*i*) Geography is a key determinant of the biogeographic usefulness to humans of various regions in prehistory. (*ii*) The richer the biogeographic endowment in broad regions of the world, the earlier was the transition to settled agriculture and, thus, the earlier was the onset of accelerated technological development and economic growth. (*iii*) Although political–institutional conditions are the most powerful proximate source of the wealth of nations, geography and initial biogeography remain significant explanatory variables even after institutions are taken into account.

Methods and Data

Definitions and measurement of variables used in the research are as follows. All data are available from D.A.H. and are posted at www.handels.gu.se/~econdhib.

Per Capita Gross Domestic Product (GDP). Per capita GDP of nation states is the best comparable, available measure of the level of national economic development. It is the standard variable used by economists to investigate institutional as compared with other sources of international variations in prosperity, partly because at any given point in time institutions vary mainly crossnationally rather than intranationally. The GDP data used are for 1997 and are expressed in 1985 US dollars. We use the largest international sample of countries for which data were available on GDP and the other variables in the analysis, except that we excluded countries whose current income per capita is based heavily on extractive wealth (mainly oil production, as in the Persian Gulf states). We obtained a sample of 112 countries.

Geography. Geography is measured by taking 100 times the average of three constituent variables, after each was normalized by dividing by its maximum value. The three constituent variables are as follows.

(*i*) Climate as measured by a four-point scale based on the Köppen classification and ordered in ascending value according to how favorable conditions are to agriculture.

Abbreviations: GDP, gross domestic product; B.C., before Christ; A.D., *anno Domini*.

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Table 1. Model timeline (not shown to scale)

Early Holocene	⇒	Neolithic transition	⇒	Industrial revolution	⇒	Present day
10,000 B.C. Nomadic hunting-gathering		8,500–2,500 B.C. Agriculture and animal husbandry		≥A.D. 1750 Mass production		A.D. 2000 Unprecedented prosperity (for some people)

1, Dry tropical or tundra and ice, classification B and E. 2, Wet tropical, classification A. 3, Temperate humid subtropical and temperate continental, classification Cfa, Cwa, and D. 4, Dry hot summers and wet winters, classification Csa, Csb, Cfb, and Cfc, which are particularly favorable to annual heavy grasses. An alternative ordering (proposed by a reviewer) would interchange scores 3 and 4, but we found that this did not affect our empirical results significantly. The data were obtained from Strahler and Strahler (7).

(*ii*) Latitude, as measured by the absolute distance from the equator in degrees of latitude.

(*iii*) The East-West orientation of continental axis, as measured by taking the distance in longitudinal degrees between the easternmost and westernmost points of each continent and dividing this number by the distance in latitudinal degrees between the northernmost and southernmost points.

Biogeography. Prehistoric "biogeography" (denoted in the model below by $\tilde{A}_n$) is measured by taking 100 times the average of the numbers of locally available wild "plants" and "animals" suited to domestication 12,000 years ago in various parts of the world, after each was normalized by dividing by its maximum value.

The term plants denotes storable annual or perennial wild grasses with a mean kernel weight exceeding 10 mg (ancestors of domestic cereals such as wheat, rice, corn, and barley). The data are from Blumler (8). The values of the plants variable range from a maximum of 33 species, in the Near East, Europe, and North Africa, to 0 species in the Pacific islands. For purposes of coding the plants variable, Eurasia was divided into three broad areas. One includes all of western Eurasia and the Near East and reaches its limit in the Indus Valley in Pakistan, where the easternmost archeological evidence of crops from the Fertile Crescent has been found (9). A second includes India and the Far East. The third includes Indonesia, the Philippines, and Papua New Guinea. America also is split up into three zones: Central, North, and South. Caribbean islands and islands near Africa are regarded as belonging to the Central American and African zones, respectively, whereas the Pacific islands are treated as independent of the Asian zone (and, as noted, had zero species suitable for domestication).

The term animals denotes the number of species of wild terrestrial mammalian herbivores and omnivores weighing >45 kg that are believed to have been domesticated prehistorically in various regions of the world. The total is 14 and are the ancient ancestors of sheep, goat, cattle, horse, pig, Bakhtrian camel, Arabian camel, llama, yak, Bali cattle, reindeer, water buffalo, donkey, and the mithan. We consider only herd domesticates and not household domesticates because of the overwhelmingly greater economic value of the former. Of the 14, western Eurasia and North Africa had access to 9, Eastern Eurasia had access to 7, Southeast Asia had access to 2, South America had access to 1, and Central and North America, sub-Saharan Africa, Australia, and the Pacific islands had access to none (6, 10).

Altogether, we have eight independent combinations of plants and animals to calibrate biogeographic endowments (biogeography) circa 10,000 before Christ (B.C.) in broad regions covering the 112 present-day countries featured in the empirical analysis. Because the European food and technology package was wholly transferred by colonialists to the neo-Europes Australia, Canada, New Zealand, and the United States, these countries are coded as having European biogeography (33 plants and 9 animals) for purposes of analyzing the connection of biogeography to present-day levels of development. The same transfer occurred by varying lesser degrees in many other former colonial nation states, but we were unable to calibrate this transfer; it is a source of imprecision in estimating the influence of effective biogeography on current national prosperity. We do not take account of the contribution of domesticates native to the Americas to European development because this reverse transfer occurred after the European conquests of the former.

Quality of Institutions. The "institutions" variable is based on ratings of the Private Risk Service Group's *International Country Risk Guide* of five political-institutional characteristics of each country, as assembled by Knack and Keefer (3). The five constituents are (*i*) quality of bureaucracy, (*ii*) rule of law, (*iii*) government corruption, (*iv*) risk of expropriation, and (*v*) risk of government repudiation of contracts. The institutions variable is created by taking 100 times the average of the scores on these variables over the period 1986–1995, after each constituent variable was divided by its maximum value, which yielded a (0, 100) index.

Analysis

Income Production 10,000 B.C. to *Anno Domini* (A.D.) 2000. We consider a time span of 12 millennia, beginning in the early Holocene at ≈10,000 B.C. and extending to the present day, around A.D. 2000. By 10,000 B.C. all continents except Antarctica had been populated by nomadic hunter-gatherers, and climatic conditions had stabilized and improved with the retreat of the glaciers and worldwide rise in temperature after the end of the last Ice Age, thereby enhancing the prospects for productive agriculture (6, 11). The timeline and associated modes of production are displayed schematically in Table 1.

The productive activity of hunting and gathering bands may be viewed for the most part as isolated, subject to little or no outside influence from remote regions or other continents. Economic growth during this era, and during all others, was determined primarily by growth of technological knowledge. Let $A_n(t)$ denote the level of technology achieved by hunter-gatherers in the n-th environment at time t, and let $\tilde{A}_n$ denote the productive potential of biogeographic initial conditions of the n-th environment during the early Holocene. $\tilde{A}_n$ is calibrated empirically by the number of domesticable species of large wild mammals and wild heavy-seeded annual grasses available 12,000 years ago in various regions of the world, bearing in mind that only a very small fraction of all plant and animal species were edible or suited to domestication in prehistory (6, 8–10).

We model the growth of technology $A_n(t)$ during this era as

$$\frac{\dot{A}_n(t)}{A_n(t)} = \gamma(\ln \tilde{A}_n - \ln A_n(t)), \quad A_n(0) = 1, \gamma > 0. \qquad [1]$$

Eq. **1** implies that the level of productive knowledge at each period was

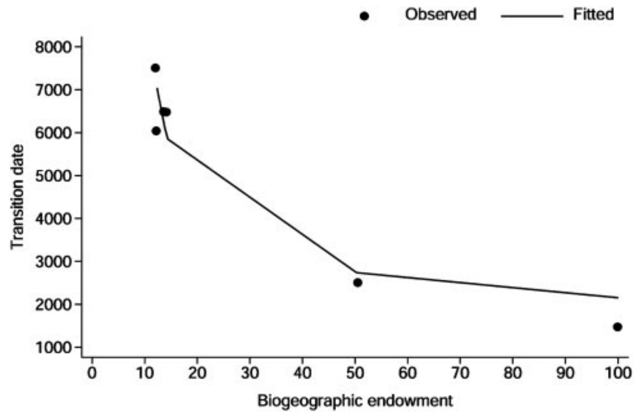

Fig. 1. Observed and fitted transition dates. The vertical axis represents the number of years after 10,000 B.C., and the horizontal axis represents our biogeography index. Note that the transition from hunting-gathering to agriculture occurred earliest in regions with the best biogeographic endowments of domesticable plant and animal species. The piece-wise, ''kinked'' appearance of the graph line is a close approximation to the continuous function actually estimated in Eq. **3**. Listed from northwest to southeast in the figure, the six observations graphed pertain to the following regions: Eastern United States, Mesoamerica, Andes and Amazonia, Tropical West Africa, China, and Southwest Asia.

$$A_n(t) = \tilde{A}_n^{1-e^{-\gamma t}}. \quad [2]$$

The parameter γ represents people's propensity to learn from nature and to exploit their biogeographic environment. It is constant over n. We assume no geographic differences in human innate productive abilities. Variation in productive success was derived solely from differences in biogeographic initial conditions $\tilde{A}_n$; a biogeographically rich environment supplied hunter-gatherers with more useful things to learn and more species to exploit. Hence, the model formalizes the hypothesis that technological change leading up to the emergence of agriculture was driven in considerable degree by ''supply-push'' environmental opportunity (6, 9, 12, 13) rather than only by ''demand-pull'' necessity, such as pressure on the food supply from exogenous population growth (14, 15), although we acknowledge that both forces undoubtedly played a role.

Perhaps the most important event in human economic history was the Neolithic transition from hunting–gathering to sedentary agriculture (the ''agricultural revolution''), when food production came to depend on domesticated plants and animals rather than on hunting and gathering wild plants and animals. We model these transitions as occurring at times t_n^A denoting the period when A_n (t) reached a threshold level A^A that was necessary to achieve agriculture. Solving Eq. **2** for transition dates t_n^A, that is, for the dates at which A_n $(t^A) = A^A$, yields

$$t_n^A = \frac{1}{\gamma} \ln\left[\frac{\ln(1/\tilde{A}_n)}{\ln(A^A/\tilde{A}_n)}\right]. \quad [3]$$

Archaeological research (6, 9, 12, 13) supplies data on the locations, biogeographic endowments, and approximate dates of six independent origins of settled agriculture spanning 8,500 B.C. to 2,500 B.C., which are identified in Fig. 1. The cases do not include Highland New Guinea, which recently again has been proposed as an independent center (16), because the evidence for this site is more equivocal than that favoring the six major cases, and it involved no animals and only a few nonstorable plants of uncertain dietary importance (17).

Letting $t = 1$ be the initial period at 10,000 B.C. and $t = 12,000$ be the terminal period at A.D. 2000, the transitions occurred in

Table 2. Estimates for the transition dates Eq. 3 (t_n^A)

Threshold level A^A	Learning rate γ	Adjusted R^2	Residual standard error
9.23 (2.14|0.013)	0.000306 (0.0001|0.040)	0.98	94.3

$n = 6$. The estimator is nonlinear least-squares. In parentheses are SE|P value.

the interval $t = 1,500$ to $t = 7,500$. Notwithstanding the small number of observations, the implication of the model in Eqs. **1-3** for the technological progression of hunter-gatherers can be tested. Nonlinear least-squares estimates of Eq. **3** are reported in Table 2. Estimates of the parameters A^A and γ are statistically significant at $P < 0.05$, and the fit of the equation to the data are excellent with 98% of the geographic variation in the timing of the Neolithic transition explained by geographic variation in the number of domesticable plant and animal species.

Fig. 1 shows the predictions generated by the regression parameter estimates in Table 2 for the number of years from period $t = 1$ (10,000 B.C.) that it took hunter-gatherer communities to make the transition to agriculture in the six cases. Eq. **2** implies that $\log A_n$ (t) approaches the corresponding limit of its biogeographic endowment, $\log \tilde{A}_n$, at rate γ per unit time with half-life satisfying $e^{-\gamma t} = (1 - e^{-\gamma t}) = 1/2$. The estimated learning rate $\hat{\gamma} = 0.000306$ means that the estimated half-life is

$$\text{half-life} = \frac{\ln 2}{\hat{\gamma}} = 2{,}265 \text{ years}. \quad [4]$$

This calculation illustrates how it could take hunter-gatherers thousands of years to exploit fully the potential of their environment's biogeographic endowment or to reach the threshold A^A at an earlier period and make the transition to agriculture.

Fig. 2 graphs the estimated time trajectories of A_n (t) that are associated with four representative biogeographic endowments. On the (0, 100) biogeography scale, the model predicts that the Neolithic transition occurs when A_n (t) crosses the estimated threshold $A^A = 9.23$, which is shown by the horizontal line in the figure intersecting the A_n (t) axis at this value. The model implies that societies enjoying the two best-endowed environments depicted (corresponding to $\tilde{A}_n$ scores of 100 and 50) make the

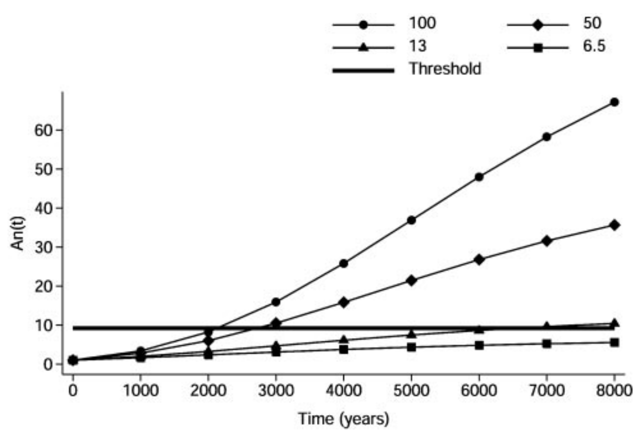

Fig. 2. Time paths of technological progress under various biogeographic initial conditions. The vertical axis represents the level of technology A_n (t), and the horizontal axis is the number of years after 10,000 B.C. The threshold to agriculture is crossed earlier in regions with better biogeographic endowments, that is, with higher values of $\tilde{A}_n$ (100, 50, 13, and 6.5) as discussed in the main text.

transition to agriculture comparatively early, as was the case in most of Eurasia. Technological progress also occurs in regions with the least well endowed biogeography shown in Fig. 2 (with an $\tilde{A}_n$ score of 6.5), as hunter gatherers gradually exploited their environment's low productive potential. But progress is slow and endowments are so impoverished that settled agriculture might never have been initiated in isolation in those regions. Communities facing these circumstances (which would include inhabitants of areas now known as Australia, New Zealand, and most of western North America) essentially remained hunter-gatherers until they were absorbed, colonized, or exterminated by states that arose in richer environments where agricultural revolutions occurred thousands of years earlier. The same fate was experienced by societies with mediocre biogeography (illustrated by $\tilde{A}_n = 13$), which Fig. 2 indicates made the Neolithic transition relatively late, >6,000 years into our model history. Examples are much of sub-Saharan Africa and South America.

Economic Growth After Agricultural Revolutions. After Neolithic transitions, technological change and economic growth were no longer limited by biogeographic initial conditions. The superior agricultural mode of production made possible specialization of economic activity and the establishment of a non-food-producing class devoted to the creation and codification of knowledge and the development of technology. By contrast to the hunting-gathering era, communities now learned about and created capital goods well beyond the constraints imposed by local environmental conditions. What we think of as "civilization" slowly emerged: for example, the invention of writing, science, engineering, formal law, mechanisms of large-scale social organization and control, technology-based military prowess, and the appearance of the first states.

The technological progress of agricultural economies entered a long era of exponential growth until the time of the industrial revolution, at which time technology reached the industrial threshold and the growth rate of technology and gross output accelerated further. But the impact of technology growth on living standards over time depends on the associated growth rate of population. Historical scholarship indicates that during most of human history population growth fully absorbed output growth in Malthusian fashion, leaving long-run per capita incomes at the subsistence level. The Malthusian link was broken only comparatively recently at approximately the time of industrial revolutions commencing in Europe around A.D. 1,750, that is around $t = 11{,}750$ and thereafter (18–22). After those transitions, per capita incomes finally began to grow steadily.

The principal hypothesis we aim to test, however, is that the effects of biogeographic initial conditions on the timing of transitions to agriculture and the onset of accelerated technological progress yielded regional development advantages that to some degree affect present-day national per capita incomes. Eq. **3** modeled those effects through the transition function

$$t_n^A = \frac{1}{\gamma}\ln\left[\frac{\ln(1/\tilde{A}_n)}{\ln(A^A/\tilde{A}_n)}\right].$$

In the empirical analyses below we bridge the disciplinary divide between economic analysis of the prosperity of current nation states and historically grounded archaeology and geography by using the estimates of A^A and γ in Table 2, along with data on biogeographic endowments $\tilde{A}_n$ in eight broad regions of the world, to generate t_n^A scores for a large cross-section of present-day countries. In Root and Schneider's (23) terms, our procedure amounts to a "scale-up" approach to calibrating the potential importance of biogeography to contemporary levels of national prosperity from parameters estimated in our microanalysis of six local cases of the emergence of agriculture, and a "scale-down" approach to mapping our measurements of regional biogeographies onto contemporary nation states. Our approach necessarily can help only to identify environmental metaconditions potentially affecting development; it says nothing about the complex dynamics of technology dispersal from the major original homelands of agriculture within (or across) the broad regions for which biogeographic conditions are measured, a topic that is being addressed with increasing rigor by the rapidly developing field of archaeogenetics (13, 24). Indeed, we know *ex post* that the technological leadership of the best endowed local homelands eventually eroded because of adverse human environmental impacts (6, 25).

The standard characterization of long-run technological progress during the agricultural and industrial eras as exponential implies that current log per capita incomes is a function of the effective duration of accelerated technological change, $T - t_n^A$. We therefore propose the baseline test equation

$$\ln y_n(T) = \alpha + \beta\cdot\left(T - \frac{1}{\gamma}\ln\left[\frac{\ln(1/\tilde{A}_n)}{\ln(A^A/\tilde{A}_n)}\right]\right),\ \alpha, \beta > 0, \qquad [5]$$

where $\ln y_n(T)$ is 1997 log GDP per capita of countries, $T = 12{,}000$ is the present-day, and $A^A = 9.23$, $\gamma = 0.000306$ are estimates from Table 2 of the agricultural revolution threshold and the learning rate, respectively. The model implies that the richer were biogeographic initial conditions in various regions of the world, the higher are present-day incomes per capita in countries falling within those regions:

$$\frac{d\ \ln y_n(T)}{d\tilde{A}_n} = \frac{\beta}{\gamma\tilde{A}_n}\cdot\left[\frac{1}{\ln(1/\tilde{A}_n)} - \frac{1}{\ln(A^A/\tilde{A}_n)}\right] > 0. \qquad [6]$$

Geography, Biogeography, Institutions, and Present-Day Prosperity. This article is mainly about the role of geography and biogeography as ultimate factors behind the more proximate influence of institutional quality that economists now commonly invoke to explain the wealth and poverty of nations. Table 3 reports results of a sequence of least-squares regression experiments using data on 112 modern economies that address the issue. Estimation results for each regression model are displayed column-wise in the table.

Regression model 1 of Table 3 shows that our index of geography accounts for ≈80% of the variation in biogeographic initial conditions $\tilde{A}_n$. Although the geography index is measured by current conditions, the stabilization of climate after the Younger Dryas means that it gives a good first approximation to relative geographic conditions circa 10,000 B.C. and afterward (with significant exceptions such as the desertification of the Sahara and parts of the Middle East during the Holocene).

Because geography is an important determinant of biogeography, it follows that geography is an important indirect determinant of the transition scores ($T - t_n^A$), which according to our model are directly determined by biogeographic initial conditions in various parts of the world. Regression model 2, in which ($T - t_n^A$) is regressed on log geography, strongly supports this logical linkage. Almost 80% of the variation in that variable is accounted for by log geography.

Regression model 3 estimates the relation of log 1997 GDP per capita to ($T - t_n^A$). This model corresponds directly to the baseline test equation proposed in Eq. **5**, and therefore it tests the strict implication of our stylized account of how biogeographic initial conditions affect contemporary prosperity. Along with regression models 4 and 5, these results show that geography and biogeography alone can explain between 50% and 60% of present-day international variation in log income per capita. Note that biogeography here means biogeographic initial endowments $\tilde{A}_n$ as transmitted through the transition score func-

Table 3. Regressions

	Regression model								
	1	2	3	4	5	6	7	8	9
Dependent variables ⇒	$\tilde{A}_n$	$(T - t_n^A)$	log y_n	log y_n	log y_n	log y_n	Quality of institutions	Quality of institutions	log y_n
Geography	1.63 (0.08|0.00)						0.628 (0.07|0.00)		
log geography		4.71 (0.23|0.00)		2.04 (0.18|0.00)	1.33 (0.39|0.00)	0.527 (0.03|0.06)			
$(T - t_n^A)$ (1,000s)			0.38 (0.04|0.00)		1.80 (0.63|0.00)	2.50 (0.04|0.00)		5.61 (0.68|0.00)	
$(T - t_n^A)^2$					−0.11 (0.04|0.01)	−0.16 (0.03|0.00)			
Quality of institutions						0.037 (0.003|0.00)			0.048 (0.20|0.00)
Adjusted R^2	0.79	0.78	0.53	0.52	0.57	0.80	0.43	0.38	0.67

$n = 112$. The estimator is ordinary linear least-squares. The variables geography, biogeography ($\tilde{A}_n$), thousands of years since the transition to agriculture ($T - t_n^A$), log 1997 GDP per capita (log y_n), and institutions are discussed in the main text. The inflection points implied by the quadratic specifications in $(T - t_n^A)$ always exceed the empirical maximum, and therefore the estimated functions are (slightly) concave over their whole range and never backward-bending. In parentheses are SE|P value of coefficient estimates. Regression intercept constants are not reported.

tion $(T - t_n^A)$. In view of the imprecise measurement of biogeographic conditions in particular, these results are remarkable evidence of the importance of geography and biogeography to present-day economic prosperity. The statistical relationship implied by regression model 5 is graphed in Fig. 3.

Taken at face value, the estimates of model 5 imply that a change from the worst geographic and biogeographic conditions to the best would yield a shift in 1997 GDP per capita from ≈\$600 to ≈\$8,800. However, incomes per capita observed in the regression sample of $n = 112$ countries are far more dispersed, ranging from \$369 (Ethiopia) to \$21,974 (Luxembourg). Hence, a more complete accounting of international variation in economic prosperity requires additional explanatory factors. As pointed out in the introduction, the leading candidate is a measure of institutional arrangements affecting the productivity of economic activity.

Regression model 6 adds to the previous model a standard measure of institutional quality used in many other studies (3–5, 26). This regression model fits 80% of the variation in log per capita incomes, which represents a significant improvement over a purely geographical and biogeographical explanation (52–57% in regression models 3, 4, and 5). Consequently, it comes much closer to tracking the full range of per capita incomes observed crossnationally. The estimates for model 6 imply that a change from the worst combination of geography, biogeography, and institutional arrangements to the best would yield a change in per capita incomes from \$350 to \$17,350.

Although these results support the common conclusion that institutional arrangements supportive of a market economy have potent influence on the wealth and poverty of nations, good institutions cannot themselves properly be regarded as a fully independent variable unaffected by geography, biogeography, and level of economic development, if only because countries that are rich because of geographic, biogeographic, and other reasons have the resources to build institutions of high quality. Consequently, the effect of institutions on per capita incomes estimated in regression model 6 almost surely mediates to some degree the effects of more ultimate geographic and biogeographic variables, and to some degree probably reflects causal influence running from high incomes to high quality institutions, rather than the reverse as sometimes is implicitly assumed. Regression models 7 and 8, for example, show that our quite rough measures of geography and biogeography can explain ≈40% of the variation in quality of institutions. Geography and biogeography might well also be mediated in part by state antiquity, as suggested recently by Bockstette, Chanda, and Putterman (27).

Moreover, although some recent studies (4, 5) have claimed that the purported effects of geography are mediated entirely by "good institutions," the results for model 6 show that biogeography and geography retain statistical significance and substantive importance even when institutional quality is included in the multiple regression. Fig. 4 shows the partial effects implied by regression model 6 of geography plus initial condition biogeography as well as the partial effect of institutions. Fig. 4 *Left* graphs the effect of geography plus biogeography on log per capita income when controlling for institutions. It shows that log per capita income rises quite steeply with geography and biogeography even after the effects of institutions are netted out. Fig. 4 *Right* shows that the same is true of the response of per capita income to institutional quality after the effects of geography and biogeography are controlled. The evidence supports the conclusion that geography (26, 28–30) and biogeography directly affect

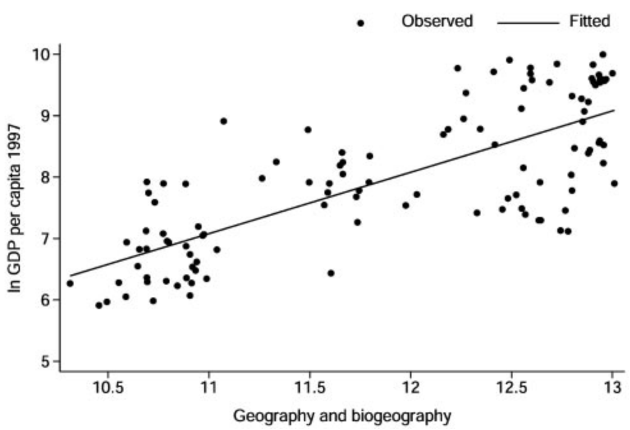

Fig. 3. Impact of geography and biogeography on present-day log per capita incomes. Geography and biogeography is the sum (linear combination) of the variables log geography, $(T - t_n^A)$ and $(T - t_n^A)^2$ after each variable was weighted by its estimated coefficient in regression model 5 (Table 3). Because the time since transition term $(T - t_n^A)$ is determined by biogeographic conditions $\tilde{A}_n$, the solid slope line in the figure represents the estimated response of log GDP per capita to geography and biogeography combined.

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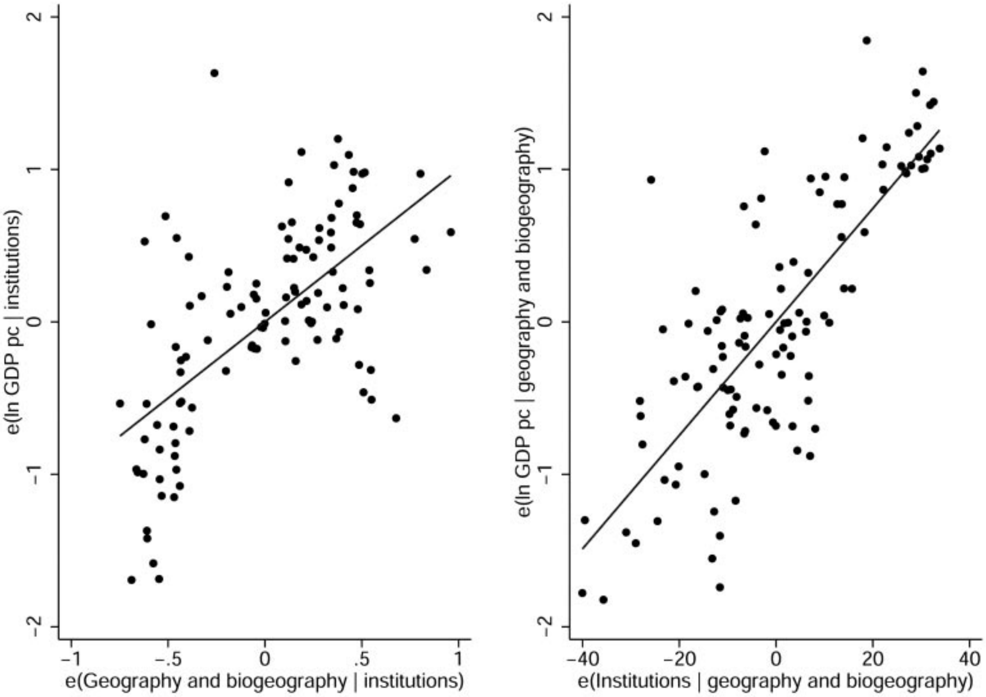

Fig. 4. Partial regression plots of the response of log GDP per capita 1997 to geography and biogeography and institutions. Geography and biogeography is the sum of the variables log geography, $(T - t_n^A)$ and $(T - t_n^A)^2$, after each variable was weighted by its estimated coefficient in regression model 6 (Table 3). The vertical axes show variation in the dependent variable log 1997 GDP per capita after controlling for institutions (*Left*) or geography plus biogeography (*Right*). The horizontal axes show variation in geography plus biogeography after controlling for institutions (*Left*) and variation in institutions controlling for geography plus biogeography (*Right*).

economic performance, rather than being wholly mediated by the influence that those variables had in shaping historical development of institutions.

It should be emphasized again, however, that geography and biogeography indisputably have prior causal status over both institutions and current per capita incomes, even though, as shown in model 9, quality of institutions has a strong connection to national levels of prosperity. In historical time, geography and biogeography are the primes mobiles of current prosperity. For this reason Fig. 3 and regression models 3, 4, and 5 of Table 3 more accurately assess the deeper effects of geographic conditions and biogeographic endowments on the wealth of nations than regression models that also include mediating variables such as institutions. This finding is true because the intervening variable quality of institutions absorbs some of the effects of its causal antecedents in multiple regression setups such as model 6, and therefore the ultimate effects of geography and biogeography are not fully registered by such single-equation regression estimates.

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