Geography, biogeography and the international distribution of prosperity

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The Neolithic transition from hunting and gathering to sedentary agriculture, which made possible the rapid technological progress that ultimately led to the Industrial Revolution, is one of the most important events in thousands of years of humankind's economic development. In this paper we present theory and evidence showing that geography and biogeography exerted decisive influence on the location and timing of transitions to agriculture, to complex social organization and, eventually, to modern industrial production. Evidence from a large cross-section of countries indicates that the effects of geographic and initial biogeographic conditions on present-day levels of economic development are remarkably strong, even when conditioned on institutional arrangements that exert powerful proximate influence on the productivity of nations.

The prosperity of nations varies enormously. Per capita incomes in countries within the top decile of the present day international distribution run about thirty times higher than incomes falling within the bottom decile. At the extremities differences in national economic prosperity exceed a factor of one hundred[1]. What explains such large dispersion of the wealth and poverty of nations?

Traditional economic theory points to accumulation of human and physical capital and to successful adoption of state-of-the-art technologies as the main sources of variation in economic productivity[2]. In recent years, however, economists have begun to appreciate more fully the importance of more fundamental, institutional sources of growth and development. Capital accumulation and technology absorption are now commonly viewed as intermediate variables that are affected decisively by institutional arrangements supporting the smooth functioning of markets; especially honest and efficient government based on the rule of law and promoting impartial enforcement of contracts, security of property and related practices safeguarding private returns to entrepreneurship, innovation, investment and hard work[3]. Empirical investigations applying standard statistical methods to cross-national data have established strong connections between such political-institutional conditions and economic performance[4-8].

In this article we demonstrate the importance of yet deeper sources of contemporary prosperity: biogeographic initial conditions in place some twelve thousand years ago. The model and empirical analyses reported ahead are broadly consistent with the sweeping framework for explaining world socio-economic and political history laid out by Jared Diamond[9]. Diamond argues that the enormous size of the Eurasian continent, its large Mediterranean zone in the western part and the East-West orientation of its major axis, meant that Eurasia was more favourably endowed in pre-history than other regions with nutritious plants suited to cultivation, animals suited to domestication, and natural corridors of transit and communication facilitating circulation of goods, people, species and ideas. Because of these geographic and biogeographic advantages, Neolithic transitions from hunting and gathering to horticulture and animal husbandry occurred earlier in Eurasia than anywhere else. The superior agricultural mode of production made possible the establishment of a non-producing class of specialists whose members were crucial for the dynamic advance of technological knowledge, which is the principal engine of secular economic growth.

Ahead we to formalize this line of thinking with a stylised dynamic model of long-run economic growth and development, and we apply standard statistical methods to test the model's implications in data. The empirical analyses support the following conclusions: (i) Geography is a key determinant of the biogeographic quality of various environments in pre-history. (ii) The richer were biogeographic endowments in various parts of the world, the earlier were Neolithic transitions to agriculture and, consequently; the earlier the onset of dynamic secular technological advance. (iii) Although market supporting institutional arrangements are the most powerful proximate source of prosperity, present-day levels of per capita income still register effects of geography and initial condition biogeography.

Income production 10,000 BC to 2,000 AD, $t \in [0,T]$

We consider a time span of twelve millennia $t \in [0,T]$, beginning during the late Pleistocene at about 10,000 BC and running to the present-day, ca. 2,000 AD. By 10,000 BC all the major continents had been populated by nomadic hunter-gatherers and climatic conditions had stabilized and ameliorated, which enhanced the prospects for productive agriculture[9,10]. The time-line modelled and associated modes of production look as follows:

Table 1 Model time-line (not shown to scale)

Late Pleistocene $\Rightarrow$	Neolithic transition $\Rightarrow$	Industrial revolution $\Rightarrow$	Present-day
$t0$ ($\approx$10,000BC)	$t1500 - t7500\ (t^A)$ (8,500BC-2,500BC)	$\geq t11750\ (t^{IR})$ ($\geq$1,750AD)	$t12000\ (T)$ ($\approx$2,000AD)
Nomadic hunting and gathering	Horticulture and animal husbandry	Mass production	Unprecedented IT-age prosperity (for some)

Let Y_n denote net real production, L_n the population of workers and $x(i)$ the quantity of intermediate capital goods employed in the n-th economy. Income production over all $n \in [1,N]$ and $t \in [0,T]$ is determined by

$$Y_n(t) = \int_0^{A_n(t)} x(i)^{\alpha}\, di\ L_n(t)^{1-\alpha}, \qquad \alpha \in (0,1) \qquad (1).$$

For simplicity and without loss of generality we take $x(i)=1$ at all i, n and t and take the population of productive workers to be "population". We therefore write the production function for income per person as

$$y_n(t) \equiv \frac{Y_n}{L_n}(t) = A_n(t) L_n(t)^{-\alpha} \qquad (2).$$

Note that A_n is conceived as the stock of intermediate capital goods, inclusive of the technological knowledge associated therewith and embedded therein. It is the driving force of economic growth in most formal models of development.

Hunter-gatherer production and Neolithic transitions $t \in \left[0, t^A\right]$

The productive activity of hunting and gathering bands may be viewed for the most part as isolated, subject to little or no outside influence. The growth of intermediate capital goods deployed in production (coterminous with the growth of knowledge and technology) depended entirely upon biogeographic endowments. Let $\tilde{A}_n$ denote the productive potential of biogeographic initial conditions of the *n*-th environment during the late Pleistocene. Ahead $\tilde{A}_n$ is calibrated empirically by the numbers of large domesticable animals and heavy-seeded annual grasses that archaeological research indicates existed in various regions of the world 12,000 years ago, bearing in mind that only a very small fraction of all plants and animals in pre-history were edible or suited to domestiction[9,11-13]. Hence in the hunter-gatherer era, A_n should be thought of as the number of such plants and animals with potential for domestication, though not yet domesticated, that have been incorporated into the subsistence economies of hunter-gatherers.

The equation of motion for $A_n(t)$ during this era is

$$\frac{\dot{A}_n}{A_n}(t) = \gamma\left(\ln \tilde{A}_n - \ln A_n(t)\right), \qquad A_n(0) = 1,\ \gamma > 0,\ t \in \left(0, t_n^A\right) \qquad (3).$$

The parameter γ represents people's propensity to learn from nature. It is constant over *n*. There were no inherent differences between societies in ability to learn about and exploit environments. Productive success derived solely from variation in biogeographic initial conditions $\tilde{A}_n$; a rich environment supplied hunter-gatherers with more useful things to learn and more species to exploit.

The foregoing differential equation has solution

$$A_n\left(t\right)=A_n\left(0\right)^{e^{-\gamma t}}\ \tilde{A}_n^{\,1-e^{-\gamma t}}\ =\tilde{A}_n^{\,1-e^{-\gamma t}} \qquad (4).$$

Perhaps the most important events in humankind's economic histories were the Neolithic transitions from hunting and gathering to sedentary agriculture – "agricultural revolutions" with production dominated by horticulture and animal husbandry. These transitions occurred at times t_n^A when $A_n\left(t\right)$ reached a threshold level A^A that was necessary to achieve agriculture. Solving equation (4) for transition dates t_n^A, that is for the dates at which $A_n\left(t^A\right)=A^A$, yields

$$t_n^A=\frac{1}{\gamma}\ln\left[\frac{\ln\left(1/\tilde{A}_n\right)}{\ln\left(A^A/\tilde{A}_n\right)}\right] \qquad (5).$$

Archaeological research supplies data on the locations, biogeographic endowments and approximate dates of just six independent origins of settled agriculture spanning *t=1500* to *t=7500* (8,500 BC to 2,500 BC). Notwithstanding the micronumerousity, the implication of equations (3)-(5) for the technological progress of hunter-gatherers can be tested. Non-linear least squares estimates of (5) are reported in Table 2.

Table 2 Estimates for the transition dates $\left(t_n^A\right)$ equation

Threshold level $\widehat{A^A}$	Learning rate $\hat{\gamma}$	Adjusted R^2	Residual standard error
9.23	0.000306	.98	94.3
(2.14|0.013)	(0.0001|0.040)		

N=6. The estimator is non-linear least squares. In parentheses are (standard error|p-value). Biogeographic endowment $\tilde{A}_n$ is an additive index scored (0,100] from archaeological data on the regional distribution of domesticable plants and animals in pre-history. (See Methods section.)

In the empirical analyses ahead we use these estimated coefficients along with data on $\tilde{A}_n$ to impute values of t_n^A for a broad cross-section of present-day nations. (See the Methods section.)

Figure 1 shows the predictions of this regression experiment for number of years from period *t=0* (from 10,000 BC) that it took hunter-gatherer communities to make the transition to agriculture in the six documented cases.

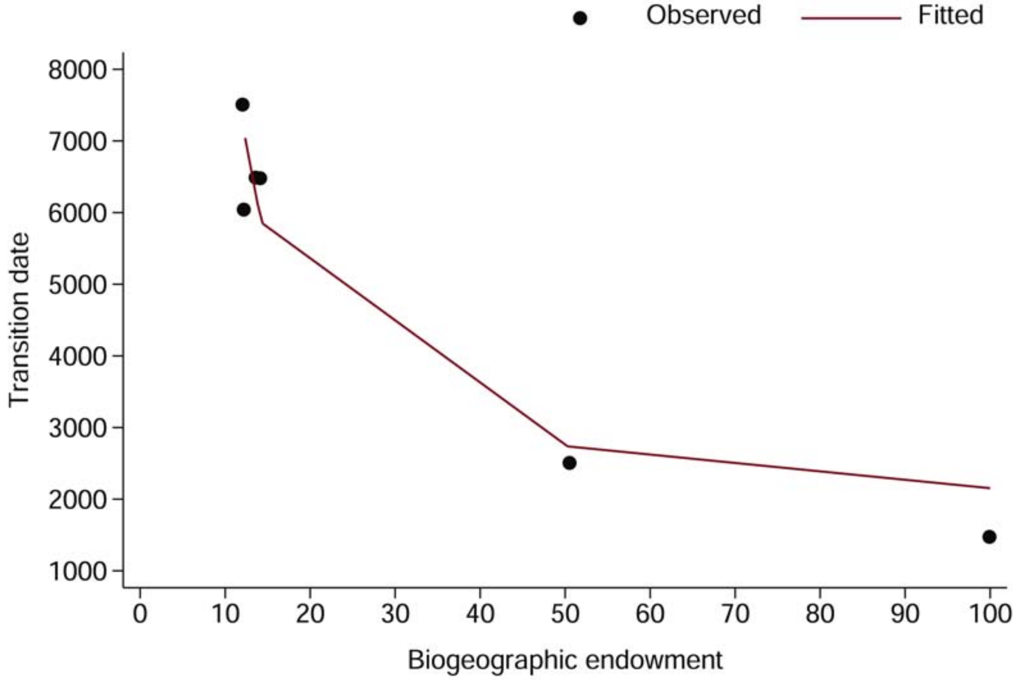

Figure 1 Observed and fitted transition dates

On the biogeography scale of $\tilde{A}_n \in (0,100]$, the agriculture threshold is estimate to be $\widehat{A^A} = 9.23$. (Table 2) Equation (4) implies that log $A_n\left(t\right)$ approaches the corresponding limit of its biogeographic endowment, log $\tilde{A}_n$, at rate γ per unit time with half-life satisfying $e^{-\gamma t} = \left(1 - e^{-\gamma t}\right) = 1/2$. The estimated learning rate $\hat{\gamma} = 0.000306$ therefore implies a half-life of

$$half - life = \frac{\ln 2}{\hat{\gamma}} = 2265 \qquad (6).$$

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

Figure 2 graphs the estimated trajectories of $A_n(t)$ from initial period $t0$ that are associated with four representative biogeographic endowments. The model predicts that the Neolithic transition occurs when $A_n(t)$ crosses the estimated threshold $\widehat{A^A} = 9.23$, 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 transition to agriculture comparatively early, as was the case in most of Eurasia[9,14,15]. Technological progress also occurs in societies with the least well-endowed biogeography shown in Fig. 2 (with an $\tilde{A}_n$ score of 6.5) as hunters and gatherers gradually exploited their environment's rather dismal productive potential. But progress is slow and conditions are so poor that settled agriculture most likely never would have been initiated in isolation. Communities facing these circumstances – which would include inhabitants of areas now known as New Zealand, Fiji, the Solomon Islands, and Samoa and much of present-day Australia and some of 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, more than 6,000 years into our model history. Examples are much of sub-Saharan Africa and South America. Hunter-gathering communities still in existence are anthropological wonders of negligible number without correspondence to any present-day national economy.

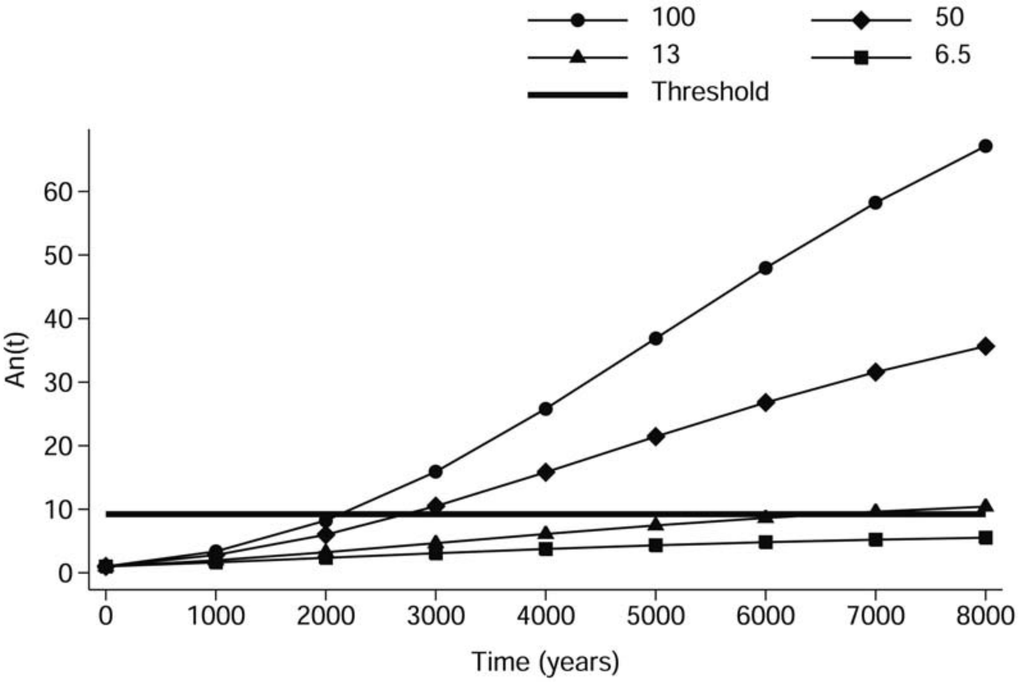

Figure 2 Time paths of $A_n(t)$ under various biogeographic initial conditions

Economic growth after agricultural revolutions, $t \in (t^A, T]$

After Neolithic transitions technological change and economic growth were no longer constrained by the static limits of local biogeographic conditions $\tilde{A}_n$. The superior agricultural mode of production made possible specialization of productive activity and the establishment of a non-producing class devoted to the creation and codification of knowledge. 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. Communities now learned about and created capital goods well beyond the limits imposed by initial environmental conditions.

The technological possibilities of agricultural economies, A_n^*, were now dynamic and entered a long era of exponential growth until the time of the industrial revolution, t_n^{IR}, at which time technology reached the industrial threshold, A^{IR} and technological possibilities made another discontinuous jump. This stylised characterization of long-run economic progress is represented by the following equations:

$$A_n^*(t) = A^A \exp\left(g^A t\right), \qquad g^A > 0,\ t \in (t_n^A, t_n^{IR}] \tag{7}$$

$$A_n^*(t) = A^{IR} \exp\left(g^{IR} t\right), \qquad g^{IR} > g^A,\ t \in (t_n^{IR}, T] \tag{8}$$

The rate at which technological knowledge was incorporated to actual production during both the agricultural and industrial eras is

$$\frac{\dot{A}_n}{A_n}(t) = \delta\left(\ln A_n^*(t) - \ln A_n(t)\right), \qquad \delta > 0 \tag{8}$$

The differential equations for the productive technology of agricultural and industrial economies have solutions

$$A_n(t) = A^A \exp\left[g^A t - \frac{g^A}{\delta}\left(1 - e^{-\delta t}\right)\right], \qquad A^{IR} > A_n(t) > A^A \tag{9}$$

$$A_n(t) = A^{IR} \exp\left[g^{IR} t - \frac{g^{IR}}{\delta}\left(1 - e^{-\delta t}\right)\right], \qquad A_n(t) > A^{IR} > A^A \tag{10}$$

In terms of exogenous variables and parameters, the technology growth rates therefore are

$$\frac{\dot{A}_n}{A_n}(t) = g^j\left(1 - e^{-\delta t}\right), \qquad \begin{Bmatrix} j = A,\ t \in (t_n^A, t_n^{IR}] \\ j = IR,\ t \in (t_n^{IR}, T] \end{Bmatrix} \tag{11}$$

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 income growth in Malthusian fashion leaving long-run per capita incomes constant at the subsistence level, $\underline{y}$, though there were short-run trends and fluctuations about the long-run subsistence equilibrium. The Malthusian link was broken comparatively recently at approximately the time of industrial revolutions commencing in Europe around 1,750 AD, that is around $t = 11750$ and thereafter[16-20].

Until the industrial revolutions at t_n^{IR} population growth therefore was

$$\frac{\dot{L}_n}{L_n}(t) = \frac{1}{\alpha}\frac{\dot{A}_n}{A_n}(t), \tag{12}$$

which left per capita output growth at zero and per capita incomes at subsistence:

$$\frac{\dot{y}_n}{y_n}(t) = \frac{\dot{A}_n}{A_n}(t) - \alpha\frac{\dot{L}_n}{L_n}(t) = 0 \Rightarrow y_n(t) = \underline{y}\,(subsistence), \qquad t \in (0, t_n^{IR}] \tag{13}.$$

After the Malthusian break following t_n^{IR} technology growth finally outstrips population growth

$$\frac{\dot{L}_n}{L_n}(t) = \frac{1}{\theta}\frac{\dot{A}_n}{A_n}(t), \qquad \theta > \alpha, \tag{14}$$

yielding positive growth of per capita incomes and rising living standards:

$$\frac{\dot{y}_n}{y_n}(t) = \frac{\dot{A}_n}{A_n}(t) - \alpha\frac{\dot{L}_n}{L_n}(t) = \left(1 - \frac{\alpha}{\theta}\right)\frac{\dot{A}_n}{A_n}(t) = \left(1 - \frac{\alpha}{\theta}\right) g^{IR}\left(1 - e^{-\delta t}\right), \qquad t \in (t_n^{IR}, T] \tag{15}$$

$$y_n(t) = \underline{y}\,\exp\left[-g^{IR}\frac{(\theta-\alpha)}{\delta\theta} + g^{IR}\frac{(\theta-\alpha)}{\delta\theta}e^{-\delta t} + g^{IR}\frac{(\theta-\alpha)}{\theta}\cdot t\right] \tag{16}.$$

At current period T equation (16) implies that log per capita incomes are

$$\ln y_n\left(T\right)=\ln \underline{y}-g^{IR}\frac{\left(\theta-\alpha\right)}{\delta\theta}+g^{IR}\frac{\left(\theta-\alpha\right)}{\delta\theta}e^{-\delta\left(T-t_n^{IR}\right)}+g^{IR}\frac{\left(\theta-\alpha\right)}{\theta}\cdot\left(T-t_n^{IR}\right) \qquad (17).$$

Solving equation (10) for t_n^{IR} we obtain

$$\begin{aligned} A_n\left(t^{IR}\right)=A^{IR}\Rightarrow t_n^{IR} &= t_n^A+\frac{1}{\delta}+\left[\frac{\ln\left(A^{IR}/A^A\right)}{g^A}+\frac{1}{\delta}W\left(\frac{-\left(A^{IR}/A^A\right)^{-\frac{\delta}{g}}}{e}\right)\right], \qquad (18) \\ &= t_n^A+\kappa, \qquad \kappa>0 \end{aligned}$$

where W is Lambert's W-function with $W\left(\;\right)$ here taking a real value falling in the interval $\left(-1,0\right)$ because $\frac{-\left(A^{IR}/A^A\right)^{-\frac{\delta}{g}}}{e}\in\left(-\frac{1}{e},0\right)$. Hence time T log incomes per capita are

$$\ln y_n\left(T\right)=\ln \underline{y}-g^{IR}\frac{\left(\theta-\alpha\right)}{\delta\theta}+g^{IR}\frac{\left(\theta-\alpha\right)}{\delta\theta}e^{-\delta\left(T-t_n^A-\kappa\right)}+g^{IR}\frac{\left(\theta-\alpha\right)}{\theta}\cdot\left(T-t_n^A-\kappa\right) \qquad (19).$$

From equation (5) we know that $t_n^A=\frac{1}{\gamma}\ln\left[\frac{\ln\left(1/\tilde{A}_n\right)}{\ln\left(A^A/\tilde{A}_n\right)}\right]$. Furthermore, for any plausible value of $\delta>0$, the exponential term $g^{IR}\frac{\left(\theta-\alpha\right)}{\delta\theta}e^{-\delta\left(T-t_n^A-\kappa\right)}$ in (19) asymptotes to zero at present-day time T, even for economies entering the industrial age late in the process. The equation for log output per capita therefore implies a linear function amenable to least-squares estimation

$$\ln y_n\left(T\right)=C+\tilde{g}\cdot\left(T-\frac{1}{\hat{\gamma}}\ln\left[\frac{\ln\left(1/\tilde{A}_n\right)}{\ln\left(\widehat{A^A}/\tilde{A}_n\right)}\right]\right), \qquad (20)$$

where $C = \ln \underline{y} - \frac{\tilde{g}}{\delta}\left(1+\frac{\kappa}{\delta}\right)$, $\tilde{g} = g^{IR}\frac{(\theta-\alpha)}{\theta} > 0$, $T = 12000$ and $\widehat{A^A} = 9.23$, $\hat{\gamma} = 0.000306$ are estimates of the agricultural revolution threshold and the learning rate, respectively, reported in Table 2. The model of course implies that the richer biogeographic initial conditions the higher present-day incomes per capita:

$$\frac{d\ln y_n(T)}{d\tilde{A}_n} = \frac{\tilde{g}}{\hat{\gamma}\tilde{A}_n}\left[\frac{1}{\ln\left(1/\tilde{A}_n\right)} - \frac{1}{\ln\left(\widehat{A^A}/\tilde{A}_n\right)}\right] > 0 \qquad (21).$$

Biogeography, institutions and present-day prosperity

Results of least-squares regression experiments for N=112 modern economies that are germane to the theoretical analysis above are reported in Table 3.

Table 3 Regressions

Dependent variables$\Rightarrow$	$\tilde{A}_n$ (1)	$\left(T-t_n^A\right)$ (2)	log y_n (3)	log y_n (4)	log y_n (5)	log y_n (6)
geography	1.63 (20.4|.00)					
log geography		4.71 (20.1|.00)		2.04 (11.1|.00)	1.33 (3.45|.00)	0.527 (1.91|.06)
$\left(T-t_n^A\right)$ 1000s ('biogeography')			0.38 (10.9|.00)		1.80 (2.86|.00)	2.50 (5.72|.00)
$\left(T-t_n^A\right)^2$					-0.11 (-2.6|.01)	-0.16 (-5.4|.00)
Institutions						0.037 (11.0|.00)
Adjusted R^2	.79	.79	.52	.52	.58	.79

N=112. The estimator is ordinary-linear least squares. Geography is an additive index scored $\in(0,1)$; see Methods. $\left(T-t_n^A\right)=\left(12,000-\frac{1}{\hat{\gamma}}\ln\left[\frac{\ln\left(1/\tilde{A}_n\right)}{\ln\left(\widehat{A^A}/\tilde{A}_n\right)}\right]\right)$ expressed in thousands and based on the estimates $\hat{\gamma},\widehat{A^A}$ reported in Table 2 and calibrations of $\tilde{A}_n$ discussed in the Methods section. The inflection points implied by the quadratic specifications in $\left(T-t_n^A\right)$ always exceed the empirical maximum and therefore the estimated functions are (slightly) concave over their whole range and never backward bending. y_n is 1997 real GDP per capita expressed in US dollars and deflated by 1985 purchasing power parity (PPP) prices. Institutions is an additive index $\in(0,100]$; see Methods. In parentheses are (standard error|p-value) of coefficient estimates. Regression constants are not reported.

Regression model (1) demonstrates that exogenous geography accounts for approximately eighty percent of the international variation in late Pleistocene biogeographic endowments $\tilde{A}_n$. Consequently, as shown in model (2), geography is an important indirect determinant of the Neolithic transition dates $\left(T-t_n^A\right)$ implied by biogeographic initial conditions in various parts of the world. Although the geography index is measured by current conditions (see the Methods section), the stabilization of climatic conditions after the Younger Dryas means that it gives a good first approximation to relative geographic conditions ca. 10,000 BC and afterward (with significant exceptions such as the desertification of the Sahara and parts of the Middle East during the Holocene). Although we do not pursue the topic here, geography is more important to the domesticable plants component of the biogeography variable than to the regional distribution of large domesticable mammals. Under the "blitzkrieg" hypothesis[21] the world distribution of large animals was significantly affected by the timing of the arrival of Homo sapiens in various parts of the world: The later Homo sapiens reached various regions the greater was their skill as "big game hunters" and the less experience their prey had with human predators, which resulted in rapid overkill and extinction of large animals in North America and Australia during the late Pleistocene.

Regression model (3) corresponds directly to the equation (20) and it therefore tests the strict implication of our stylised model of economic development over twelve millennia for the effect of biogeographic initial conditions on contemporary prosperity. Along with models (4) and (5) these results show that geography and biogeography alone can explain between fifty and sixty percent of present-day international variation in log output per capita. Note that 'biogeography' here means biogeographic initial endowments $\tilde{A}_n$ as transmitted to per capita incomes through the transition function $\left(T - t_n^A\right)$ as defined in Table 3. In view of the imprecise measurement of biogeographic conditions in particular, these results are remarkable evidence of the importance of geography and biogeography to economic prosperity. The statistical relationship implied by regression model (5) is graphed in Figure 3.

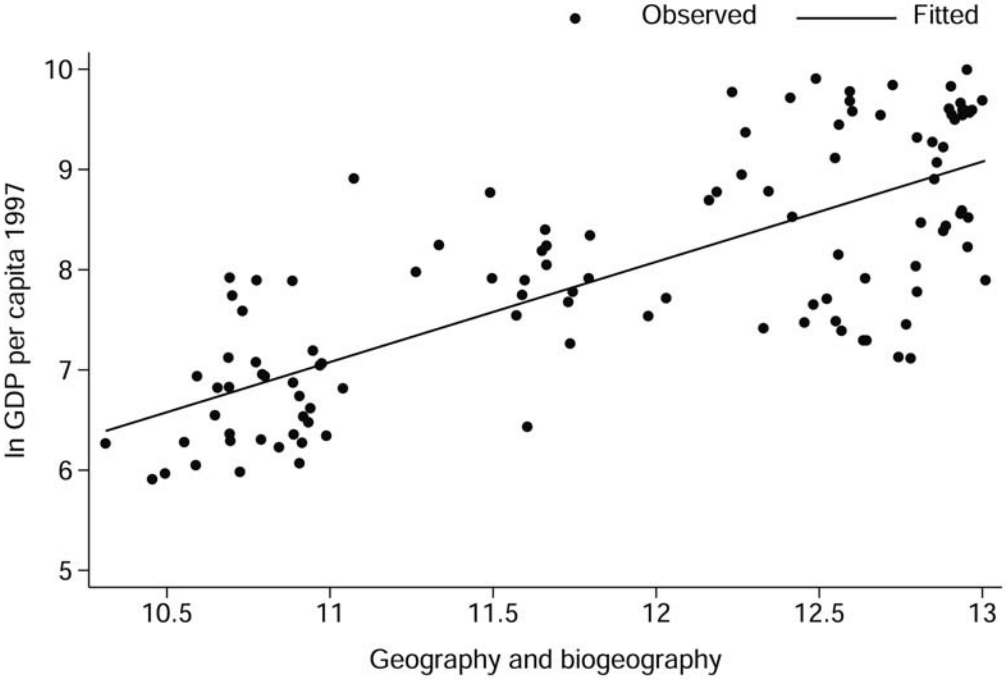

Figure 3 Impact of geography and biogeography on present-day per capita incomes. 'Geography and biogeography' is the sum log Geography, $\left(T-t_n^A\right)$ and $\left(T-t_n^A\right)^2$ weighted by the corresponding estimated coefficients of model (5) Table 3. The solid line is the regression slope of log GDP per capita on the linear combination.

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 around 600 dollars to around 8,800 dollars. However, incomes per head observed in the regression sample of N=112 countries are far more dispersed, ranging from 369 (Ethiopia) to 21974 (Luxembourg). 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 specification a standard measure of institutional conditions affecting security of property, rule of law and enforcement of contracts ("Institutions") that is identical or very similar to that used in many other studies[4-8,22]. (See Methods.) This model fits nearly eighty percent of the variation in log per capita incomes and comes much closer to tracking the full range observed cross-nationally. The estimates 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 dollars. 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, institutions and prosperity are almost surely jointly endogenous, if only because rich countries have the resources to build institutions of high quality. Consequently, the estimated effect of institutions on current log per capita incomes likely represents to some degree the consequences of reverse causation.

The same cannot be said, however, of our measurements of geography and biogeography, which are indisputably exogenous with respect to current incomes. Problems of joint endogeneity and reverse causation are therefore decisively ruled out with respect to these variables. Contrary to the conclusions of some studies[6-8], our results demonstrate that geography and biogeography retain statistical significance and substantive importance even when conditioned on institutional quality. This is true when geography and linear and quadratic terms in $\left(T - t_n^A\right)$ are included in a regression model jointly with Institutions, as in model (6) Table 3, or are included separately with institutions, as in regression experiments not reported that are available by request. The evidence therefore strongly favours the claim that geography and biogeography directly affect economic performance[22-25] rather than being wholly mediated by whatever influence they may have had in shaping historical development of institutions. Figure 4 shows the partial effects implied by regression model (6) of geography and initial condition biogeography by comparison to the partial effect of institutions.

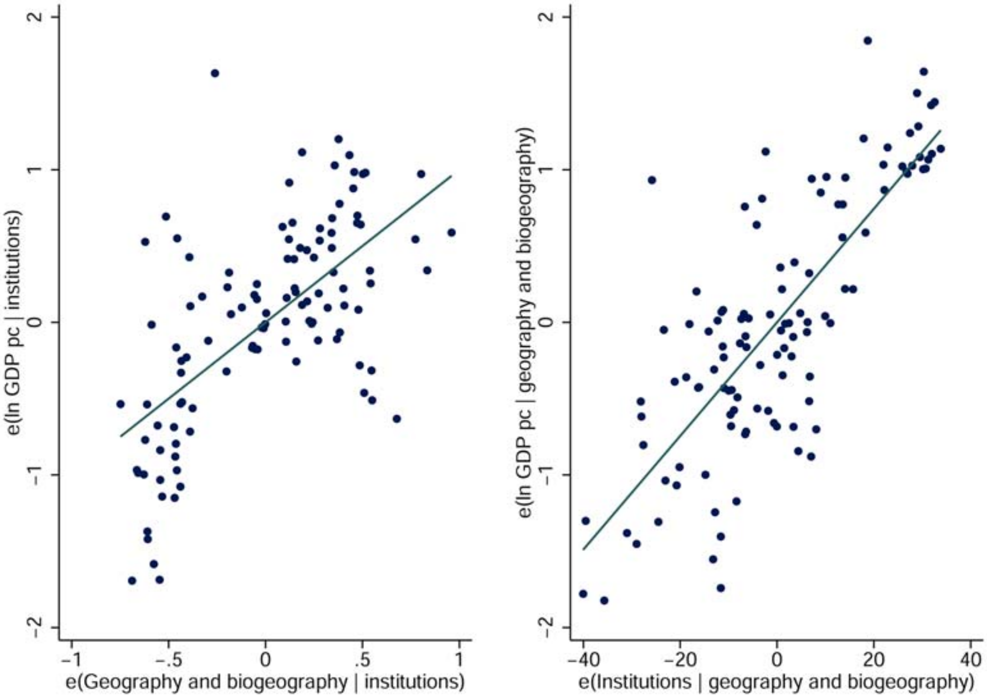

Figure 4 Partial regression plots of the response of log GDP per capita 1997 to geography and biogeography and institutions. 'Geography and biogeography' is the sum of log geography, $\left(T-t_n^A\right)$ and $\left(T-t_n^A\right)^2$ weighted by the corresponding estimated coefficients of model (6) Table 3.

It should be emphasized again, however, that institutional quality is an endogenous variable that most likely was affected historically by biogeographic endowments and geographic conditions[9]. In historical time our evidence therefore implies that geography and biogeography are the primes mobiles of current prosperity. Consequently, regression model (5) Table 3 and Figure 3 more accurately register the deeper effects of geographic conditions and biogeographic endowments on the wealth and poverty of nations than models that also include institutions, because the endogeneity of the latter attenuates estimated effects of the former.

Methods

Where not adequately specified in the main text, measurement of variables in the analysis was as follows. All series are available from the corresponding author.

Geography

Geography is one hundred times the average of three constituent variables after each was normalized $(0,1]$ by division of its maximum value in the N=112 country sample. Geography therefore varies $\left(0,100\right)$. The constituents are: (1) Climate as measured by a four point scale based of the Köppen classification and ordered in ascending value according to how favorable conditions are to agriculture: 1=dry tropical or tundra and ice, Köppen classification B and E. 2=wet tropical, Köppen classification A. 3=temperate humid subtropical and temperate continental, Köppen classification Cfa, Cwa and D. 4=dry hot summers and wet winters, Köppen classification Csa, Csb, Cfb and Cfc, which is particularly favorable to annual heavy grasses. The data were obtained from Strahler and Strahler[26]. (2) Latitude as measured by the absolute distance from equator in latitude degrees. The data are from the World Bank[27]. (3) East-West orientation of axis as measured by the distance in longitudinal degrees between the eastern and westernmost points of each continent and dividing this number by the distance in latitudinal degrees between the northernmost and southernmost points.

Biogeography

Biogeography $\left(\tilde{A}_n\right)$ is one hundred times the average of Plants and Animals after each was normalized $(0,1]$ by division of its maximum value. Plants denotes the number of annual or perennial wild grasses known to exist in pre-history with a mean kernel weight exceeding 10 milligrams. The data are from Blumler[11]. The geographical distribution ranges between 33 species in the Near East, Europe, and North Africa to 0 in the Pacific islands. Eurasia was divided into three subcontinents that had different and independent experiences of plant and animal domestication. The Western part reaches its limit in the Indus Valley in Pakistan, where the easternmost archeological evidence of crops from the Fertile Crescent have been found[13]. Southeast Asia includes Indonesia, the Philippines, and Papua-New Guinea. America was split up into three zones of independent agricultural origins; Central, North, and South. Caribbean islands and islands near Africa are regarded as belonging to the Central American and African zones respectively, while the Pacific islands (which are not in the sample analysed) are independent of the Asian zone of agricultural origin and hence had zero species suitable for domestication.

The variable $\left(T - t_n^A\right) = \left(12{,}000 - \frac{1}{\hat{\gamma}} \ln\left[\frac{\ln\left(1/\tilde{A}_n\right)}{\ln\left(\widehat{A^A}/\tilde{A}_n\right)}\right]\right)$ used in the regressions shown in Table 3 is created for each country from the biogeography variable $\tilde{A}_n$ discussed above and estimates of $\hat{\gamma}, \widehat{A^A}$ reported in Table 2. The European food and technology package was wholly transferred by Britain to the neo-Europes Australia, Canada, New Zealand and the United States and these countries are therefore imputed with Britain's value of $\left(T - t_n^A\right)$, 9847. The same transference occurred by varying lesser degrees in many other former colonial nation states but we were unable to calibrate this. It is a source of imprecision in estimation of the influence of effective biogeography on current incomes.

Animals denotes the number of domesticable mammals weighing more than 45 kilos, which are believed to have been present in pre-history in various regions. 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[9]. Of these 14, western Eurasia and North Africa had access to 9, Eastern Eurasia 7, Southeast Asia 2, Central and North America, Sub-Saharan Africa, Australia and the Pacific islands 0[12]. Early hunter-gatherers across the world typically had access to between 3-4 domesticable animals.

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[4]. The constituents are (1) quality of bureaucracy, (2) rule of law, (3) government corruption, (4) risk of expropriation and (5) risk of government repudiation of contracts. Scores on these variables were averaged over the period 1986-1995 and multiplied by one hundred after division by the maximum value, which yielded a $(0{,}100)$ index.

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Competing interests statement

The authors declare that they have no competing financial interests.

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