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HIGHER SCHOOL OF ECONOMICS

Andrey Shcherbak

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GENETIC ADAPTATION TO
ENVIRONMENT: THE EFFECT OF
LACTASE PERSISTENCE ON
CULTURAL CHANGE**

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*Andrey Shcherbak*¹

DOES MILK MATTER? GENETIC ADAPTATION TO ENVIRONMENT: THE EFFECT OF LACTASE PERSISTENCE ON CULTURAL CHANGE

Considering diet as often a product of adaptation to geographic environment, this paper suggests that not only the amount of food (food abundance) is important, but what kind of foods people eat may also affect social change. One of the reasons for variation in diet is food intolerances as a result of adaptation to the environment. This paper investigates one case – lactase persistence. This trait is associated with different genotypes of the LCT gene. Lactase persistence is mostly spread among northern Europeans, and is also found among some African and Asian nomadic populations. Such a unique trait is usually explained in the gene-culture coevolution framework: selective pressure for it had to be followed by the expansion of dairy production and herding. Empirical analysis based on 78 populations reveals strong and positive association between a lactase persistent population and the distribution of emancipative values. The suggested causal mechanism is a change in demographic trends: the effect of lactase persistence on the emancipative values is mediated through historically lower fertility and lower child mortality rates. This demographic transition results in higher value of human life, formation of human capital, economic development and finally cultural change.

JEL classification: I15, Q57

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¹ National Research University Higher School of Economics, Research Fellow, Laboratory for Comparative Social Research, the Research Fellow; E-mail: ascherbak@hse.ru

Introduction

Development in a broad sense – understood as social, economic and cultural change – has many explanations. Some scholars put emphasis on historical legacies, religious traditions, institutional solutions, technological innovation or even good luck. Without any previous attempts to challenge the significance of these factors, this paper endeavors to make a contribution to this discussion. The suggested interdisciplinary approach stresses the importance of genetic diversity as a factor of social and cultural change. Genetic diversity may be also considered as an outcome of human adaptation to the environment – in particular, geographic conditions. The variety of ecological niches may be reflected in the variety of social structures.

This paper particularly focuses on the relationship of lactase persistence and cultural modernization. Some populations show unprecedented high levels of lactase tolerance, especially in North Western Europe; surprisingly, these societies happened to be pioneers of modernization. This study assumes that it is not a spurious correlation, and lactase tolerance turned out to be a significant factor of development from a historical perspective. One may argue only about indirect relationship between the ability to digest lactase and development, and causal mechanisms are the key to understanding this phenomenon.

Existential conditions and cultural change

Why are non-social factors like natural disasters, climate, geography, infections and genetic diversity so important? These factors determine the environment where human populations live; they are factors of existential hardships that these populations face on the everyday basis. Physical environment affects cultural adaptation and development, including social norms. Jared Diamond in his seminal work “Guns, germs and steel” (1997) argues that climate and geography have an enormous impact on human development. The abundance and variety of crops and animals for potential domestication allowed an earlier shift from hunter-gathering to sedentary agriculture – and a dramatic rise in the production of food. As a result, population increases and social structures became more complicated.

Existential conditions have an impact on people's life perceptions: under harsh conditions, people perceive life as a source of threats and under comfortable ones as a source of opportunities.

How can culture be dependent on existential conditions? In their seminal paper, Gelfand et al. (2011) argue that societies which live under harsh conditions – with higher population density, lower food supply and production, higher infant and child mortality and with higher probability of natural disasters, famine, epidemics and territorial disputes with neighbors – are likely to have tight cultures. A tight culture is defined as one with dominating rigid cultural norms, multiple taboos (stressing obedience, conformism and collectivism) and severe sanctions for their violation. A loose culture is defined as a culture with flexible norms, few taboos and mild sanctions for their violations. Empirical analysis shows that tight cultures are associated with authoritarian institutions. Culture is functional to historical and ecological contexts.

Culture is understood within the framework of the revised modernization theory – as a value system, and cultural change is understood as value shift. Here I rely on the emancipative values concept from Welzel and Inglehart. In its last version this approach is presented as a theory of emancipation (Welzel 2013). On an empirical level, emancipative values measure a country's mean emphasis on freedom of choice and equality of opportunities based on twelve items from the World Values Survey polls. The emancipation theory holds a few assumptions about a value shift. First, objective improvements in ordinary people's conditions are required – for example, higher life expectancies, longer education, broader information access and better technological equipment (Alexander, Welzel, Inglehart 2014). Second, when these improvements spread on a large scale, people change their attitude to their lives – from life as a source of threats to the life as a source of opportunities. As Welzel and Amy argue, “In the course of this transformation, people's actions change from what external needs force them to do to what inner drives encourage them to do” (Alexander, Welzel, Inglehart 2014: 4). Finally, societies ascend the “utility ladder”: people rely on universal freedoms to take advantage of opportunities offered by a better life.

Empirical analysis shows that developed countries have higher means of emancipative values scores. The emancipative values index (EV) is also highly correlated with other indicators of development – such as the Human Development Index, Freedom House score and GDP per

capita. It is consistent with the revised modernization theory that argues that socio-economic progress is a precondition for cultural and then institutional change (like a transition to democracy). Therefore, this study suggests an additional link between existential conditions and cultural orientations.

Value change is measured by the spread of EV and in this context it is the key indicator of modernization and emancipation. EV scores are highly and positively correlated with previous measures for value change (self-expression values) and conventional indicators of development – HDI, GDP per capita and Freedom House score.

Genes and food traditions

Diet is an essential part of the environments where people live. One would expect that like water, infections and climate, diet should have a significant impact on social and cultural change. Climate, geography and food production are closely connected. As Diamond argues (1997), geographic conditions of Eurasia were the most favorable for earlier sedentary agriculture due to abundance of domesticated cereals and animals. Ever-increasing food production led to earlier population growth and the emergence of division of labor, social stratification, urban settlements, and ancient states. In other words, Diamond stressed the importance of the *amount* of food available to human populations: abundance of food accelerates social development. But he did not really focus on *what kind* of foods people eat, and whether it could have any social effect. In fact, a diet is a product of adaptation to environment. For two different populations, a similar number of calories may be comprised of various products. This paper argues that this difference can be important for understanding social and cultural change from a historical perspective.

Genes often play an important role in the adaptation to an environment. For example, the ‘thrifty genotype hypothesis’ argues that the human genotype is historically designed for hunter-gatherers. A set of diseases is caused by progress and civilization, including obesity, diabetes, and hypertension. One possible explanation of this phenomenon is that social and cultural progress makes some genes ‘irrelevant’. For thousands of years hunter-gatherer populations were living in the ‘feast-famine’ cycle. To ensure survival during periods of famine, certain genes

evolved to regulate the efficient intake and utilization of fuel stores. Now, the combination of a continuous and permanent food abundance and physical inactivity eliminates the evolutionarily programmed biochemical cycles emanating from feast-famine and physical activity-rest cycles, which in turn abrogates the cycling of certain metabolic processes, ultimately resulting in metabolic derangements such as obesity and Type 2 diabetes (Chakravanty, Booth, 2004; Brooks, 2011). For many thousands of years human populations adapted to low-carbohydrates, low-cholesterol, low-calories and low-salt diet; and the thrifty genotype reflected that. At the present time, change in lifestyle, population size, economy, climate change and diet are among factors affecting genetic selection.

The combination of geographic conditions, climate and available sources of food causes genetic adaptation to diet. Research provides evidence of genetic adaptation to the consumption of milk, sugar, mushrooms, starch, beans, etc. (Kozlov et al., 2005; Borinskaya et al., 2009; Perry et al., 2007). The frequency of genes responsible for the digestion of these products varies significantly among populations. In many cases, low or high frequency of a particular gene/allele is associated with a specific food intolerance.

One of the most interesting cases is maldigestion of lactase (milk). Lactose intolerance is an inability to digest lactose, a sugar found in milk. Lactose is normally broken down by an enzyme called lactase. Lactase activity has an expressed age relation: normally, after two years children show reduced production of lactase. Lactose intolerance or hypolactasia is associated with the gene LCT. *LCT* C/T -13910* genotypes are associated with lactase intolerance among European populations (e.g., Ingram et al., 2009; Itan et al., 2010). Genotype C/C was reported to be responsible for hypolactasia.

The frequency of lactase intolerance (primary hypolactasia) varies dramatically among populations from 2% (Danes) to 100% (Chinese, Japanese, and Vietnamese) (Kozlov et al., 2005; Borinskaya et al., 2006).

How to explain this variation? There are four main theories that explain uneven distribution of lactase persistence. First, it is '*the arid environment hypothesis*' that argues that in arid areas milk was the only pure liquid available for drinking. Therefore, populations had to adapt to avoid death from dehydration or diarrhea. This concept applies to pastoralist populations.

Second, it is *the gene-culture coevolution theory* that supposes a nutritional advantage of lactose digestion in pastoral populations. Some studies argue that lactose deficiency is found among populations which have never practiced dairy farming: absence of dairy products leads to hypolactasia. Bloom and Sherman (2005) extend this analysis further by showing that the distribution of lactose intolerance is also correlated with the historical distribution of communicable diseases of cattle. Hence, the ecology of disease influenced the likelihood of herding being adopted by our ancestors, and this in turn generated a selective force for a change in our digestive system.

Third, *the calcium assimilation theory* suggests that carriers of the lactase persistence allele(s) are favored in high-latitude regions, where sunshine is insufficient to allow accurate vitamin-D synthesis. The lowest frequencies of hypolactasia were found in North-Western Europe, in the areas with the lowest levels of insolation. A low level of insolation means there is a deficit of vitamin D; milk and dairy products are calcium-rich and a substitute for vitamin D. Lactose activity after infancy among North-Western European populations was likely to be an instrument of genetic adaptation to the environment (Borinskaya et al., 2006; 2009). Moreover, this area shows the highest genetic variation of cattle. Recent genetic evidence indicates that lactase persistence has evolved independently in African and European populations, perhaps associated with the independent development of dairying. Other studies argue that in some North-Western countries lactose persistence could be better explained not by adaptation and strong selection pressure for lactose tolerance but immigration of lactose tolerant populations (Vuorisalo et al., 2012).

Forth, *the reverse cause hypothesis* suggests that a dairy diet was introduced after the mutation (an ability to digest milk) became more common.

Some studies revealed that the calcium assimilation hypothesis is a more plausible explanation for lactase persistence in Europe, and gene-culture evolution in Africa (Gerbault et al., 2009). Moreover, archeological data shows that in Medieval Europe *LCT*C/T-13910* polymorphism has similar frequencies as in contemporary Europe (Kruettli et al., 2014). Another study suggested that contemporary Berber populations possess the genetic signature of a past migration of pastoralists from the Middle East and that they share a dairying origin with Europeans and Asians, but not with sub-Saharan Africans (Myles et al., 2005). In Neolithic Europe LP allele frequencies were extremely low, even among early farmers (Burger et al., 2007). Only since

7900 years ago may one find evidence for the use of dairy products in Europe (Gebrault et al., 2011). Scholars argue about the effect of migration (Vuorisalo et al., 2012) and positive selection on this trait (Gebrault et al., 2011). Although in terms of evolution it is an example of unprecedented fast positive selection, in general, genetic drift takes millennia. Therefore, allele frequency is treated as a constant from a historical perspective.

In other geographic areas various genotypes were reported to be associated with lactase intolerance: LCT^*C/C -13907 in Africa and LCT^*G/G - 13915 in North Africa and Middle East (Itan et al., 2010).

Table 1. Lactase intolerance frequency, % population.

Population	LCT* C/T -13910 genotype frequency	Lactase intolerance. share of population
Dutch	0.344	0.02
Danes	0.212	0.03
Swedes	0.069	0.03
Irish	0.148	0.04
English	N/A	0.060
Finns	0.173	0.170
Germans	0.437	0.148
Estonians	0.486	0.280
Hungarians	0.641	0.370
French	0.542	0.370
Russians	0.740	0.36-0.53
Greeks	0.925	0.450
Italians	0.829	0.710
Koreans	1.000	0.750
Iranians	0.810	0.860
Han	1.000	0.920
Malaysians	1.000	0.880
Japanese	1.000	1.000

Source: the ALFRED database; Borinskaya et al., 2009; Borinskaya, unpublished data.

Lactase persistence and social effects

There are few papers that focus on the social effects of variation in lactase intolerance among populations. They reveal the relationship between lactase persistence and population density, expansion, marriage patterns, cultural restrictions and diseases.

Cook in his recent paper (2014) tested the effect of lactose persistence on pre-colonial population density in Eurasia and revealed strong and positive relationship between the digestion of milk and an increase population density. He argued that for preindustrial societies that are entrapped in a 'Malthusian economy' (where any improvement in technology leads to a temporary increase in income and to a permanent increase in population) milk is an essential source of calories (as well as proteins, vitamins, etc.) that affects population growth and population density. Moreover, a farmer who is able to digest milk immediately gains an additional resource from his set herd of cattle and is able to support a larger family. Finally, cow milk can be regarded as a substitute for mother's milk. The use of cow milk would have reduced weaning time, shortening the postpartum infertility period (Cook, 2014: 5). Cook reveals through a number of specifications that country-level variation in the frequency of lactase persistence is positively and significantly related to population density in 1500 CE.

In another paper Cook (2014a) tests the interaction effect between the frequency of lactose persistence and potato consumption on early industrial population growth (1700-1900) and shows that the marginal effect of potatoes on post-1700 population growth is positively related to milk consumption. He assumes that milk and potatoes are complimentary: milk is high in protein and fat, while potatoes are high in calories and carbohydrates. In both papers Cook used the population level data on lactose persistence, but he converted them into country level figures using historical data for ethnic composition.

In their book, Cochrane and Harpending (2009) argue that a high frequency of the European lactose-tolerance mutation (the 13910-T allele) was the driving advantage for Indo-European expansion. They argue that raising cattle for dairying is much more efficient than for slaughter: It

produces about five times as many calories per acre (Cochrane and Harpending, 2009: 181). It means that Proto-Indo-Europeans could raise and feed more warriors on the same amount of land “and that is a recipe for expansion” (Cochrane and Harpending, 2009: 181). After the steppe, the Indo-European expansion continued on into Europe, where dairying was ecologically competitive with early agriculture and produced a far more aggressive culture. Most likely, Indo-European culture became more warlike as their mobility, superior numbers, and better nutrition allowed them to win battles more often than other people (Cochrane and Harpending, 2009: 184). Therefore, lactose tolerance became a driving force of Proto-Indo-European expansion.

Reilly in his article (2013) focuses on the relationship between lactase persistence and the proliferation of consanguineous marriage patterns (marriage between second cousins or more closely related individuals) in the Middle East (from 15.3% in Morocco to as high as 65% in Sudan), especially among Bedouins. He suggests that high rates of LP among Bedouins are a key explanation. In the arid climate, without access to (safe) water, camel milk was the only source of fluid (and food) available for pastoralist Bedouins. Among camel-breeding Bedouins, who depended heavily on the lactase persistence allele for their subsistence, any marriage practice that maximized the frequency of this allele in the lineage would be favored over alternative marriage strategies. As a result, the selective pressure exerted by LP alleles led to the proliferation of two particular marriage strategies – consanguineous marriage and “virtual consanguineous” marriage (Reilly, 2013: 375).

Baten and Blum in their recent paper (2014) studied the determinants of the biological standard of living in the 19th–20th centuries, using average heights as a proxy. They revealed that high-quality nutrition – milk consumption and meat consumption – were among the major determinants of height from a global perspective. Their sample included countries from Europe, Asia, Africa, America and Australia. Until the mid-20th century local availability of cattle, milk and meat per capita determined the stature of populations. To separate the ability to digest milk and the availability of cattle, they use LP as an instrumental variable in their models. Higher levels of lactose tolerance lead to higher levels of milk consumption – resulting in higher statures.

In another paper Koepke and Baten (2008) focused on height determinants only in Europe but looked at a deeper historical perspective – from 1 to 1800 AD. Using cattle bone shares as proxies for meat and milk consumption, they argued that along with land per capita,

specialization in milk cattle agriculture was the main height determinant in the Malthusian world. Thus, historically LP and milk consumption are strongly associated with better biological standards of living.

Simoons (1973) describes a “non-milking attitude” in the societies without a dairy products culture. People of eastern Asia and tropical Africa share certain feelings about milking domestic animals and consuming their milk (Simmons, 1973: 84). In both areas, many people say that they do not know how to milk animals or it is unnatural to manipulate the udder of an animal. In eastern Asia, people sometimes protest the practice of milking as one of stealing essential food from the young nursing animal. Moreover, both Asian and African non-milkers believe that milk is an unclean animal fluid, like urine; non-milkers sometimes protest that milk is a disgusting white substance that both smells and tastes bad (Simmons, 1973: 84).

Cramer (1989; 1994) revealed an association between dietary galactose (a monosaccharide commonly ingested in a double sugar form combined with glucose in lactose) and ovarian function. Significant positive correlations were noted between ovarian cancer incidence, per capita milk consumption, and lactase persistence. He also argued that age-specific fertility rates in various countries correlate with the prevalence of adult hypolactasia and per capita milk consumption.

Nowadays, in modernizing societies like China and India, despite the absence of a tradition of dairying, milk is understood as an essential element of the modernization agenda (Wiley, 2011). Milk is strongly associated with calcium, and the latter with an increase in average height in society. Therefore, milk becomes a synonym for nation’s growth and strength: to catch up with the West means to narrow the gap in average height between East and West. More milk means a more visible achievement of modernization. To sum up, previous studies stress the role of social effects, mostly in the domain of historical demography.

Lactase intolerance and cultural change

The literature review demonstrates that the ability to digest milk is likely to be a nutritional advantage for populations from a historical perspective. Scholars stress its importance from a historical demographic and economic perspective. Genetic studies allow us to treat LP as a constant within populations/ethnic groups; it allows the incorporation of LP as an independent

variable in historical quantitative research. Making one more step further, I incorporate lactase persistence into the emancipation theory as a vital element of existential conditions. I assume that LP had a long-term positive effect on the improvement of existential conditions.

Milk was a new, nutritious, and energy-rich source of food, and individuals able to capitalize on this would have been at an advantage. Lactose tolerance is much more common in populations with a long history of livestock agriculture than in those with little or only recent history (Bruessow, 2013). Milk is a reserve food resource in times of famine or just before the next harvest when food reserves are at their annual low. Even when accounting for the lower productivity of prehistoric cows and the milk needed for raising the calves, it was estimated that about 200 kg of milk were then a surplus per cow and per weaning period (Gerbault et al., 2011). A liter of whole milk contains approx. 720 calories; dairy products from the same amount of milk contain only about 400 calories. Moreover, milk is rich in proteins and vitamin D; it is an important supplement to the basic monocereal diets.

I suggest that such a nutritional advantage might have contributed to lower inequality in those societies. Inequality is understood not in income or status terms but rather in a) nutritional (well-fed elites vs. starving lower classes with poor monocereal diets), b) exposure to disease (better diet is associated with better health), c) physical strength (better diet and better health make people stronger; that's crucial in the cold arms age) and d) reproductive advantage (better health and lower exposure to disease) terms. My guess is that lower classes had more opportunities and resources to protect their autonomy against claims from ruling elites. Lactose persistence and milk consumption thus contributed to the formation of individual autonomy. Early spread of individual autonomy became an advantage for modernization, and later for human empowerment. Individual autonomy and modernization are associated with the distribution of emancipative values. Some scholars provide historical evidence that the distribution of income in Europe was “unusually equal” compared to Asia (Jones, 2003: 5).

Thus, lactase tolerant societies had greater chances for social and cultural modernization. What are the causal mechanisms of this change?

My hypotheses are

H1: The higher the share of population with the lactose persistence phenotype in a given country, the higher the Emancipative Values score.

H2: The causal mechanism is the demographic change: the effect of lactase persistence on the emancipative values is mediated through historically lower fertility and child mortality rates.

Data and variables

Given the nature of my approach, I am going to test the effect of LP from a historical perspective. I assume that earlier changes affected the chances for modernization. Therefore, for my independent variables I take historical estimates of country-level predictors from various sources. The emancipation theory usually indicates the Modern time as the starting point of modernization. Ideally, I would prefer to have numerous estimates from different time points in history for most of the variables. Unfortunately, it is not possible for most of the indicators. Nevertheless, I try to take the earliest estimates for my independent variables.

My key dependent variable is **Emancipative Values (or *Obedient-vs.-Emancipative Values*)** - Emancipative values are a multi-point index from minimum 0 to maximum 1.0 based on twelve items from the WVS. On the conceptual level, emancipative values appreciate a life free from external domination, therefore these values emphasize equal freedoms for everyone. Thus, emancipative values involve a double emphasis on freedom of choice and equality of opportunities. The higher the index is, the more emancipated, progressive and modernized a given society is. The highest scores are among such countries as Sweden (0.781), Norway (0.681), Denmark (0.638), Germany (0.608) and Netherlands (0.604); “outsiders” are Yemen (0.216), Jordan (0.227), Iraq (0.231), Pakistan (0.239) and Nigeria (0.260). These index values were taken from Welzel (2013). This index strongly correlates with previous measures for cultural modernization – Secular-Rational vs. Traditional values and Self-Expression vs. Survival values (Inglehart, Welzel, 2005).

Lactase persistence frequency – frequency of the LP phenotype among selected 78 populations. I take population-level data from Ingram et al. (2009) and convert them into country-level data using Cook’s approach (2014), which is based on ethno-linguistic approximation.

LCT* C/C –13910 – frequencies of *LCT* C/C –13910* genotype among the selected 41 populations. To be included in the sample, a population had to be referred with a country from

the WVS database. Therefore, I had to omit multiple small ethnic groups, like Yakuts, Chukchi, Sardinians, Basque, etc. Data was taken from the ALFRED database and Borinskaya (unpublished data).

The description of all other variables as well as descriptive statistics can be found in the Appendix (see Tables S1 and S2).

In this paper I adopt Cook’s empirical strategy to create a country-based estimate for lactase persistence frequency. Cook (2014; 2014a) converts population-based data on lactase persistence (phenotype) into country-based data in three steps. Firstly, he takes data on the contemporary ethnic composition of existing polities from Alesina (2003). Secondly, he adjusts data on lactose persistence for populations from Ingram (2009) to ethnic groups indicated in Alesina using linguistic approximation. Finally, he calculates country level estimates for lactose persistence for 118 countries. This method is not an ideal one; some cases are likely to be biased, but it helps to shift to country-level data. Cook calculated lactose persistence values for 1500 CE; however, he provided a matrix of ethnic/country composition for contemporary states. I used this matrix to calculate estimates of lactase persistence; in some cases I used Ingram’s (2009) calculations of country level frequency of milk digestors (2009: supplementary material). My new sample includes 78 cases (Europe – 41, Asia – 25, Africa – 12).

Table 2. Means for lactase persistence among regions.

Total (N=78)	Europe (N=41)	Asia (N=25)	Africa (N=12)
0.472	0.633	0.301	0.276

Source: Ingram et al. (2009). Cook (2014)

Results

My first step was to test the relationship between the frequency of LP and the Emancipative Values Index (EVI). To do that I ran several OLS models with EVI as a dependent variable (see Table 3). Model 1 includes only the independent variable – LP. The effect is strong and with

predicted sign (0.637). In model 2 I use a conservative sample (only 28 cases), without an ethnolinguistic approximation – where ethnic majority can be easily matched with polity; instead of LP frequency (phenotype), I use LCT*C/C – 13910 frequency (genotype). Again, the effect is strong and significant (-0.724); the negative sign means that the lower genetic inability to absorb lactose (hypolactasia), the higher the EVI score. In model 3 and 4 I use another dependent variable – the Human Development Index, one of the most popular indicators of modernization. In all models LP and LCT*C/C – 13910 are significant and with predicted sign (0.521 and 0.545, respectively). In Model 5 I included income per capita (log GDP per capita) in 2000 as a control variable: the revised modernization theory argues that income growth always precedes value change. The effect of LP remains strong and significant (0.465). In Model 6 I also added continental dummies (Asia and Africa); the effect of LP is significant again (0.308). Finally, in model 7 I also added several geographic and historical variables – Ln Millennia of agriculture, Ln Land Productivity and Ln Absolute Latitude – to control for geography, history of agriculture and initial quality of arable land. Even in this specification, the effect of LP is significant (0.340) and among controls only absolute latitude is insignificant. All these models show that the effect of LP is significant and not sensitive to various controls. The H1 hypothesis is confirmed. From a long-term perspective, lactase tolerant societies had higher chances for modernization and transition to emancipative values.

Table 3. The effect of Lactase Persistence on Emancipative Values Index.

	<i>Standardized Beta – coefficients</i>						
	<i>Model 1</i>	<i>Model 2</i>	<i>Model 3</i>	<i>Model 4</i>	<i>Model 5</i>	<i>Model 6</i>	<i>Model 7</i>
			<i>HDI</i>	<i>HDI</i>			
Lactase persistence frequency	0.637*** (0.03)		0.521*** (0.051)		0.465*** (0.041)	0.308*** (0.051)	0.340*** (0.058)
LCT C/C – 13910 genotype frequency		-0.724*** (0.051)		-0.545*** (0.048)			
Log income 2000					0.382*** (0.009)	0.417*** (0.010)	0.460*** (0.011)
Ln millennia of Agriculture							-0.255 ** (0.027)
Ln Absolute Latitude							0.035 (0.015)
Ln Land Productivity							0.240 ** (0.009)
Continental	N	N	N	N	N	Y	Y

dummies							
<i>R-square</i>	0.405	0.525	0.273	0.297	0.538	0.573	0.684
<i>Adjusted R-square</i>	0.397	0.507	0.263	0.271	0.525	0.549	0.648
<i>Observations</i>	78	29	77	29	77	77	70

*- significance on 0.1 level, ** - significance on 0.05 level, ***- significance on 0.01 level

Now the key question is how to explain the relationship between the prevalence of lactase persistence and the distribution of Emancipative Values from a historical perspective? My next step is to test my second hypothesis about potential causality. To do that I ran two path-analysis models.

Causal mechanism

The suggested causal mechanism that can explain the relationship between LP and Emancipative Values is *demography*: LP is crucial for a demographic transition that stresses the importance of individual autonomy.

I find strong correlations between LP and fertility rate in 1800 CE ($r=-0.542$, $p=0.000$, $N=76$), child mortality in 1800 CE ($r=-0.453$, $p=0.000$, $N=78$) and milk consumption in 2000 CE ($r=0.714$, $p=0.000$, $N=74$) (both Pearson's correlations). I expect Lactase persistence to be associated with lower fertility. According to Oded Galor's 'unified growth theory' (2011), lower fertility (even if only somewhat lower) is crucial for economic development because it frees up time for human capital formation and innovation at the grassroots level of society.

To test my causal hypothesis I created path-analysis models, where the Emancipative Values Index is the dependent variable and LP is the independent variable. I ran two models: Model 1 tested the effect of LP on EVI via Child mortality 1800 and Fertility 1800. Model 2 added Pathogens Index as an additional control. All models were run in MPlus.

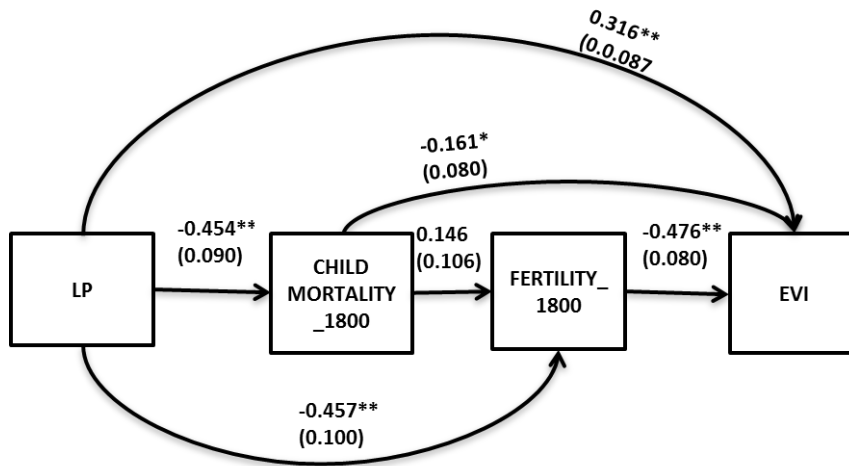


Figure 1. Model 1.

CFI = 1.000, RMSEA = 0.000, SRMR = 0.00, AIC = 828.840, BIC = 857.121, N = 78

Model 1 (see Fig. 1) shows that LP has a strong effect both on Child mortality (-0.454), Fertility (-0.457) and EVI (0.316). Child mortality has a weak but significant effect on EVI (-0.161) and no effect on Fertility. Finally, Fertility has a strong effect (-0.476) on EVI. All signs are as predicted by theory; the fit indices indicate the high quality of the model. The only insignificant link in the model – between child mortality and fertility – just says that the relationship between these two factors has a more complex nature than one might assume.

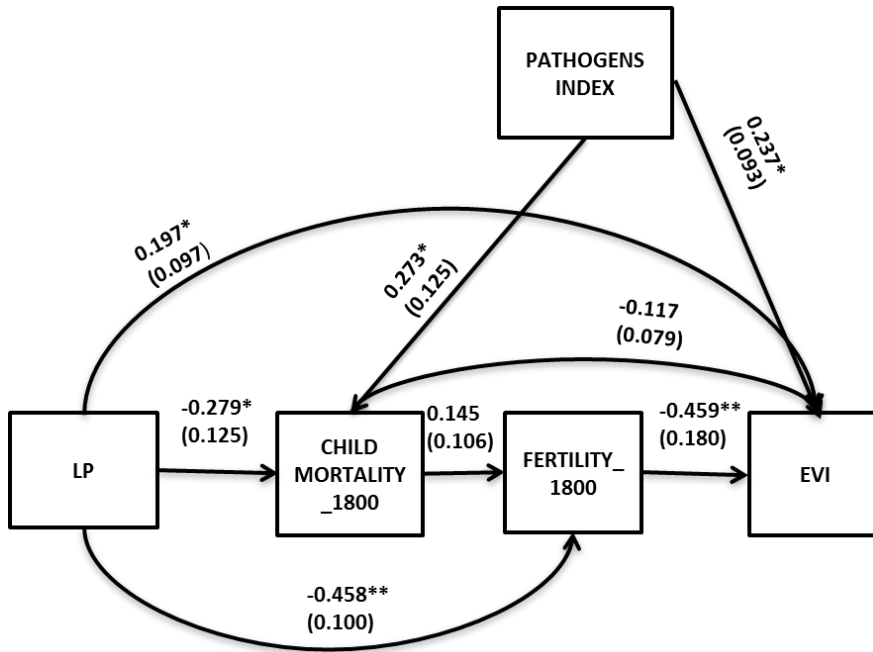


Figure 2. Model 2.

CFI = 1.000, RMSEA = 0.000, SRMR = 0.017, AIC = 822.046, BIC = 855.040, N = 78

Model 2 (see Fig. 2) shows similar results to the previous model. With some insignificant links omitted for better quality of the model, LP has a strong effect on Fertility (-0.458), Child mortality (-0.279) and EVI (0.197). Fertility has a strong effect on EVI (-0.459). Again, all signs are as predicted by theory; the fit indices indicate the high quality of the model. The Pathogens Index is significant for Child mortality (0.273) and EVI (0.237). In general, this model shows that Fertility is the most significant component between LP and EVI. This finding is consistent with the ‘unified growth theory’ by Galor (2011).

Discussion and Conclusion

Recent studies (Thorhill et al., 2009; Murray and Schaller, 2010) show that climate and pathogens load are vital for the development of human populations. High pathogens load impedes social, economic and cultural development. A higher historical pathogens load is associated with higher levels of collectivism, and a lower level of individualism (Murray and

Schaller, 2010). Societies under threat of frequent epidemics are much more intolerant to out-groups – what promotes collectivism and authoritarianism.

A severe environment means more existential hardship for human societies. In-group solidarity, collectivism is a psychological response to existential hardship. Moreover, collective discipline favors authoritarian institutions as a tool of enforcement. Where existential pressure is not perceived as a vital threat, individualism has more chances to expand (Welzel and Inglehart, 2013). Welzel and Inglehart (2013) also focus on the critical significance of the open access to water resources, which is defined as ‘cool-water’ environments. These environments combine 1) fairly low average annual temperatures with 2) continuous rainfall over all seasons and 3) the presence of permanently navigable waterways. The regular precipitation in CW-environments makes fresh water permanently accessible to everyone (Welzel and Inglehart, 2013:8-9). Moreover, relatively cold waters are safer due to lower levels of infestation. Access to a water supply is an important precondition to existential autonomy, and vice versa, control over water supply historically opens a route to despotism (Wittfogel, 1957).

Lactase persistence as a product of genetic adaptation to the environment is a unique feature of European societies. Milk and dairy products became an essential part of the European diet, especially in North-Western Europe. This paper argues that LP affected not only diet *per se* but social and cultural change from a historical perspective. Our tests reveal a strong and positive relationship between LP and the Emancipative Values Index as an indicator of modernization. Interestingly, developed countries are milk-drinkers and lactase tolerant. We argue that it is not a spurious correlation; historically, lactase tolerant societies had more opportunities for development. We assume that milk and dairy products were not only a nutritional advantage but also of social and economic benefit. A possible causal mechanism was suggested and tested. It puts emphasis on demographic change: lactose tolerance is associated with lower fertility rates and child mortality rates. Later this process resulted in individualization and higher education rates.

Alternative mechanism stresses the effect of LP on social and economic structure: lactase tolerant societies could maintain more non-agricultural producers and had higher urbanization rates. Europeans had a specific type of agriculture based on the integration of crop growing and cattle husbandry. In fact, they had more cattle and could substitute human muscle power with

animal muscle power. Thus, a larger share of manpower could be ‘liberated’ and channeled to war and industry. Lactose tolerant societies had a slightly more cattle per capita and higher urbanization rates. Urbanization is an important prerequisite for modernization. However, although OLS tests have provided some evidence to this mechanism, the path-analysis has revealed statistical insignificance of all tested models.

Our study stresses the importance of human adaptation to the environment – not only on the social level, but also on a biological one. Lactase persistence and a relatively higher level of dairy products (very rich in animal proteins) turned out to be an advantage – both nutritional and social – for European populations.

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Appendix

Table S1. Description of variables

Concept	Year	Description	Source
Emancipative Values Index	1995-2005	Emancipative values are a multi-point index from minimum 0 to maximum 1.0 based on twelve items from the WVS. On the conceptual level, emancipative values appreciate a life free from external domination, for which reason these values emphasize equal freedoms for everyone. Thus, emancipative values involve a double emphasis on freedom of choice and equality of opportunities.	Welzel (2013)
Lactose persistence frequency	Timeless	Frequency of the LP phenotype among selected 78 populations.	I take population-level data from Ingram et al. (2009) and convert them into country-level data using the Cook's approach (2014), which is based on ethnolinguistic approximation. Cook's online appendix to his papers (2014)
Pathogens Index	Timeless	Index of historic pathogen prevalence, for 7 diseases (leishmaniasis, schistosomes, trypanosomes, malaria, filaria, dengue, typhus), from D.Murray&M.Schaller. The higher values – the higher is the historical pathogen load.	For detailed description of data see Murray and Schaller (2010)
Fertility rate 1800	1800 (the earliest year	Historical estimates of fertility rate in year	www.gapminder.org

	possible)	1800, children per woman with projections.	
Child mortality rate 1800	1800 (the earliest year possible)	Historical estimates of child mortality in the year 1800, per thousand children by age of five.	www.gapminder.org
Log Income per capita 2000	2000	GDP per capita, PPP (current international dollars)	World Development Indicators database
In Millennia of agriculture,	Since the onset of Neolithic revolution	The millennia since the majority of a country's population adopted agriculture for subsistence.	I take this data from These data are from the Cook's online appendix to his papers (2014). Originally, this data are from Putterman and Trainor (2006).
In Absolute Latitude	Timeless	The absolute value of a country's representative latitude. Representative latitude is given by the centroid latitude of a country	I take this data from the Cook's online appendix to his papers (2014). Originally, from <i>The World Factbook</i> (2011).
In Land Productivity	Timeless	Land productivity is the first principle component between a country's fraction of arable land and the country's suitability of agriculture. The fraction of arable land comes from the <i>World Development Indicators</i> . Suitability of agriculture is an index capturing soil and climate conditions favorable for agriculture.	I take this data from the Cook's online appendix to his papers (2014).

Table S2. Descriptive statistics for all variables

	N	Min.	Max.	Mean	St.Dev.
Emancipative Values Index	78	.22	.72	.4168	.10973
Lactase persistence frequency	78	.040	.976	.47204	.246867
LCT C/C -13910 genotype frequency	29	.038	1.000	.62066	.295869
Pathogens index 7 items	78	-1.05	1.19	-.0383	.60993
ln land productivity	70	-3.398	1.613	.36856	1.152701
ln millenia of agriculture	75	.336	2.351	1.74821	.422244
ln absolute latitude	74	.000	4.159	3.42073	.799500
fertility rate in 1800	76	4.04	8.10	5.9266	.98583
child mortality rate in 1800	78	322.40	540.44	409.5469	51.22916
HDI 2013	77	.435	.944	.75816	.126525
Log GDP per capita. PPP (cur. Int. dollars)	77	6.20	10.99	9.0236	1.12003

Andrey Shcherbak

Laboratory for Comparative Social Research, National Research University Higher School of Economics. 55-2, room 309, Sedova ul., St.-Petersburg, Russia 192171.
ascherbak@hse.ru

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