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Genetic influence on social outcomes during and after the Soviet era in Estonia

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The etiology of individual differences in educational attainment and occupational status includes genetic as well as environmental factors[1–5] and can change as societies change[3,6,7]. The extent of genetic influence on these social outcomes can be viewed as an index of success in achieving meritocratic values of equality of opportunity by rewarding talent and hard work, which are to a large extent influenced by genetic factors, rather than rewarding environmentally driven privilege. To the extent that the end of the Soviet Union and the independence of Estonia led to an increase in meritocratic selection of individuals in education and occupation, genetic influence should be higher in the post-Soviet era than in the Soviet era. Here we confirmed this hypothesis: DNA differences (single-nucleotide polymorphisms, SNPs) explained twice as much variance in educational attainment and occupational status in the post-Soviet era compared to the Soviet era in both polygenic score analyses and SNP heritability analyses of 12 500 Estonians. This is the first demonstration of a change in the extent of genetic influence in the same population following a massive and abrupt social change – in this case, the shift from a communist to a capitalist society.

Socioeconomic status (SES), a composite index of educational attainment and occupational status, has been shown to be associated with a range of life outcomes from life satisfaction and happiness, to physical and mental health, and even life expectancy[8–12]. Individual variation in SES in a population has often been assumed to be explained entirely by environmental factors. Twin and adoption studies, however, suggest that individual differences in SES are substantially genetic in origin[1–5], with heritability estimates from twin studies of about 50%, meaning that around half of the individual differences in SES can be explained by inherited differences in individual's DNA sequence. It is now possible to estimate heritability directly from DNA using hundreds of thousands of DNA differences (single nucleotide polymorphisms, SNPs) genotyped on microarrays (SNP chips) in samples of thousands of unrelated individuals[13]. Data of this sort are available for many traits, including SES, as a by-product of genome-wide association (GWA) studies. Unlike GWA analysis, which aims to identify specific SNPs associated with a trait, SNP heritability relates overall similarity between individuals across all SNPs on a SNP chip to the individuals' phenotypic similarity on a trait, without knowing which SNPs are associated with the trait.

SNP heritabilities have been estimated as about 20% for educational attainment, occupational status, and combined SES [4,14–18]. SNP heritability (20%) is less than heritability estimates from twin studies (50%) because SNP heritability, like GWA analysis, is limited to the additive effects of common SNPs included on SNP chips. For this reason, SNP heritability is the ceiling for GWA studies.

GWA data can also be used to create genome-wide polygenic scores (GPS) that aggregate thousands of SNP associations across the genome to predict the trait of interest. Individual SNP associations typically account for less than 0.1% of the variance, so are not individually useful for prediction. GPS can be created for each individual and correlated with a trait in an independent sample, which yields an index of what could be called *GPS heritability*, the extent to which GPS can explain variance in a trait. A GPS from a GWA study of educational attainment (*EduYears*)[19] predicts 4% of the variance of educational attainment in independent samples[19–22]. No GWA studies of occupational status have been reported, but educational attainment and occupational status correlate about 0.50 phenotypically[23–25], and the *EduYears* GPS for educational attainment predicts 2% of the variance of occupational status[21], 2% of the variance of SES[21,26], and 7% of the variance of family SES using children's DNA[27]. GPS heritability (2-7%) is lower than SNP heritability (20%) in part because GPS heritability is limited to specific SNPs shown to be associated with a trait and it includes the trait's measurement error.

Heritability -- including GPS, SNP and twin heritability -- refers to the proportion of individual differences that can be explained by inherited differences in individuals' DNA in a particular population at a particular time. It describes what is, not what could be[28]. The reported heritability of educational attainment and occupational status from twin studies differs across birth cohorts and across countries[2,3,5,19,6,7,29]. Specifically it has been hypothesized that heritability of educational attainment can change following reform in educational policy[2,6]. Higher heritability estimates in twin studies have been noted in countries where educational curriculum is highly standardized, such as the UK, because the standardization reduces environmental differences between schools[30]. However, research so far has yielded mixed results, with some studies showing change in heritability estimates following a change in curriculum, or changes in the heritability of achievement across birth cohorts, and other studies not showing such an effect[3,6,29]. The major limitation to date is that most research has been greatly underpowered; the twin method requires several thousand twin pairs to achieve sufficient power to detect such gene-environment interactions[31].

Few studies have investigated changes in SNP heritability as a function of environmental change[4,19]; this method requires several thousand unrelated individuals to detect gene-environment interactions. Only one study has explored secular changes in GPS heritability. Using *EduYears* GPS, GPS heritability of educational attainment was reported to be greater in older as compared to younger cohorts in Sweden[19]. This decline in heritability is opposite to the results found in a twin study in Norway[2] and also in recent meta-analyses of twin data[3]. However, no evidence has yet been reported for significant changes in GPS or SNP heritability estimates following a major and abrupt social change.

Here we use GPS heritability and SNP heritability to estimate genetic influence on individual differences in educational attainment and occupational status for 12 500 adults participating in the Estonian Genome Centre, University of Tartu (EGCUT). EGCUT affords the unique opportunity to compare heritabilities in a single population before and after the collapse of the Soviet Union. Estonia was occupied by the Soviet Union after World War II and regained independence in 1991[32].

The post-Soviet era is generally assumed to be more meritocratic in the sense that access to education and occupation is to a greater extent based on ability[32,33]. Given that education- and occupation-related abilities are substantially due to inherited DNA differences between individuals, the greater equality of opportunity implied by meritocracy should diminish the impact of environmental inequalities such as privilege or privation. Inherited DNA differences will remain and will account for a relatively larger portion of differences among individuals. In this sense, heritability can be viewed as an index of equality of opportunity and meritocracy. In an entirely genetically driven meritocracy, genetic differences in ability would account for all individual differences in educational attainment and occupational status. Environmental differences that convey privilege or privation would account for none.

We used the EGCUT sample to test the hypothesis that heritability of educational attainment and occupational status differs after a major environmental change. We compared SNP heritability and GPS heritability for educational attainment and occupational status before and after the collapse of the Soviet Union in Estonia. If independence led to greater meritocracy in terms of increased environmental opportunity, the heritability of educational attainment and occupational status should be higher for individuals who lived the majority of their studying and working lives in independent Estonia as compared to those who lived during the Soviet Union.

Supplementary Table 1 shows means and standard deviations for height, educational attainment, occupational status and SES for the whole sample, males and females separately and for historical eras separately. ANOVA results indicate that historical group and sex explained up to 4% variance for the SES variables. For subsequent analyses, we controlled for sex effects by using sex-regressed standardized residuals.

Figure 1 compares GPS heritability in the Soviet and post-Soviet eras for the *EduYears* GPS (see Methods). For the whole sample, GPS heritability was 1.9% for occupational status and 2.3% for educational attainment (Figure 1). Using the less stringent cut-off of 15 years (Figure 1a), GPS heritability was significantly greater in the post-Soviet era compared to Soviet era for occupational status and educational attainment (see Supplementary Table 2 for all comparisons). These results are based on a GPS calculated at a 0.1 GWA study p-value threshold, which provided on average the best prediction across phenotypes and across historical eras. (Supplementary Figure 1 shows variance explained across multiple thresholds.)

The more stringent cut-off of 10 years yielded even larger GPS heritability differences (Figure 1b). For occupational status, GPS heritability was significantly greater in the post-Soviet era (5.6%) compared to the Soviet era (1.7%). Similarly for educational attainment, GPS heritability was significantly greater in the post-Soviet era (6.1%) than the Soviet era (2.1%). (See Supplementary Table 2 for all comparisons, including the composite SES score.)

<< Insert Figure 1 here >>

The GPS heritability estimates for composite SES (see Supplementary Figure 1) in the post-Soviet era (~7%) are in line with the GPS heritability estimates obtained in the UK[27] , a meritocratic society, for family SES using offspring GPS. The difference arises from a significantly lower GPS heritability in the Soviet era. The results were very similar when additional analyses were run using variables that were not sex corrected (Supplementary Figure 2) and taking the transition period between Soviet and post-Soviet era into account (Supplementary Figure 3).

GPS heritability was also calculated for males and females separately (Supplementary Figure 4). The difference between GPS heritability in the Soviet and post-Soviet era was substantially greater for females compared to males, especially when a stricter cut-off of 10 years was used. This finding suggests that increased meritocracy after the Soviet era especially favored women, although the sample size and therefore the power of analyses were reduced when the sample was divided by gender.

We explored the extent to which the difference in GPS heritability between the Soviet and post-Soviet era differs by birth cohort. We divided the sample into birth cohorts using 10-year and 5-year intervals (Supplementary Figure 5). The difference in GPS heritability was greatest between the oldest and youngest birth cohort, the two birth cohorts that most clearly represent the Soviet versus post-Soviet. During the Soviet era, GPS heritability estimates fluctuate across birth cohorts but do not show a general trend of increasing GPS heritability, which could suggest that birth order itself underlies the Soviet versus post-Soviet GPS heritability difference. (See Supplementary Figure 6 for the distribution of sample size and SES for the Soviet and post-Soviet birth cohort groups and Supplementary Figure 7 for the distribution of *EduYears* GPS for the Soviet and post-Soviet birth cohort groups.)

We also calculated GPS scores using summary statistics from a GWA analysis of household income and social deprivation[14], although this study was conducted using only the UK Biobank sample (N~112,000). However, these GPS scores are much less powerful predictors, explaining less than 1% of variance in independent samples. For this reason, these GPS scores explained less than 1% of the variance in our SES variables regardless of the historical era (Supplementary Figure 8-9).

We also used height as a control variable. *EduYear*s GPS heritability was less than 1% regardless of the historical era (Supplementary Figure 10). This slight association is to be expected because height correlates significantly but slightly with SES variables. For example, the genetic correlation between household income (a good proxy for SES) and height has been shown to be around 0.2[14].

Turning to SNP heritability, it should be noted our sample had much less power to detect SNP heritability differences between the Soviet and post-Soviet groups. For the whole sample, SNP heritabilities were 15% (SE 0.03) for occupational status and 18% (SE 0.03) for educational attainment (Figure 2). Despite having less power to detect SNP heritability, SNP heritabilities were almost twice as high in the post-Soviet than the Soviet era for educational attainment using age 15 as a cut-off (Figure 2). In the Soviet era, SNP heritabilities were 17% (SE 0.04) for occupational status and 18% (SE 0.04) for educational attainment. In contrast, in the post-Soviet era, SNP heritabilities were 23% (SE 0.16) and 37% (SE 0.14), respectively. Although SNP heritabilities were larger in the post-Soviet era, these differences were not significantly different as is evident from the standard errors.

<< Insert Figure 2 here >>

Height was also used as control variable for analyses of SNP heritabilities. SNP heritability was 32% for height in the whole sample. For the Soviet era, SNP heritabilities was 33% for height, however, the post-Soviet estimates were not significantly different (40%) (Supplementary Figure 11).

Our main finding is that heritabilities are higher for SES variables in the post-Soviet era as compared to the Soviet era in the same Estonian population. GPS heritability for the composite SES measure (mean of educational attainment and occupational status) was 7.5% in the post-Soviet era and 2.3% in the Soviet era using the more stringent cut-off of 10 years. The variance in SES explained by the *EduYears* GPS seems small compared to the twin study estimates of about 50% and SNP heritability estimates of about 25%. However, we are only in the early stages of GPS research and the predictions are becoming stronger. SNP heritabilities showed a similar trend as GPS heritabilities: SNP heritabilities for educational attainment were twice as high in the post-Soviet era (37%) as compared to the Soviet era (17%).

A possible explanation for the increased heritability is increased meritocracy in Estonia following the restoration of independence in 1991. By meritocracy, we refer to equal opportunity for access to education and occupation and, when selection occurs, to meritocratic selection based on talent and effort, which are substantially influenced by genetic factors, rather than on environmentally driven privilege or discrimination. A meritocratic mechanism for the increased heritability of educational attainment and occupational status in the post-Soviet era would be genotype-environment correlation in the sense that individuals with equal opportunities are better able to select or to be selected for educational and occupational environments correlated with their genetic propensities. When environmental differences in access to education and occupation diminish, genetic differences increasingly account for educational attainment and occupational status.

There are of course other possible explanations for increased GPS heritability in the post-Soviet era. The largest increase in GPS heritability was observed for the participants who were in the youngest cohort when Estonia regained the independence. Much has changed in the society after the collapse of the Soviet Union, including wealth, culture, values -- all of which might contribute to the change in GPS heritability for the cohort who lived, studied and worked the majority of their lives in independent Estonia. Migration and changing population dynamics could also have affected the study results, although it should be noted that there was substantial migration during the Soviet era (within the Soviet Union) as well as after the Soviet era. However, we see no substantive hypothesis about the increased heritability following the collapse of the Soviet Union as obvious as increased meritocracy, although this cannot be definitely tested. One point in favor of the meritocracy hypothesis is that GPS heritability for SES in modern post-Soviet Estonia is similar to GPS heritability in the UK, presumably a meritocratic society. The difference is that GPS heritability for SES is lower in the Soviet era.

Another possible explanation is methodological. GPS scores were calculated for *EduYears* on the basis of a meta-analytic GWA of heterogeneous cohorts. If the GWA discovery sample weights were closer to the post-Soviet sample in the present study, then more variance would be explained in the post-Soviet compared to Soviet sample.

Equal educational opportunities

The meritocracy hypothesis assumes that educational and occupational success was less meritocratic in the Soviet era. In the Soviet era, access to primary education was universal and universal secondary education was introduced in the 1960s. However, the quality of teaching and even the curricula varied widely across schools[34,35]. Within schools, students were divided into one of the three different tracks, with limited movement between tracks: vocational training, secondary education and (special) secondary education[36]. This tracking was partly done based on merit (school achievement), but social-political ranking played a significant part as well. The number of students admitted to each track depended on the economic and social goals of central planning at the time; individual aspirations and ability were not considered to be as important[35]. Access to tertiary education from lower ‘ranks’ in the social-political system was limited; for example, students who were religious were not admitted[34,36]. In this way, the Soviet education system created environmental inequalities both directly and indirectly[35]. Importantly, university education was not as highly valued in society as it is now and this was accompanied by limited competition for university places, with an average of only two applicants per position. Admissions to university remained low throughout the Soviet era, which restricted any selection, meritocratic or not.

Since regaining independence, education in Estonia has become more meritocratic in terms of educational opportunity. Many educational reforms were introduced after the collapse of the Soviet Union with the aim of building a more egalitarian and effective educational system. Currently, almost all students complete elementary education and the rate of completing secondary education is among the highest in the OECD countries. Estonian equality in education is now above the OECD average, with limited variation in teaching standards between schools. The quality of teaching is considered to be excellent according to international standards and Estonia is ranked among the highest performing educational systems according to PISA surveys in 2012 and 2015[37,38]. This overall educational excellence, and the limited number of selective or private schools, suggests that there is equal opportunity and access to good education for all at primary and secondary level of education. We hypothesized that equality of opportunity should increase the heritability of educational achievement by making it possible for children to select, modify and choose educational experiences correlated with their education-related genetically influenced propensities, which include appetites as well as abilities. Educational achievement in turn contributes importantly to eventual educational attainment and occupational status.

For tertiary education, in addition to self-selection, students are now selected for university largely on the basis of ability and prior achievement, rather than environmentally driven privilege. Selection is not based on socio-political or religious considerations as in the Soviet era. Nor is selection based on the ability to pay tuition, because almost all university education is free. There is also greater opportunity for selection for university admission in the post-Soviet era because university applications and admissions increased exponentially in the 1990s; for example, applications to University of Tartu have increased threefold compared to the Soviet era[34].

Equal access to occupation

During the Soviet era, the economy and labor market was mainly characterized by centralized control, with the majority of workforce assigned to jobs in manufacturing and agriculture. Occupational status was determined more by loyalty to the communist party than by ability, achievement or qualifications. Recommendations for job positions and promotion always came from party leaders, although educational qualifications were also needed for certain positions[39]. The economy and labor market had very limited workforce mobility[36].

Inequality in occupations during the Soviet era was even more dramatic for females than males. During the Soviet era there was an increase in participation of women in workforce, meaning that both men and women were largely employed. However, this did not lead to occupational equality; women often did jobs requiring lower level of skills[40]. Although Soviet ideology argued for gender equality, this was not carried out in practice[41].

The transition from the Soviet Union to a prosperous independent Estonia was more difficult than anticipated. After the restoration of independence in Estonia the living standards were low, the economy was struggling, and the situation worsened with a major recession until 1994 when Estonia joined the European Union[32,33]. Equality of opportunity increased as the Estonia became more integrated with the west[42].

These historical events may explain why *EduYears* GPS did not explain more variance in SES in the transition time compared to the Soviet era. Our results suggested that *EduYears* GPS heritability is greatest for the youngest participants who had lived, studied and worked in independent Estonia the longest. Gender equality in Estonia started to improve, albeit gradually, after the collapse of the Soviet Union[43]. This was mirrored by an interesting facet of the results in the present study showing that GPS heritability increased more dramatically for females compared to males following the collapse of the Soviet Union. These results further support the meritocratic hypothesis specifically in relation to gender.

Future research directions

The present analyses excluded participants who were younger than 25 at the time of data collection because they may not yet have achieved their highest educational qualifications or reached their highest occupational status. Linking the EGCUT database with data from the Estonian Department of Education will make it possible in the future to include those individuals who were excluded as they complete their education and reach their ultimate occupational status. This will increase the size of our post-Soviet sample and thus the power of our SNP and GPS heritability comparisons. Because these individuals grew up completely in the post-Soviet era, we predict that they will show even greater heritability of SES. Increased sample size would also provide greater power to investigate further gender differences in GPS heritability.

Another interesting direction for research concerns the relationship between education and fecundity. Decreased fecundity in Iceland among highly educated citizens has been reported to result in lower GPS scores for *EduYears,* although the effect is very small[20]. According to Statistics Estonia, the population in Estonia has been decreasing for decades (http://www.stat.ee/news-release-2017-008), although it increased for the first time in 2016. We plan to investigate the extent to which decreasing fecundity comes disproportionately from highly educated individuals, in which case we might expect lower average GPS in the most recent birth cohorts. Our preliminary analyses did not support this hypothesis in that the average *EduYears* GPS did not differ across birth cohorts (Supplementary Figure 12), although we did not study fecundity here.

Studying parent-offspring resemblance to understand intergenerational social mobility is also part of our future research plans in EGCUT. Intergenerational social mobility is often assumed to be solely due to environmental factors. For example, the OECD uses parent-offspring resemblance in SES outcomes to assess intergenerational social mobility, assuming that this resemblance is environmentally mediated. Our current results and results from other studies show that educational and occupational outcomes are partly explained by genetic factors. Because parents and offspring are on average 50% similar genetically, parent-offspring resemblance is also likely to show genetic influence for SES. From this perspective, parent-offspring resemblance could be viewed as an index of equality rather than inequality. In other words, if environmental inequalities were eliminated, genetic resemblance between parents and offspring would completely account for parent-offspring resemblance.

While our analyses provided evidence for changes in GPS and SNP heritabilities following the major social change from a communist to a capitalist society, no definite conclusions can be drawn. It will be necessary to replicate the results of the present analyses using data from a different country that has gone through similar abrupt social change. A country that used to be part of the Soviet Union and has regained independence would be ideal; however, we are not aware of such a replication sample available at this time. We hope that our results lead to future molecular genetic studies researching gene-environment interactions of this sort that are now possible using GPS scores.

Another direction for future research is to consider intermediate phenotypes such as cognitive abilities that might mediate these changes in the distal outcomes of educational attainment and occupational status. In addition, the precision and power of all of these SNP and GPS analyses will increase as the power of GWA studies increases.

Meritocracy or social justice?

In closing, we wish to emphasize that we are not advocating meritocracy, although these issues are more an issue of values than science. At first glance meritocracy seems unquestionably good, but it could have unintended consequences such as creating social inequalities if societal rewards such as wealth are doled out on the basis of genetically driven abilities. The word meritocracy was coined by Michael Young whose book, *The Rise and Fall of the* Meritocracy[44], was meant as a cautionary tale about the dangers of meritocracy. The value system underlying meritocracy is that the point of education is to get better test scores in order to get better jobs, and that the point of occupations is to achieve high status and make lots of money. A different way to look at education is as a time to learn basic skills but also to learn how to learn and to enjoy learning. It is a decade when children can find out what they like to do and what they are good at doing, finding their genetic selves. If education were universally good, there would be no need for selection, especially at the level of primary and second education, and thus there would be no need to apply meritocratic criteria.

Similarly with occupations, where selection cannot be avoided, we will end up with a lot of frustrated people if we only value high-status occupations that earn lots of money. Society needs people who are good care workers, nurses, plumbers, public servants, and people in the service industry. To the extent that selection is necessary it should be meritocratic, but it is possible to imagine an occupational system that is not driven so much by monetary reward. For example, society could choose to reduce income inequality with a tax system that redistributes wealth.

In his book, *The Myth of Meritocracy,* James Bloodworth (2016)[45] argues that meritocracy leads to an inherent inequality of opportunity and reward based on genetic differences. He suggests that we need to replace meritocracy with what he calls a just society in which everyone could live well.

Methods

Sample

The sample for the present study was drawn from the Estonian Genome Centre, University of Tartu (EGCUT) sample. Ethical approval was granted by the Research Ethics Committee of the University of Tartu (approval 245/T-16).

EGCUT is a population-based study with a sample size of over 52 000 individuals (all participants ≥18 years of age), which comprises 5% of the adult population in Estonia. Genome-wide genetic data are available for approximately 20 000 of these individuals. EGCUT has been shown to be representative of the Estonian population in terms of age and geographical location while females are overrepresented, 66% female as compared to 55% in the adult population in Estonia[47]. EGCUT is also reasonably representative in terms of educational attainment when compared to national figures from the Department of Statistics Estonia (http://www.stat.ee/phc2011) (Supplementary Table 4). The initial sample for the present study included all participants with available genotypic and phenotypic data. All individuals who were 25 or younger were excluded from the analyses, as it is possible that these young individuals had not yet reached their highest educational level and highest occupation. The sample size before exclusions included 17 990 participants (7 409 males and 10 581 females). After exclusions (removing participants who were under 25 at the time of data collection and following quality control) the sample size was reduced to 12 490. Sample size for each measure separately is presented in Supplementary Table 1.

The sample was divided into two historical eras: the Soviet era and the post-Soviet era. Estonia regained independence in 1991; consequently, all participants who were born on or after 1976 went into secondary or further education in the post-Soviet era (i.e., they were aged 15 or younger when Estonia regained independence) and the rest of the sample was aged 16 or older when Estonia regained independence. This is an arbitrary cut-off that does not take into account the transition time between communist to capitalist society since societal changes take time to have an effect on people's lives. We assumed that young individuals were in the middle of their educational career, still making decisions about their universities and post-graduate degrees. We therefore repeated the analyses allowing for a transition period before and after the collapse of the Soviet Union assigning participants who were 16-25 year olds in 1991 to a 'transition' group. In addition, we used another cut-off to define the Soviet and post-Soviet groups, assigning all participants who were aged 10 or younger at the time of the restoration of independence in Estonia to the post-Soviet group and participants who were older than 10 years to the Soviet group.

Measures

Educational attainment

Educational attainment was assessed using a 10-point self-reported scale from no elementary education to postgraduate degree. The measure and scoring followed closely the International Standard Classification of Education (ISCED: http://www.uis.unesco.org/Education/Pages/international-standard-classification-of-education.aspx). However, some participants were studying towards an undergraduate or postgraduate degree at the time of the data collection, so additional points were added to the scale. Our measure included the following 10 categories (rather than the 8 categories that were in the original scale) for educational attainment: (1) no educational qualifications, (2) elementary school education, (3) basic education/ junior grade of high school, (4) secondary school/high school education, (5) vocational qualification/community college, (6) professional higher education, (7) studying towards university degree, (8) university degree, (9) studying towards postgraduate degree, (10) postgraduate degree.

Occupational Status

Occupational status was assessed with two questions: "What is your professional status right now?" and "What has been your main professional status (the occupation you kept the longest)?" These occupational status responses were scored according to the International Standard Classifications of Occupations (ISCO: http://www.ilo.org/public/english/bureau/stat/isco/). ISCO is a widely used and reliable measure[48–51]. ISCO classification assigns occupational status to broad groups (as well as more specific subgroups), taking into account the skills and education level required for occupation as well as the potential earnings. The present study used nine occupational status groups, classified in ISCO as the following categories, scored from 1 to 9 respectively: (1) elementary occupations (cleaners, helpers, laborers), (2) plant and machine operators, assemblers, (3) craft and related trades workers, (4) skilled agricultural, forestry and fishery workers, (5) service and sales workers, (6) clerical support workers, (7) technicians and associate professionals, (8) professionals, (9) legislators, senior officials and managers. The current occupational status and the main occupational status correlated 0.46. Both the current and the main occupational status had missing data; therefore, to increase power and sample size, a composite measure of occupational status was created by taking the mean of current and the longest held occupations; if only one measure were available then that measure was used. The same measure was used for both the Soviet and post-Soviet eras. Although, the classification of occupational status and the potential pay could have been different during the Soviet era, we assume that occupational positions (and the prestige of them) still fit into the broad ISCO categories.

SES

Because educational attainment and occupational status correlated 0.62, we calculated a mean as an index of general socioeconomic status (SES). SES is usually operationalized as a composite measure that includes income as well as occupational status and educational attainment. Although the measure of SES used in the present study does not include family income, occupational classification takes into account the potential earnings and prestige of the occupation. Therefore, we consider our composite measure of occupational status and educational attainment to be a reasonable index of SES.

Height

Height was used as control variable in the analyses; we had no hypothesis about changes in the SNP or GPS heritabilities following the shift from a communist to a capitalist society. Height was assessed in person by the researchers and was measured in cm.

Genotyping

Venous blood was collected from all 52 000 participants of EGCUT. DNA and plasma were immediately extracted from the blood and stored in EGCUT Core Laboratory of EGCUT in Tartu, Estonia. Genome-wide genotyping was assayed for 20 000 participants using three Illumina arrays: Illumina HumanCoreExome, Illumina Human370 CNV and Illumina OmniExpress in the Core Laboratory of EGCUT in Tartu, Estonia. Data were harmonized across the three arrays and harmonized data were used for all analyses (see Quality Control).

Quality Control

Genotype quality control were performed using Illumina GenomeStudio 3.1 and PLINK 1.07[52]. Standard quality control analyses were conducted at both the individual level and the SNP level excluding individuals with genotype call rate < 95%, sex discrepancies (using the heterozygosity rate of X-chromosome) and excess heterozygosity (mean±3SD). Additionally, duplicates and multidimensional-scaling (MDS) outliers were excluded. At the SNP level, we excluded SNPs with minor allele frequency (MAF) < 1%, call rate < 95%, failure of the Hardy-Weinberg Equilibrium (HWE) exact test (threshold $1*10^{-6}$), A/T or C/G and sex chromosome SNPs were removed. Phasing and imputation of the cleaned data were performed using ShapeIT v2[53] and IMPUTE v2.3.1[54] with 1000 Genomes Phase 3 Oct 2014 imputation reference panel based on 5 008 haplotypes[4] (www.1000genomes.org). IMPUTE2 builds custom-reference panels for each individual to be imputed and so is the best-suited software for imputing genotype data from Estonians, for whom no population-specific reference panel exists.

After imputation, further quality control was carried out. SNPs with MAF < 1%, and SNPs with poor imputation quality (info score < 0.30) or failure of the HWE exact test (threshold $1*10^{-6}$) were removed. We harmonized the genotyped datasets across the 3 arrays removing duplicate individuals and duplicate markers. Other standard quality control methods were applied removing SNPs and samples with call rate <0.97. The quality control was performed on each array separately, and was repeated after harmonization. After harmonization and quality control the final sample included 4 052 281 variants and 16 397 individuals (see Supplementary Table S5 for number of SNPs dropped after each step of quality control).

To control for ancestral stratification, principal component analyses were performed after pruning to remove markers in linkage disequilibrium (200kb window using R^2> 0.05). The first 10 principal components were used as covariates in the genetic analyses.

Statistical Analyses

Means and variances for measures were calculated, comparing the Soviet era and post-Soviet era, as well as sex differences. Mean differences were tested using ANOVA (Supplementary Table 1). Because significant, though small, sex differences emerged for both occupational status and educational attainment, explaining 2-4% of the variance in SES measures, we corrected the measures for mean sex differences using the regression method. In addition, we repeated the analyses without sex correction and calculated the variance explained by GPSs created separately for males and females. No correction for multiple testing was done, as all analyses tested just one hypothesis and we were interested in the effect size rather than the significance level.

Genome-wide polygenic scores

Genome-wide polygenic scores (GPSs) aggregate the effects of individual SNPs shown to be associated with the trait in a GWA study[55]. GPSs were calculated for 16 398 participants using p-values and β- weights obtained from summary statistics from the Okbay et al (2016) GWA analysis[19] of years of education

(*EduYears*) with the PRSice program[56] using multiple p-value thresholds (0.001; 0.05; 0.1; 0.2; 0.3; 0.4; 0.5). Of the 293 723 participants in the *EduYears* GWAS, the present study excluded 23andMe participants, for legal reasons, and excluded all participants from EGCUT, resulting in a sample of 208 596 individuals (see Supplementary Table 6 for cohort description). SNPs were clumped in PRSice for linkage disequilibrium, using a cut-off of R^2=0.1 within a 250-kb window. GWA summary statistics were obtained from the sample of 208 596 individuals, and p-values and β- weights were used to calculate the *EduYears* GPS. Delta R^2 are reported as the estimates of variance explained by adding the GPS to the regression model that included 10 principal components to control for population stratification.

We also calculated GPS scores using p using p-values and β- weights obtained from summary statistics from the Hill et al (2016) GWA analysis[14] of household income and social deprivation with the PRSice program[56] using the same procedure.

The difference in GPS heritabilities was evaluated using Fisher's exact test with Z to r transformation that assesses the significance in the difference in correlation coefficients in independent samples using both the effect sizes and sample sizes in the two samples[57].

SNP heritability

SNP heritability estimates genetic and residual (environmental) components of variance directly from DNA using unrelated individuals and hundreds of thousands of SNPs (single nucleotide polymorphisms) from thousands of individuals[58]. Using GCTA software, a genetic relatedness matrix was calculated weighting the pairwise genetic similarities with allele frequencies across all genotyped SNPs[58,59]. Individuals found to be even remotely related (relatedness >0.05) were removed from the analyses. We repeated the analyses when using the more stringent cut-off of 0.025, but this did not make any difference in SNP heritability estimates. This matrix of pair-by-pair genetic similarities were then compared to the matrix of pair-by-pair phenotypic similarity using residual maximum likelihood estimation[58,59]. This method only assesses additive effects captured by the common SNPs genotyped on the DNA array, and does not take into account gene-gene or gene-environment interactions or rare DNA variants, but these are unlikely to have a strong influence on the phenotype[58,60]. Prior to SNP heritability analyses we adjusted educational attainment and occupational status for sex using regression; standardized residuals were used in all analyses. To correct for the slight skew in the data, all measures were transformed to a normal distribution using the van der Waerden rank-based transformation[61,62].

Statistical power

Power for estimating SNP and GPS heritability was estimated using the online tool GCTA-GREML power calculator[63] and AVENGEME R code[55,64]. Our sample provided more than 80% power to detect GPS associations that explained 4% variance under the following circumstances: GWAS discovery sample size of 208 596, our target sample of 12 500 participants (the power did not change when we calculated power with a target sample of 2100 or a target sample of 680 for post-Soviet subgroups); number of independent SNPs in the GPS=20,000; proportion of variance explained in discovery sample =4%, covariance between genetic effect sizes in the discovery and target sample =4%; and proportion of SNPs with no effects on the discovery trait = 99%; range of p-values from GWA summary statistics= 0.00- 0.5). These assumptions are somewhat arbitrary, but the power calculations did not change when parameters for the power calculations were changed (for example, changing the proportion of SNPs with no effects on the trait in the discovery sample to 50%). In addition, the power of our sample sizes to detect the expected GPS effect is supported by a much simpler approach: *EduYears* GPS predicts around 4% of variance in independent samples, a correlation of 0.20, which requires a sample size of only 150 for 80% power (p = .05, one-tailed (http://www.sample-size.net/correlation-sample-size/).

Power for estimating SNP heritability is 99% to detect a SNP heritability of 20% for the whole sample. For the Soviet-era subsample, we had 99% power to detect a SNP heritability of 20%, but power was only 24% in the post-Soviet era (the power to detect heritability of 35% was 64% in the post-Soviet era). Therefore, little confidence is warranted for assessing differences in SNP heritability in the Soviet and the post-Soviet groups.

Supplementary information accompanies this article.

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Author Contributions

Conceived and designed the experiments: KR, RP. Analyzed the data: KR, MT, EK, JRIC. Wrote the paper: KR, MT, EK, TE, AM, RP. All authors approved the final draft of the paper.

Data availability

For information on data availability, please see the Estonian Genome Centre, University of Tartu (EGCUT) data access policy. This can be found at: http://www.geenivaramu.ee/en/biobank.ee/data-access

Conflict of interest: The authors declare no conflicting of interest.

References

1. Lykken, D. T., Bouchard Jr., T. J., McGue, M. & Tellegen, A. The Minnesota Twin Family Registry: some initial findings. *Acta Genet Med Gemellol* **39,** 35–70 (1990).
2. Heath, A. C. *et al.* Education policy and the heritability of educational attainment. *Nature* **314,** 734–736 (1985).
3. Branigan, A. R., Mccallum, K. J. & Freese, J. Variation in the heritability of educational attainment: An international meta-analysis. *Soc. Forces* **92,** 109–140 (2013).
4. Rietveld, C. A. *et al.* GWAS of 126,559 individuals identifies genetic variants associated with educational attainment. *Science,*. **340 (**6139), 1467–71 (2013).
5. Tambs, K., Sundet, J. M., Magnus, P. & Berg, K. Genetic and environmental contributions to the covariance between occupational status, educational attainment, and IQ: A study of twins. *Behav. Genet.* **19,** 209–222 (1989).
6. Colodro-Conde, L., Rijsdijk, F., Tornero-Gómez, M. J., Sánchez-Romera, J. F. & Ordoñana, J. R. Equality in educational policy and the heritability of educational attainment. *PLoS One* **10,** e0143796 (2015).
7. Lichtenstein, P., Pedersen, N. L. & McClearn, G. E. The origins of individual differences in occupational status and educational level: a study of twins reared apart and together. *Acta Sociol.* **35,** 13–31 (1992).
8. Adler, N. E. *et al.* Socioeconomic status and health: the challenge of the gradient. *Am. Psychol.* **49,** 15–24 (1994).
9. Cutler, D. M. & Lleras-Muney, A. *Education and health: insights from international comparisons*. *NBER Working Papers* (2012).
10. Cutler, D. M., Lleras-Muney, A. & Vogl, T. *Socioeconomic status and health: dimensions and mechanisms*. *NBER Working Papers* (2008).
11. Batty, G. D., Deary, I. J. & Gottfredson, L. S. Premorbid (early life) IQ and Later Mortality Risk: Systematic Review. *Ann. Epidemiol.* **17,** 278–288 (2007).
12. von Stumm, S., Deary, I. J. & Hagger-Johnson, G. Life-course pathways to psychological distress: a cohort study. *BMJ Open* **3,** e002772 (2013).
13. Yang, J., Lee, S. H., Goddard, M. E. & Visscher, P. M. Genome-wide complex trait analysis (GCTA): Methods, data analyses, and interpretations. *Methods Mol. Biol.* **1019,** 215–236 (2013).
14. Hill, W. D. *et al.* Molecular genetic contributions to social deprivation and household income in UK Biobank (n = 112,151). *Curr. Biol.* **26,** 3083–3089 (2016).
15. Marioni, R. E. *et al.* Molecular genetic contributions to socioeconomic status and intelligence. *Intelligence* **44,** 26–32 (2014).
16. Benjamin, D. J. *et al.* The genetic architecture of economic and political preferences. *Proc. Natl. Acad. Sci.* **109,** 8026–8031 (2012).
17. Davies, G. *et al.* Genome-wide association study of cognitive functions and educational attainment in UK Biobank (N=112 151). *Mol. Psychiatry* **21,** 758–67 (2016).
18. Hyytinen, A., Ilmakunnas, P., Johansson, E. & Toivanen, O. *Heritability of lifetime income*. *Helsinki Centre of Economic Research* (2013).
19. Okbay, A. *et al.* Genome-wide association study identifies 74 loci associated with educational attainment. *Nature* **533,** 539–542 (2016).
20. Kong, A. *et al.* Selection against variants in the genome associated with educational attainment. *Proc. Natl. Acad. Sci.* **114,** E727-32 (2017).
21. Belsky, D. W. *et al.* The genetics of success: how single-nucleotide polymorphisms associated with

educational attainment relate to life-course development. *Psychol. Sci.* **27,** 957–972 (2016).

22. Hugh-Jones, D., Verweij, K. J. H., St. Pourcain, B. & Abdellaoui, A. Assortative mating on educational attainment leads to genetic spousal resemblance for polygenic scores. *Intelligence* **59,** 103–108 (2016).

23. Hollingshead, A. Four factor index of social status. *Yale Journal of Sociology* **8,** 21–52 (1975).

24. Sirin, S. R. Socioeconomic status and academic achievement: a meta-analytic review of research. *Rev. Educ. Res.* **75,** 417–453 (2005).

25. White, K. R. The relation between socioeconomic status and academic achievement. *Psychol. Bull.* **91,** 461–481 (1982).

26. Domingue, B. W., Belsky, D. W., Conley, D., Harris, K. M. & Boardman, J. D. Polygenic influence on educational attainment. *AERA Open* **1,** 2332858415599972 (2015).

27. Selzam, S. *et al.* Predicting educational achievement from DNA. *Mol. Psychiatry* **22,** 267–272 (2017).

28. Knopik, V. S., Neiderhiser, J. M., DeFries, J. C. & Plomin, R. *Behavioral Genetics. 7th ed*. (Worth Publishers, New York, 2017).

29. Baker, L. A., Treloar, S. A., Reynolds, C. A., Heath, A. C. & Martin, N. G. Genetics of educational attainment in Australian twins: Sex differences and secular changes. *Behav. Genet.* **26,** 89–102 (1996).

30. Samuelsson, S. *et al.* Environmental and genetic influences on prereading skills in Australia, Scandinavia, and the United States. *Journal of Educational Psychology* **97,** 705–722 (2005).

31. Hanscombe, K. B. *et al.* Socioeconomic status (SES) and children's intelligence (IQ): in a UK-representative sample SES moderates the environmental, not genetic, effect on IQ. *PLoS One* **7,** e30320 (2012).

32. Laar, M. *Estonia's way*. (Pegasus, Tallinn, Estonia, 2007).

33. Laar, M. The Estonian economic miracle. *Backgrounder* **2060,** 1–12 (2007).

34. Saar, E. Changes in intergenerational mobility and educational inequality in Estonia: Comparative analysis of cohorts born between 1930 and 1974. *Eur. Sociol. Rev.* **26,** 367–383 (2010).

35. Saar, E. Transitions to Tertiary Education in Belarus and the Baltic Countries. *Eur. Sociol. Rev.* **13,** 139–158 (1997).

36. Titma, M., Tuma, N. B. & Roosma, K. Education as a factor in intergenerational mobility in soviet society. *European Sociological Review* **19,** 281–297+i (2003).

37. OECD. *Education policy outlook: Estonia*. (2016).

38. OECD. *Equity and quality in education - supporting disadvantaged students and schools*. (2011).

39. Titma, M. & Roots, A. Intragenerational mobility in successor states of the USSR. *Eur. Soc.* **8,** 493–526 (2006).

40. Carnaghan, E. & Bahry, D. Political attitudes and the gender gap in the USSR. *Comp. Polit.* **22,** 379–399 (1990).

41. Katz, K. *Gender, work and wages in the Soviet Union: a legacy of discrimination*. (Palgrave Macmillan UK, 2001).

42. Boughton, J. *Tearing down walls: the International Monetary Fund, 1990-1999*. (2012).

43. Silova, I. & Magno, C. Gender equity unmasked: democracy, gender, and education in Central/Southeastern Europe and the former Soviet Union. *Comp. Educ. Rev.* **48,** 417–442 (2004).

44. Young, M. *The rise and fall of the meritocracy*. (Penguin Books, 1965).

45. Bloodworth, J. *The myth of meritocracy*. (Biteback Publlishing, 2016).

46. Piketty, T. *Capital in the twenty-first century*. (Harvard University Press., 2014).

47. Leitsalu, L. *et al.* Cohort profile: Estonian Biobank of the Estonian Genome Center, University of Tartu. *Int. J. Epidemiol.* **44,** 1137–1147 (2015).

48. Ganzeboom, H. B. G. A New International Socio-Economic Index [ISEI] of occupational status for the International Standard Classification of Occupation 2008 [ISCO-08] constructed with data from the ISSP 2002-2007; with an analysis of quality of occupational measurement in ISS. *Annu. Conf. Int. Soc. Surv. Program. , Lisbon* (2010).

49. Ganzeboom, H. B. & Treiman, D. J. in *Advances in Cross-National Comparison. A European Working Book for Demographic and Socio-Economic Variables.* (eds. Hoffmeyer-Zlotnik, J. H. P. & Christof Wolf) 159–193 (New York: Kluwer Academic Press., 2003).

50. Wolf, C. The ISCO-88 International Standard Classification Of Occupations in cross-national survey research. *Bull. Methodol. Sociol.* **54,** 23–40 (1997).

51. Kromhout, H. The use of occupation and industry classifications in general population studies. *Int. J. Epidemiol.* **32,** 419–428 (2003).

52. Purcell, S. *et al.* PLINK: A tool set for whole-genome association and population-based linkage analyses. *Am. J. Hum. Genet.* **81,** 559–575 (2007).

53. Delaneau, O., Zagury, J.-F. & Marchini, J. Improved whole-chromosome phasing for disease and population genetic studies. *Nat. Methods* **10,** 5–6 (2013).

54. Howie, B. N., Donnelly, P. & Marchini, J. A flexible and accurate genotype imputation method for the next generation of genome-wide association studies. *PLoS Genet.* **5,** e1000529 (2009).

55. Dudbridge, F. Power and predictive accuracy of polygenic risk scores. *PLoS Genet.* **9,** e1003348 (2013).

56. Euesden, J., Lewis, C. M. & O'Reilly, P. F. PRSice: Polygenic Risk Score software. *Bioinformatics* **31,** 1466–1468 (2014).

57. Fisher, R. . On the probable error of a coefficient of correlation deduced from a small sample. *Metron* **1,** 3–32 (1921).

58. Yang, J. *et al.* Common SNPs explain a large proportion of the heritability for human height. *Nat. Genet.* **42,** 565–9 (2010).

59. Yang, J., Lee, S. H., Goddard, M. E. & Visscher, P. M. GCTA: a tool for genome-wide complex trait analysis. *Am. J. Hum. Genet.* **88,** 76–82 (2011).

60. Visscher, P. M., Hill, W. G. & Wray, N. R. Heritability in the genomics era — concepts and misconceptions. *Nat. Rev. Genet.* **9,** 255–266 (2008).

61. Lehmann, E. *Nonparametric Statistical Methods Based on Ranks*. (Holden-Day, San Francisco, CA, 1975).

62. Van Der Waerden BL. On the sources of my book Moderne Algebra. *Hist. Math.* **2,** 31–40 (1975).

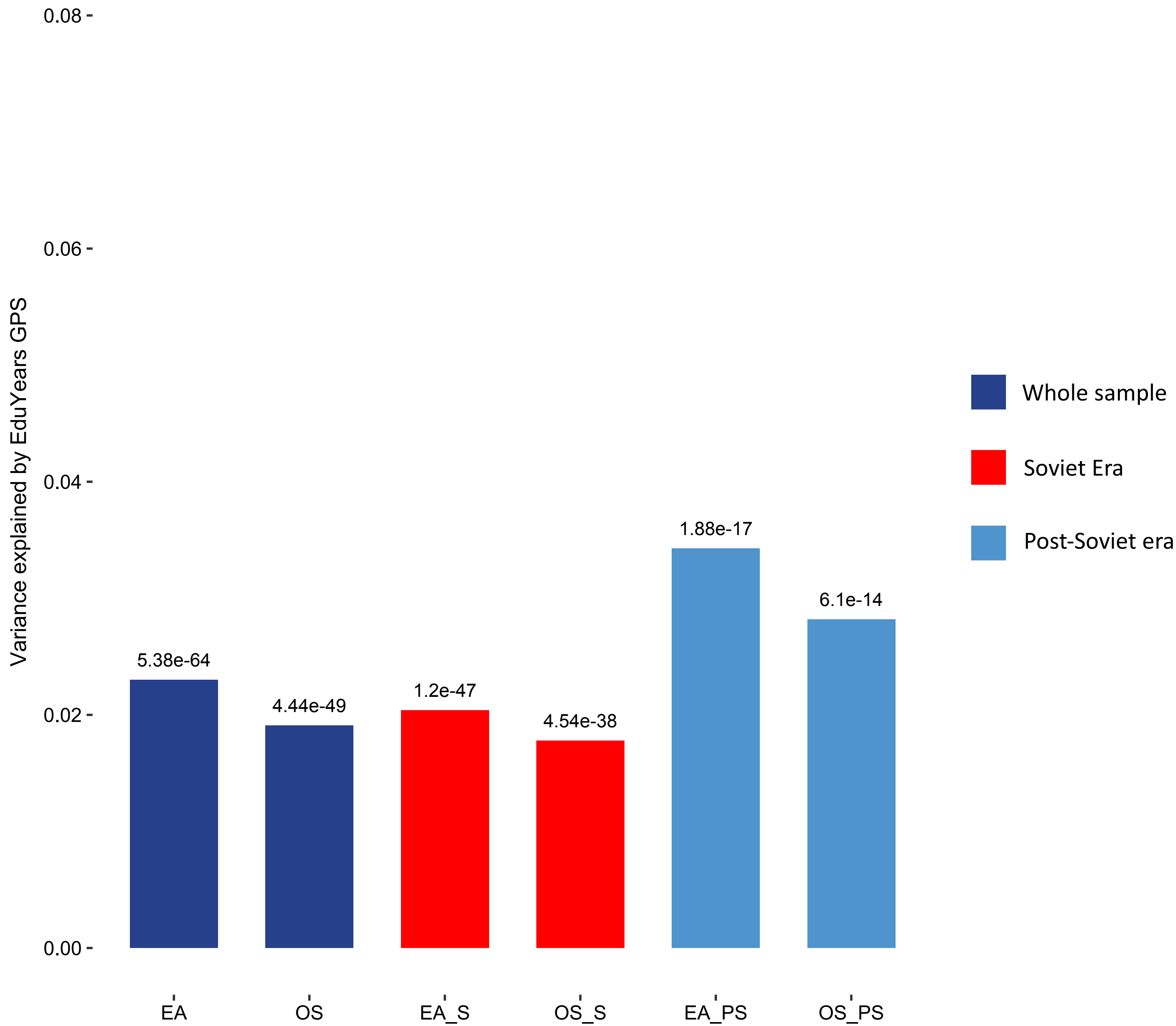
63. Visscher, P. M. *et al.* Statistical power to detect genetic (co)variance of complex traits using SNP data in unrelated samples. *PLoS Genet.* **10,** e1004269 (2014).

64. Palla, L. & Dudbridge, F. A fast method that uses polygenic scores to estimate the variance explained by genome-wide marker panels and the proportion of variants affecting a trait. *Am. J. Hum. Genet.* **97,** 250–259 (2015).

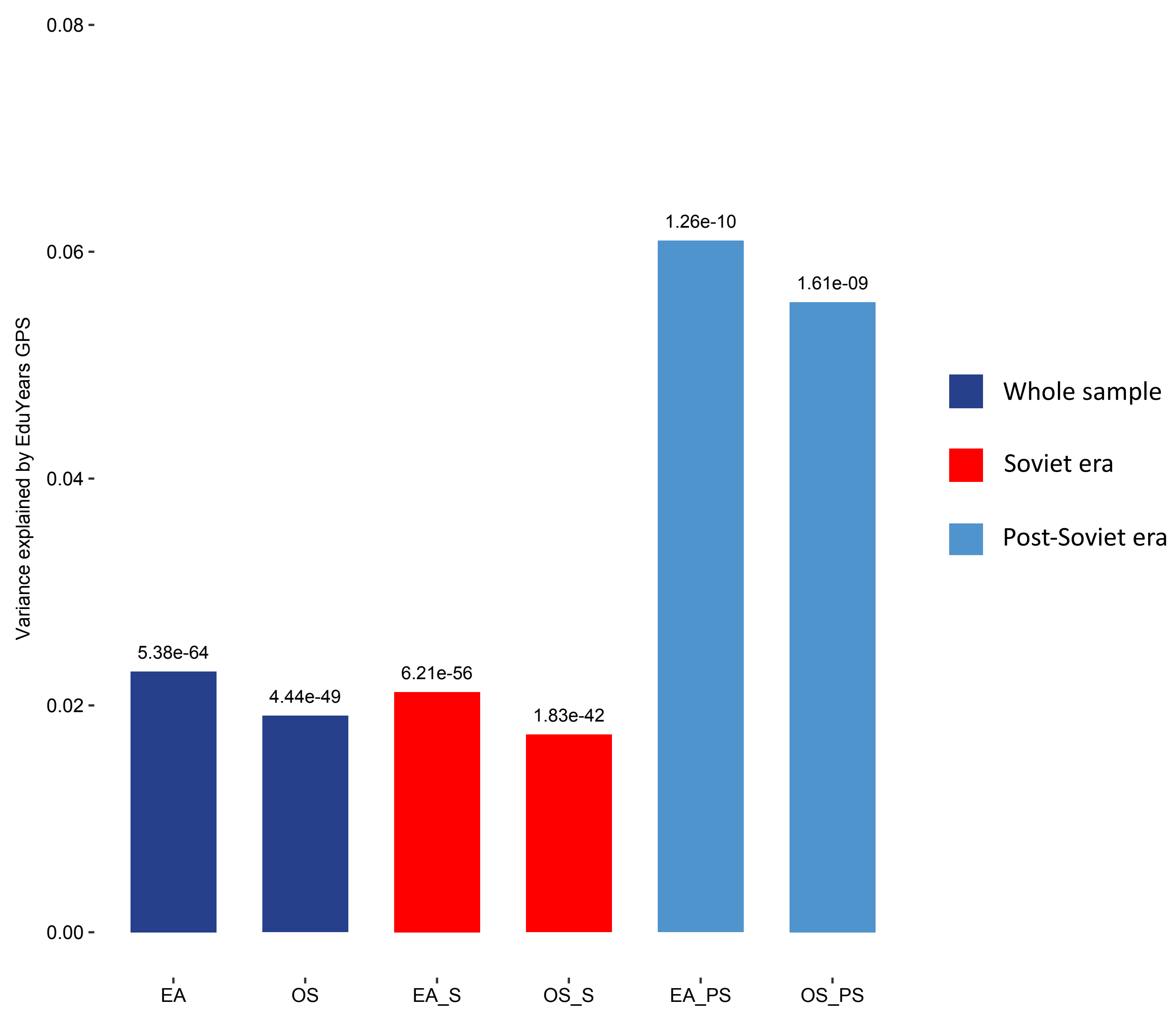
Figures

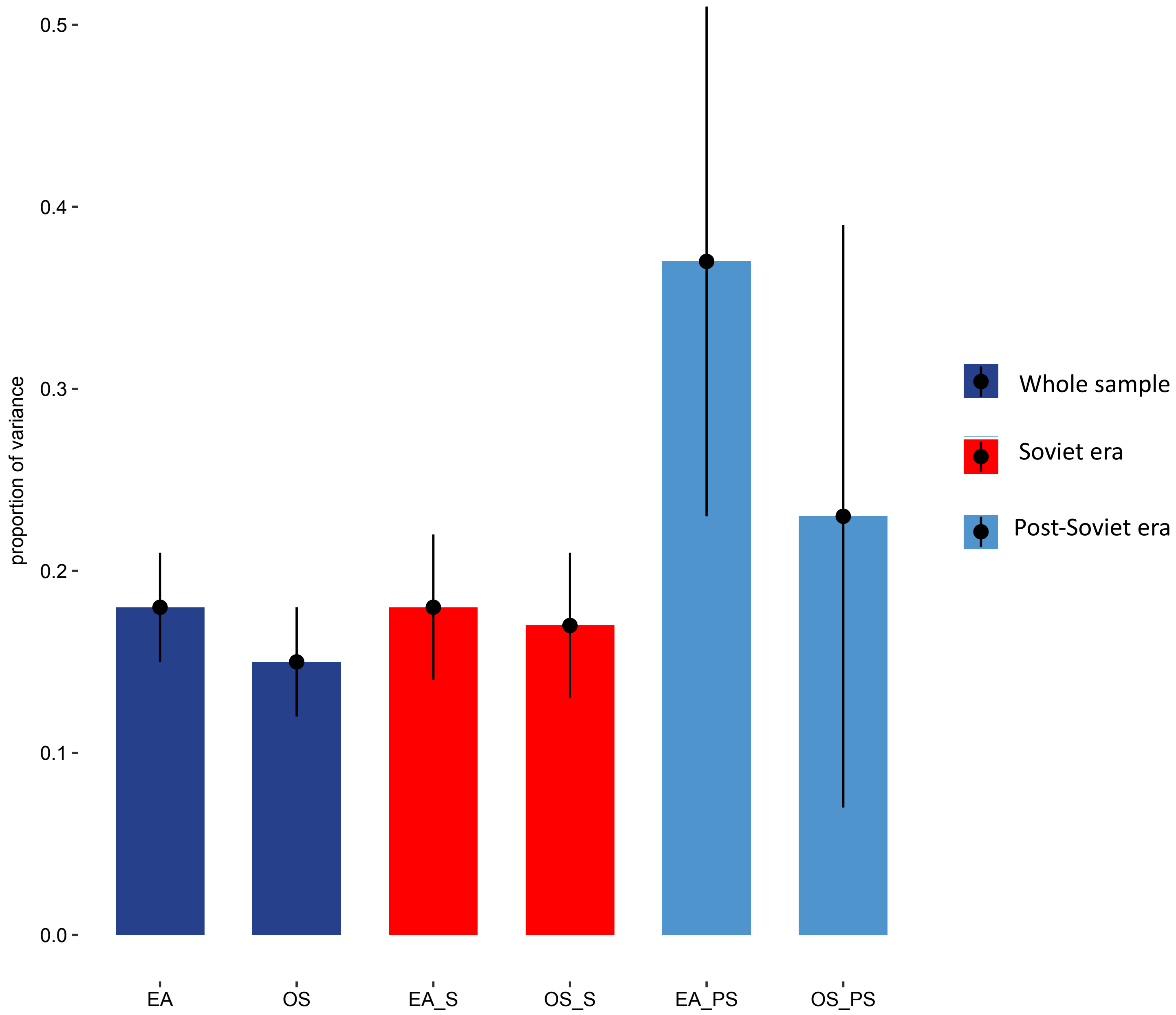
Figure 1. Variance explained by *EduYears* GPS in the post-Soviet (PS) and Soviet (S) groups. We calculated GPS using a 0.1 GWA study p-value threshold for educational attainment (EA) and occupational status (OS) for the whole EGCUT sample (N(EA)=12 483; N(OS)= 11 419) and when divided into historical eras using two cut-offs: (a) The post-Soviet (PS) group included participants 15 or younger when independence was regained and the Soviet (S) group included the rest of the participants (N(EA_S)=10 381; N(EA_PS)=2 102; N(OS_S)= 9 417; N(OS_PS)= 2 002); (b) The post-Soviet (PS) group included participants 10 or younger when independence was regained and the Soviet (S) group included the rest of the participants (N(EA_S)=11 808; N(EA_PS)=675; N(OS_S)= 10 767; N(OS_PS)= 652).

Figure 2. SNP heritabilities showing the proportion of variance explained by additive effects of common SNPs (SE as error bars) for the whole EGCUT sample and for the Soviet and post-Soviet groups using a cut-off of 15 years. SNP heritabilities were adjusted for population stratification. (N(EA)=12 483; N(OS)= 11 419; N(EA_S)=10 381; N(EA_PS)=2 102; N(OS_S)= 9 417; N(OS_PS)= 2 002).



0.08
0.06
0.04
0.02
0.00
Variance explained by EduYears GPS
5.38e-64
4.44e-49
1.2e-47
4.54e-38
1.88e-17
6.1e-14
EA
OS
EA_S
OS_S
EA_PS
OS_PS
Whole sample
Soviet Era
Post-Soviet era


0.08
0.06
0.04
0.02
0.00
Variance explained by EduYears GPS
5.38e-64
4.44e-49
6.21e-56
1.83e-42
1.26e-10
1.61e-09
EA
OS
EA_S
OS_S
EA_PS
OS_PS
Whole sample
Soviet era
Post-Soviet era



proportion of variance
0.0
0.1
0.2
0.3
0.4
0.5
EA
OS
EA_S
OS_S
EA_PS
OS_PS
Whole sample
Soviet era
Post-Soviet era