Divergent selection on height and cognitive ability: evidence from Fst and polygenic scores

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Abstract

Tests of selection based on population differentiation were performed on two highly polygenic traits important for success and satisfaction in life: height and educational attainment (EA).

Polygenic scores (PGS) of EA and height, computed across three public genomic databases revealed differences between populations (1000 Genomes, HGDP, gnomAD) that matched the average IQ and height of ethnic groups (r ~0.9).

A moderately strong correlation between latitude and EA PGS (r= 0.68), significantly deviating from the correlations of random SNPs, suggests the implication of climate (seasonality or winter temperature) for selection on cognitive abilities.

The global Fst index revealed population differentiation at height and EA loci, significantly deviating from random SNPs.

Substantial LD decay between Africans and Europeans was found (r= 0.6) but there was no correlation between Linkage disequilibrium (LD) decay and population differences in polygenic scores (r= 0.015, p= 0.45) for EA, and slight inflation of height PGS difference due to LD decay (r= -0.04, p= 0.0315).

implying that LD decay does not produce a bias in polygenic scores of non-European populations. Finally, it is shown that PGS differences are more sensitive to SNP significance than Fst, reflecting the major limitations of Fst as an index of selection.

1. Introduction

Many studies over the last decade have established the highly polygenic nature of many human traits (Lo et al., 2015; Shi et al., 2016; Boyle et al., 2017). This discovery was aided by technical advances in the science and technology of genomics, which enabled genome-wide association studies (GWAS) on large samples to detect thousands of variants with tiny effect on human traits. This genetic architecture contrasts with the classical Mendelian model where effects are driven by rare variants with large effect.

Despite these advances, polygenic adaptation has proven difficult to disentangle because causal variants only undergo subtle changes in allele frequency. Moreover, the arrays used by GWAS usually tag causal variants, that is they identify variants that are only

in linkage disequilibrium with the causal variant. Whilst the effect of causal variants is generally homogeneous across ethnic groups (Ishigaki et al., 2020), tag variants have decreased predictive power in populations that are ancestrally different from the GWAS reference sample, due to a phenomenon known as LD-decay. The latter is due to recombination events which shuffle the genetic material (Vos et al., 2017). Another issue that affects GWAS and selection methods relying on GWAS summary statistics is population stratification, which can inflate signals of selection due to co-variance between genes and the environment.

Methods to detect directional selection usually exploit population differentiation in allele frequencies (Piffer, 2013; Berg & Coop, 2014). Other methods are based on within-population variation: selection scans based on singleton density score (SDS) (Field et al., 2016) or tests that analyze the correlation between derived allele frequencies (DAF) and GWAS effect size and direction (Uricchio et al., 2019).

Other tests rely on the correlation between allele frequencies and environmental variables, such as annual temperature or rainfall, or proxies for climate such as latitude (Limborska et al., 2002; Eisenberg, Kuzawa and Hayes, 2010).

This paper will use tests relying on between-population variation and correlation with latitude to identify signals of polygenic adaptation on two highly polygenic traits: Educational attainment and height. Population differentiation at education-related genetic variants has been shown by previous studies (Piffer, 2013; Piffer, 2015, Piffer, 2019). Recently a study found strong directional selection on educational attainment in Britain over the last 2k years (Stern et al., 2021).

The correlation between polygenic scores and average population trait and Qst-Fst (Whitlock & Guillaume, 2009) test are complementary approaches to detect polygenic selection.

These two traits were chosen because they are 1) socially relevant since they both affect success in life (academic, occupational and mating success); 2) highly polygenic and 3) GWAS relying on very large sample sizes are available. Moreover, education is highly genetically correlated to intelligence, and can be used as a proxy for cognitive abilities.

Finally, two novel measures of selection are introduced: 1) the correlation of GWAS allele frequencies across pairs of populations and 2) the ratio between allele frequency difference and mean absolute allele frequency difference.

2. Methods

Polygenic scores were computed using GWAS SNPs meeting the standard significance threshold ($p< 5 \times 10^{-8}$) and weighed by effect size.

The inclusion criteria for GWAS were sample size and predictive power: the GWAS with the largest sample size and predictive power were used to compute polygenic scores: for education, Lee et al. (2018) study, which included 1.1 million participants and had the highest predictive power (~9%) and largest sample size among GWAS of education and cognition. The EA MTAG polygenic score was chosen because it encompassed several cognitive abilities and had the largest predictive power; for height, the GWAS meta-analysis comprising 700,000 individuals by Yengo et al. (2018) had the largest sample size, but the highest predictive power (42.8%) was achieved by Chung et al. (2019), albeit with a somewhat smaller sample size (N= 456,837).

Polygenic scores were computed using the three largest publicly available population genetics datasets: 1000 Genomes, gnomAD and HGDP.

Average height for populations was obtained from Wikipedia (https://en.wikipedia.org/wiki/Average_human_height_by_country) and was available for 12 populations in 1000 Genomes. The HGDP sample included mostly tribes that were not represented in national height statistics c for which it would be difficult to get a precise estimate, hence they were reported without attempting to compute the correlation with phenotypic height. The average height for gnomAD was obtained from National Health Statistics (Fryar et al., 2018) for ethnic groups in the US represented by the gnomAD samples (Hispanic, East Asian, European (non Finnish), African-American). The average height for Finns was obtained from Wikipedia. The average height of Ashkenazi Jews was obtained from a recent study on the genetics of height among a sample consisting mostly of Ashkenazi Jews (Zeevi et al., 2019).

The random SNPs were matched by MAF and LD (with a threshold r^2=0.1) using SNPSNAP.

The absolute allele frequency difference was calculated as the mean absolute difference of the allele frequencies

Fst and allele frequencies were calculated using Plink 1.9 and polygenic scores for each population were computed using R (version 3.6). Code and data are available on OSF: https://osf.io/6dvfc/

3. Results

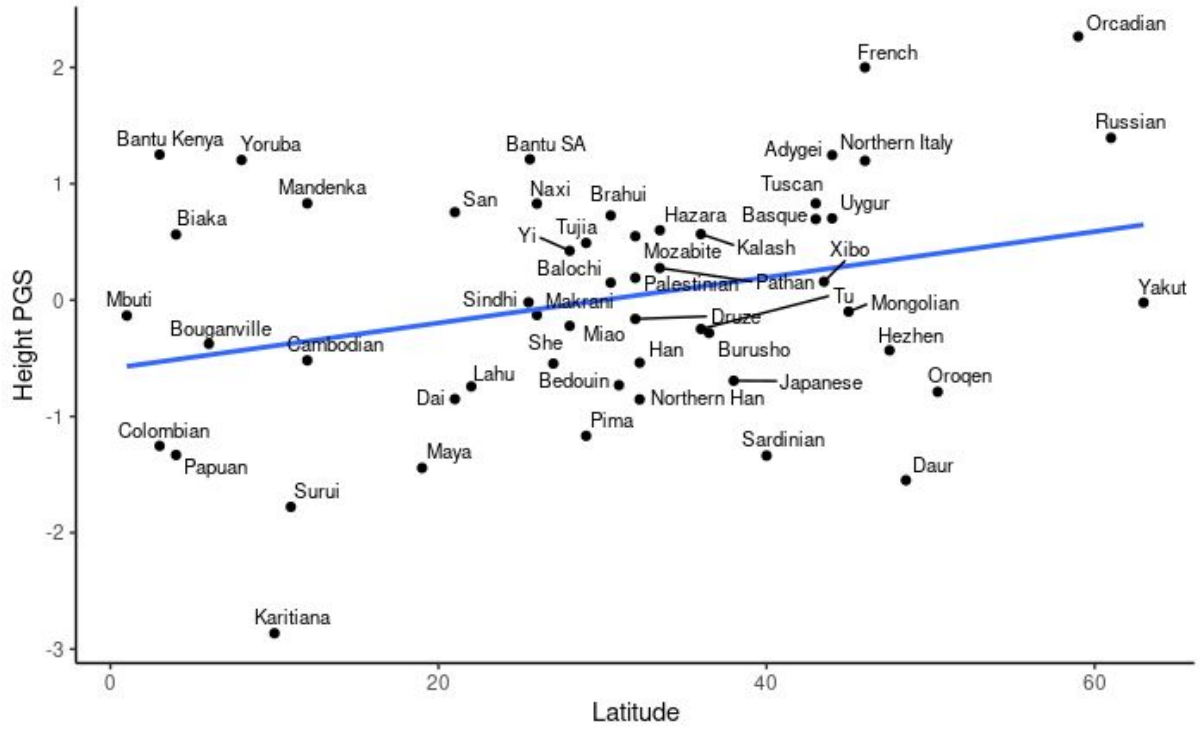
Height PGS

The polygenic scores for height were calculated using Chung et al. (2019)'s GWAS, using the effect size in the Lasso+CTPR meta-analysis, which provided the best predictive power. The PGS showed substantial inter-population variation. The highest values were obtained by

northern Europeans (Finns, Orcadians, Northern Europeans from Utah) and the lowest by Native Americans (Karitiana, Surui) and Southeast Asians (Dai, Vietnam).

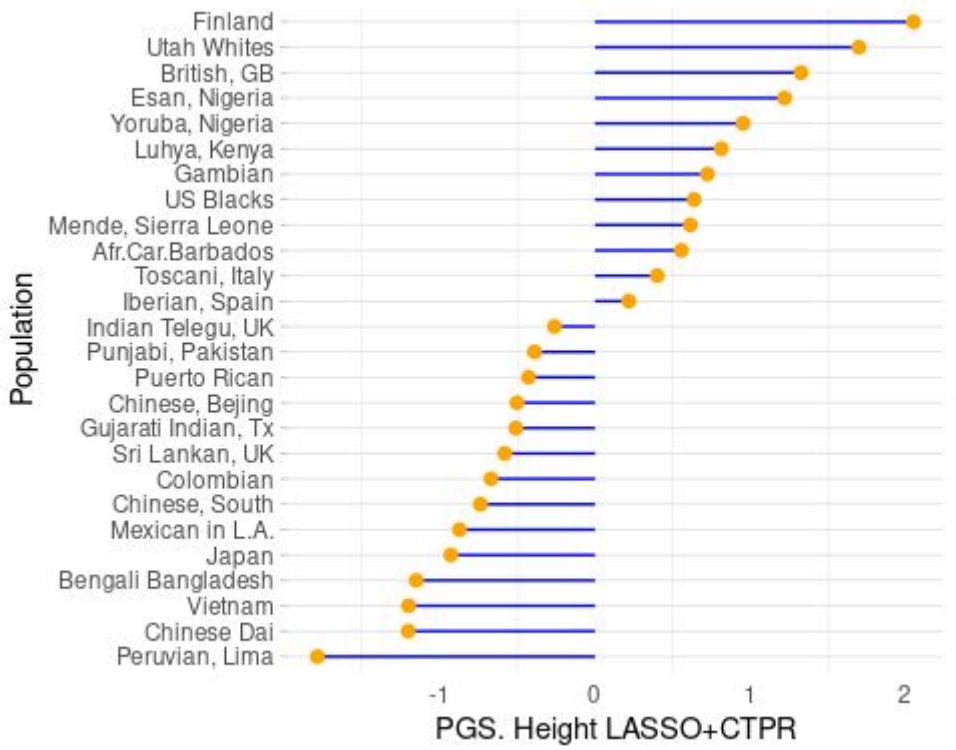
There was a weak, positive correlation (r= 0.321) between height PGS and latitude (figure 1).

Figure 1. Scatterplot (Height PGS x Latitude): HGDP populations.



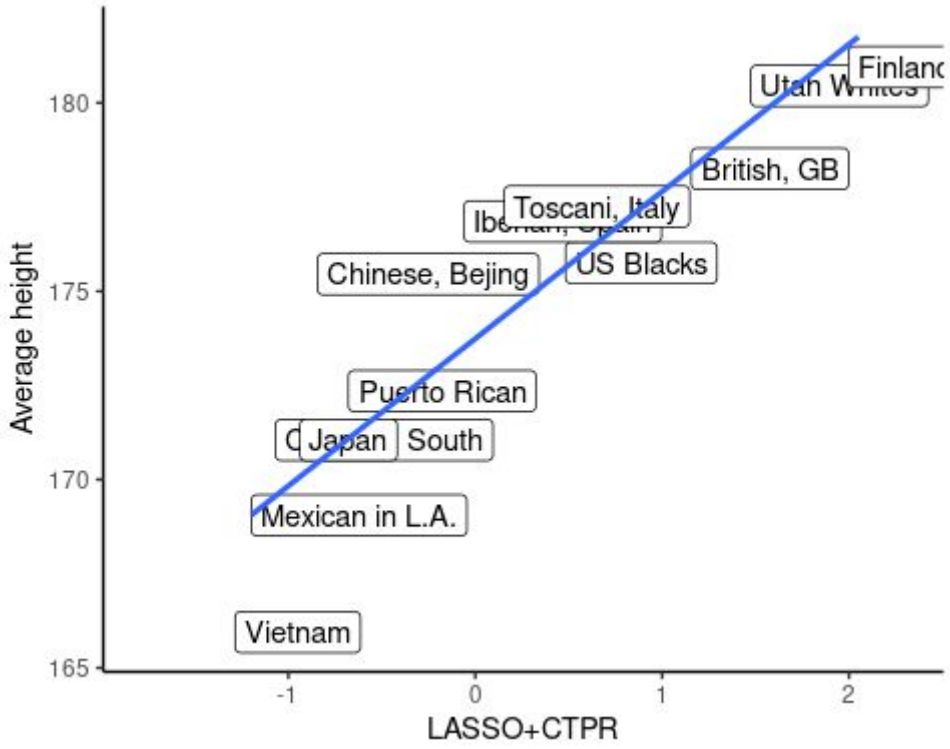
The height PGS in the 1000 Genomes (figure 2) showed higher scores for Europeans and Africans, and lower for Latin Americans and East Asians.

Figure 2. Height PGS: 1000 Genomes



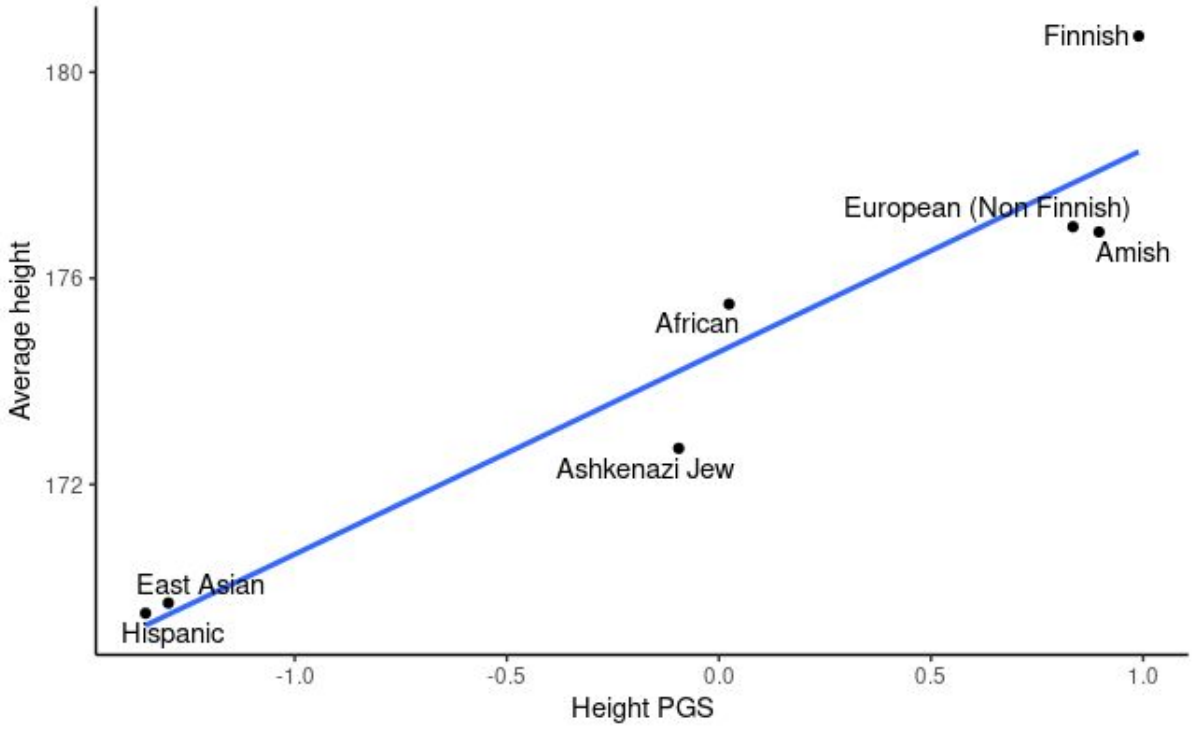
The PGS had a strong correlation with average population height (r= 0.923) (figure 3).

Figure 3. Scatterplot (Height PGS x average height).



In the gnomAD dataset, the correlation between height and PGS was r=0.949 (figure 4).

Figure 4. Scatterplot (Height x PGS): gnomAD.

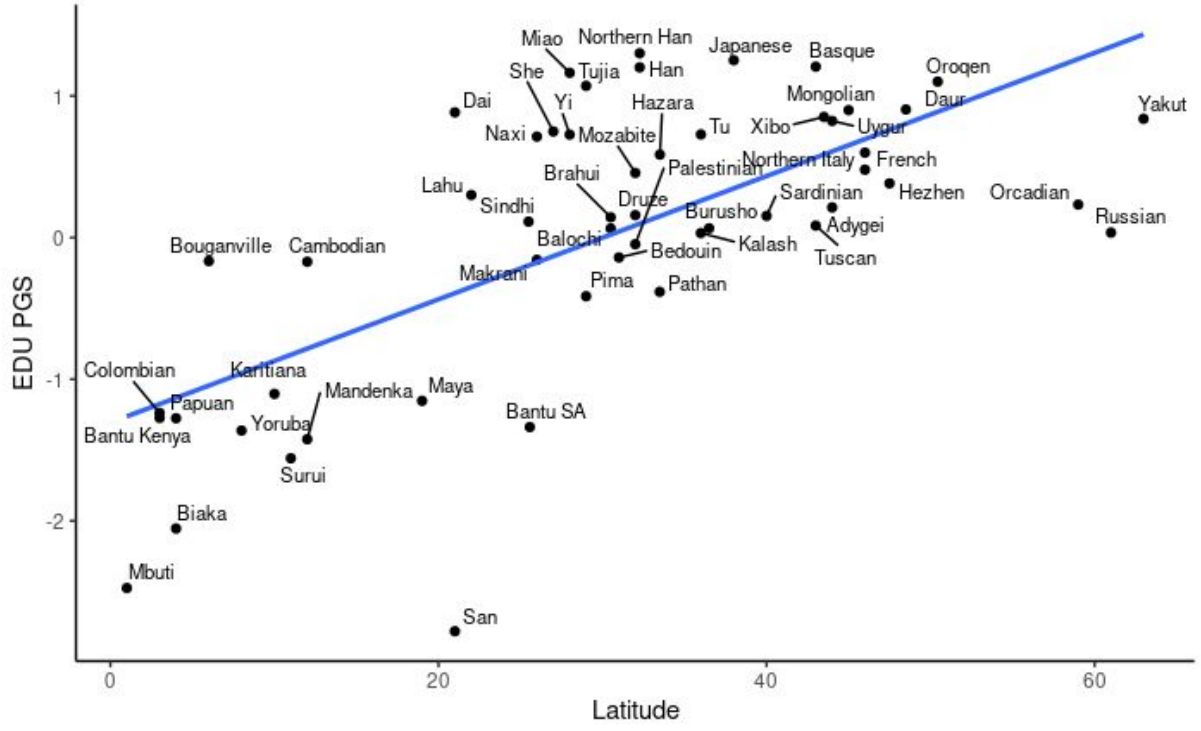


Education

There was a strong, positive correlation (r= 0.675) between EDU PGS and latitude (figure 5).

HGDP

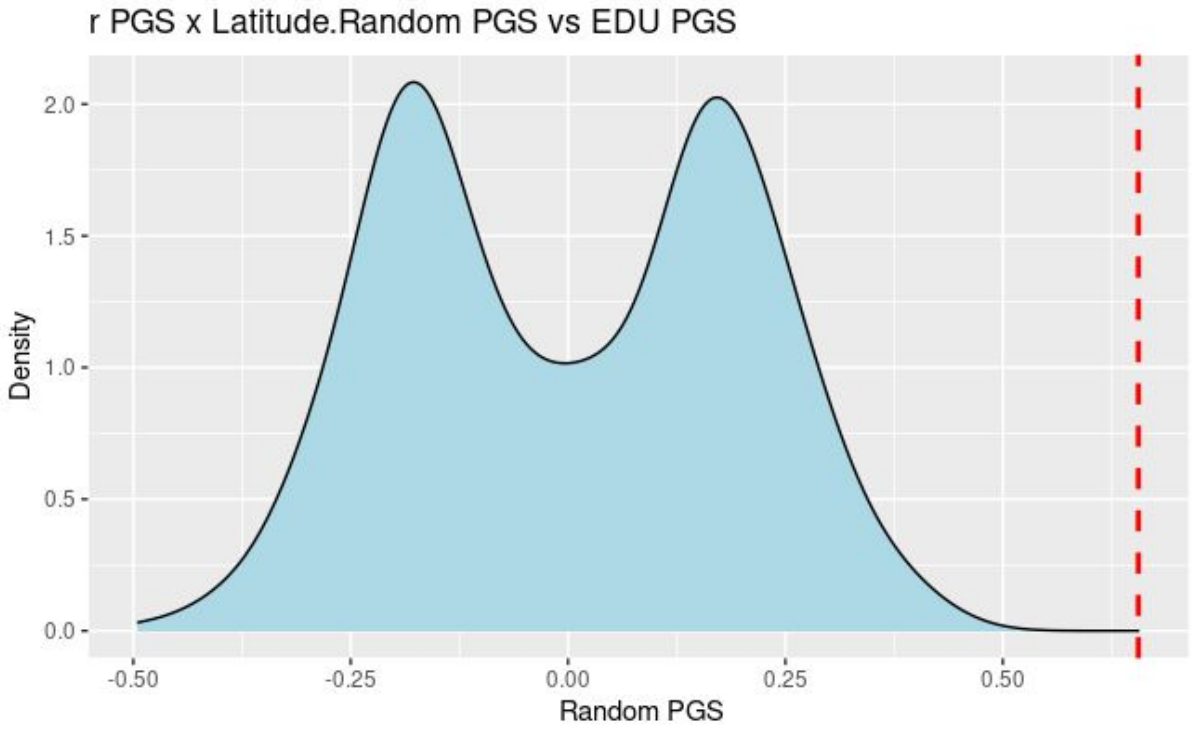
Figure 5. Scatterplot (EDU PGS x Latitude): HGDP populations.



Monte Carlo simulation

1000 random polygenic scores were generated to compute the null distribution of correlation coefficients. The correlation between the clumped EDU PGS and latitude (significantly deviated from the null (Z= 3.29, p= 0.0009).

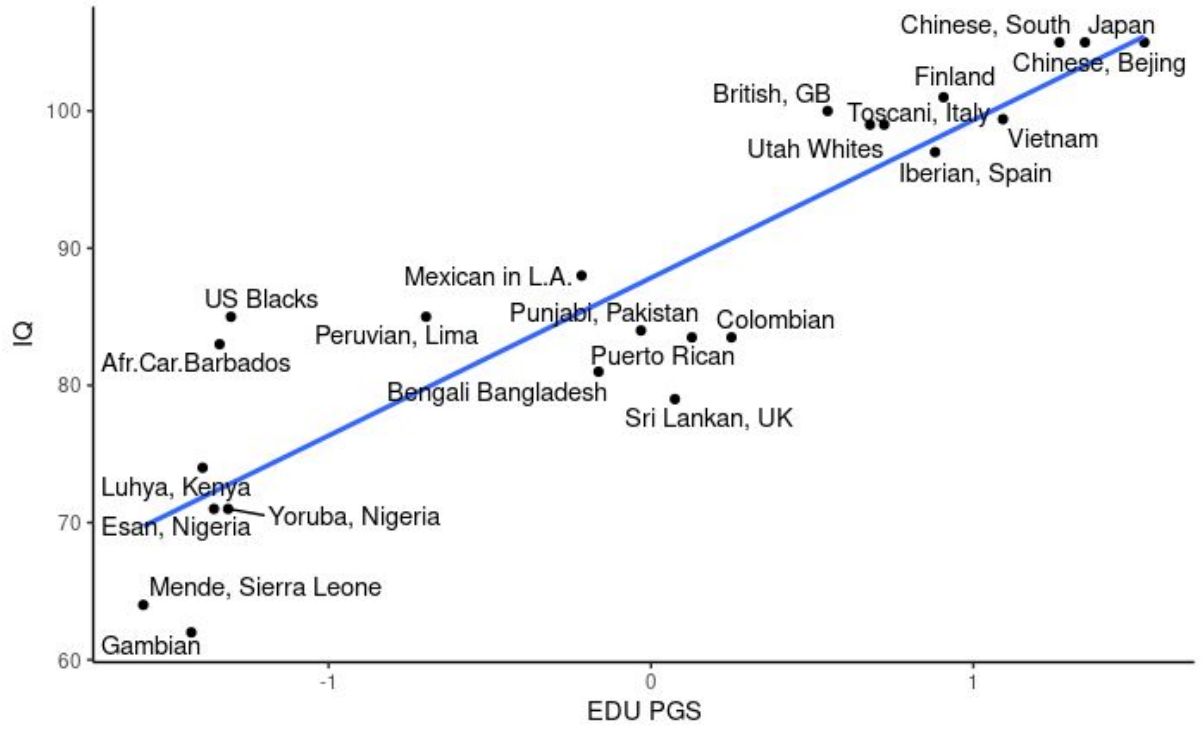
Figure 6. Density plot (correlation with latitude).



1000 Genomes

Among the 1000 Genomes populations, the correlation between EDU PGS and average IQ was r= 0.903 (figure 6).

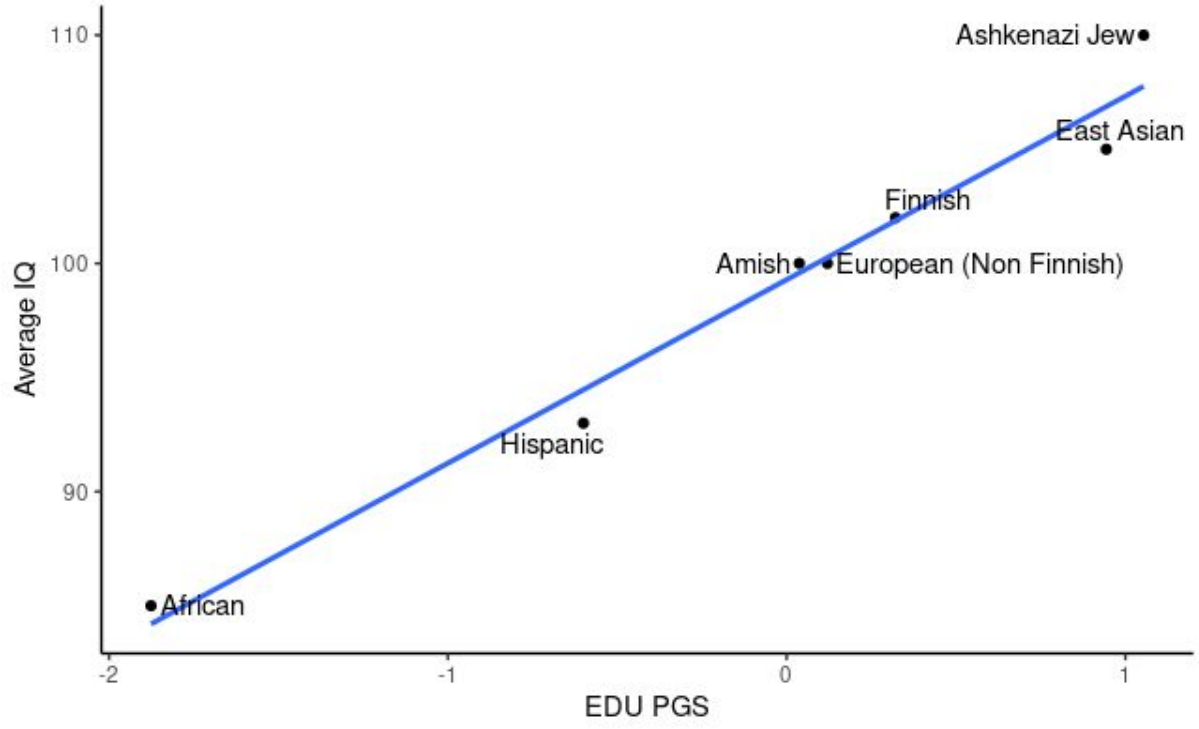
Figure 6. Scatterplot (EDU PGS x IQ): 1000 Genomes.



gnomAD

The correlation between IQ and edu PGS was r= 0.985.

Figure 7. Scatterplot (EDU PGS x IQ): gnomAD.



Correlation between height and education (PGS and average height)

The population-level correlation between EDU and height PGS was close to 0 (r= 0.02, -0.304, 0.03 in gnomAD, 1000 Genomes and HGDP, respectively).

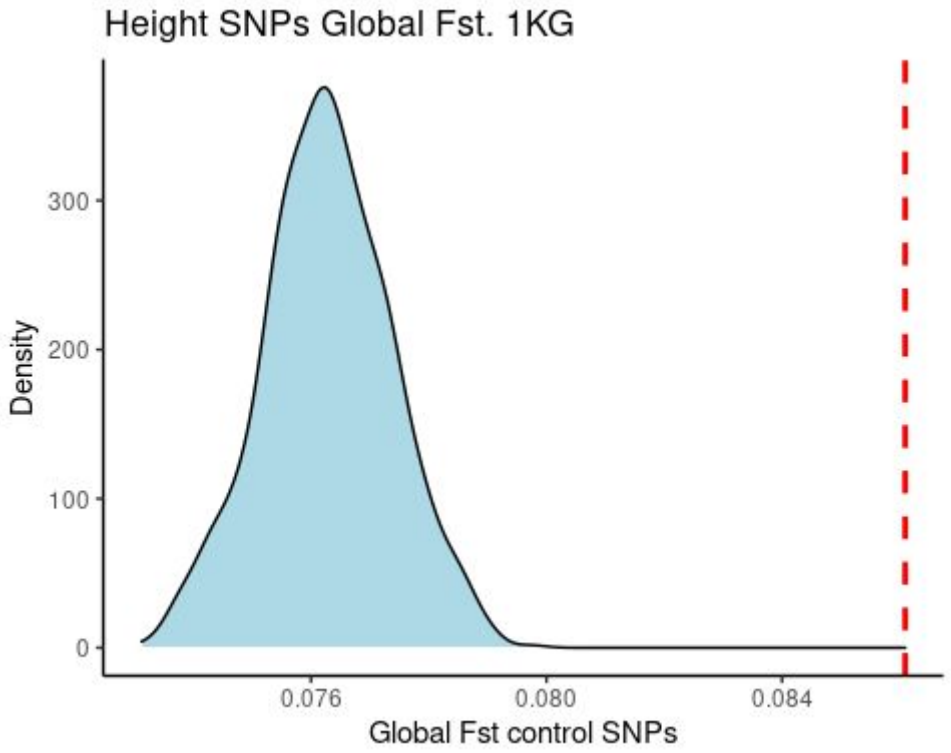
Global Fst

A version of the Qst-Fst test, known as Fst enrichment test (Guo et al., 2018) was used to detect divergent selection. A more powerful version is used here, which avoids the issue of multiple comparisons found in pairwise tests: global Qst-Fst. The trait-associated SNPs were matched (after LD clumping) to random SNPs stratified by MAF and not in close LD (r< 0.1). This process was repeated 1000 times to generate a distribution of mean Fst under neutrality.

The GWAS by Yengo et al. (2018) was used to compute Fst values for height-associated SNPs because the Chung et al. (2019) GWAS summary statistics lacked the p value needed to perform LD clumping.

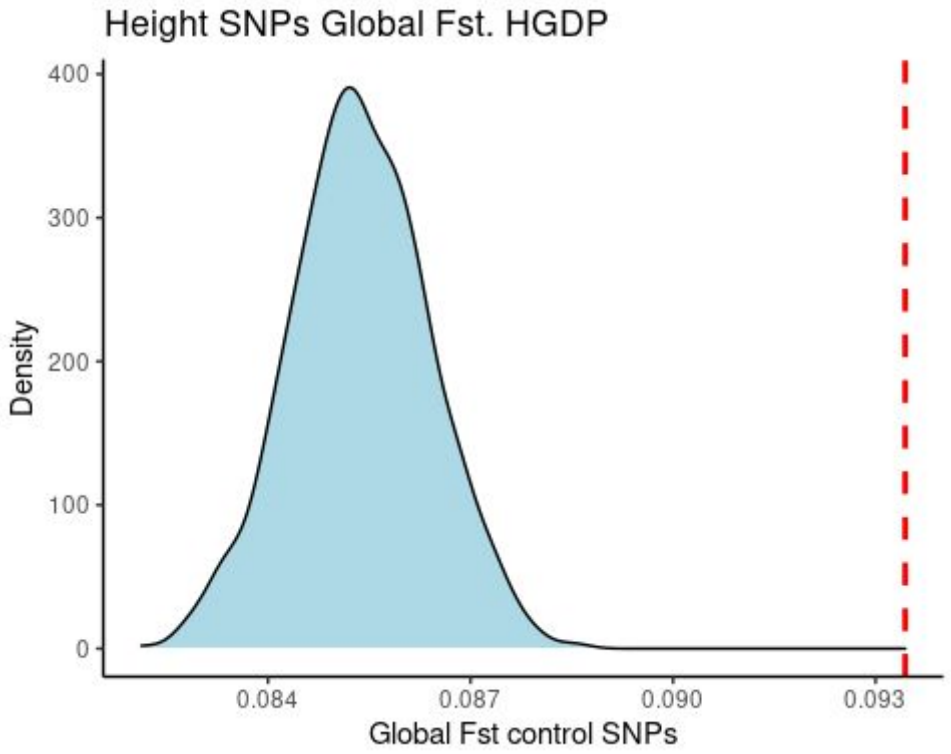
In 1KG, the height PGS had higher average Fst than random SNPs,significantly deviating from Fst values of random PGS (figure 8).

Figure 8. Global Fst for height SNPs and random SNPs. 1000 Genomes



A similar deviation from random SNPs was observed in the HGDP dataset (figure 9).

Figure 9. Global Fst for height SNPs and random SNPs. HGDP



The global Fst enrichment test yielded positive results for education too (figures 10 and 11).

Figure 10. Global Fst for EDU SNPs and random SNPs. 1000 Genomes

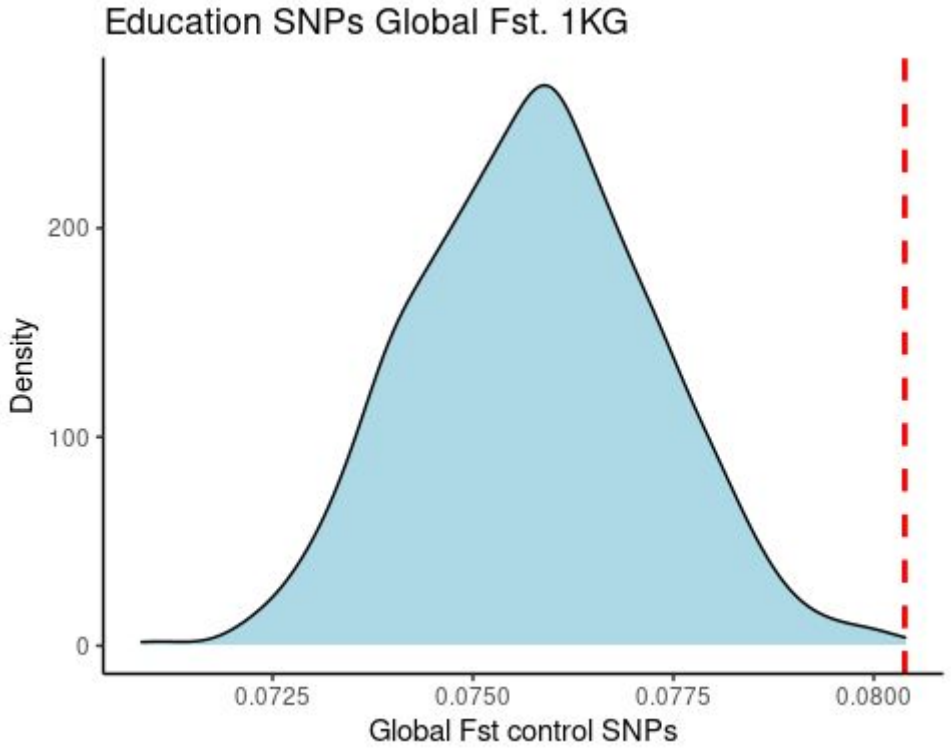
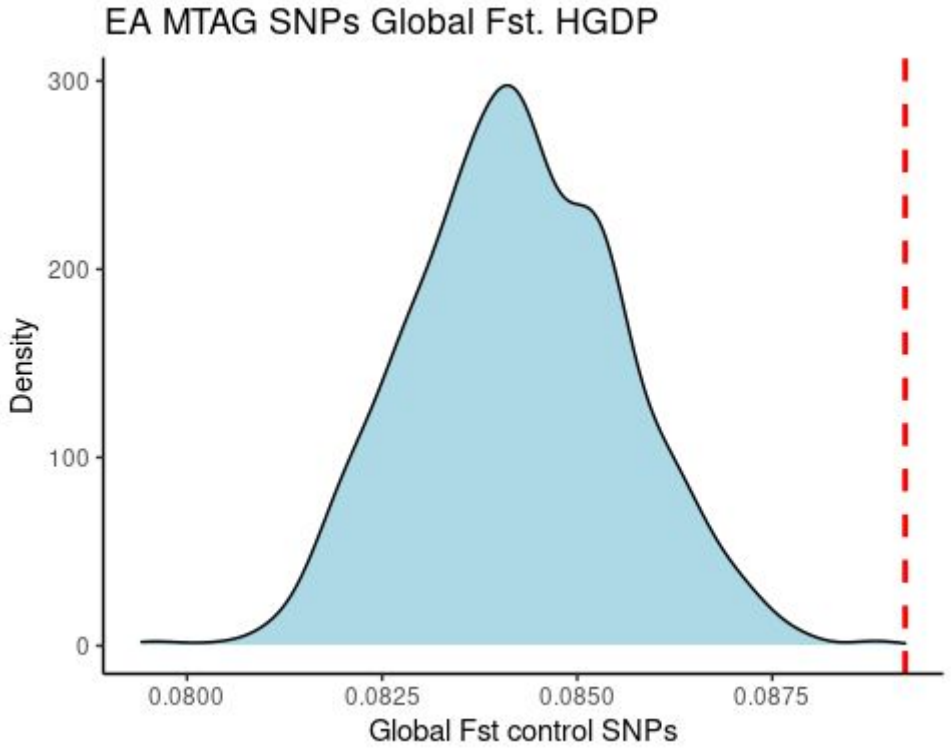


Figure 11. Global Fst for EDU SNPs and random SNPs. HGDP



The Fst values for random and GWAS SNPs and the Z scores + empirical p values are reported in table 1.

Table 1. Fst, Z score and p values for height Fst enrichment test.

	Fst GWAS	**Fst random**	**Z**	**p**
Height 1KG	0.086	0.076	9.04	0.001
Height HGDP	0.089	0.084	3.679	0.0009
EDU 1KG	0.080	0.076	3.11	0.002
EDU HGDP	0.093	0.085	7.945	0.0009

Controlling for LD decay

The SNPs that reached genome-wide significance (P 5 × 10−8) in the largest GWAS of educational attainment (Lee et al., 2018) were selected. Those with minor allele frequency (MAF) <0.01 in the 1000 Genomes database among Europeans (CEU) and Africans (YRI) were removed. There were 2,596 SNPs satisfying these criteria. To explore the different LD patterns across populations, the SNPs were uploaded to LDlink, and all variants -/+ 500 Kb of the query variant with a pairwise R2 value greater than 0.01 were downloaded using CEU and YRI as reference populations. There were 4,696,863 and 5,739,447 variants for CEU and YRI, respectively.

The two files were merged and 1,680,781 overlapping SNPs were retained.

For each query variant, the correlation between the pairwise R2 values for CEU and YRI was computed. The correlation coefficient was used as an index of differential LD decay across Europeans and Africans relative to the query variant. That is, the higher the correlation between the CEU and YRI R2 values, the lower the amount of trans-ethnic LD decay.

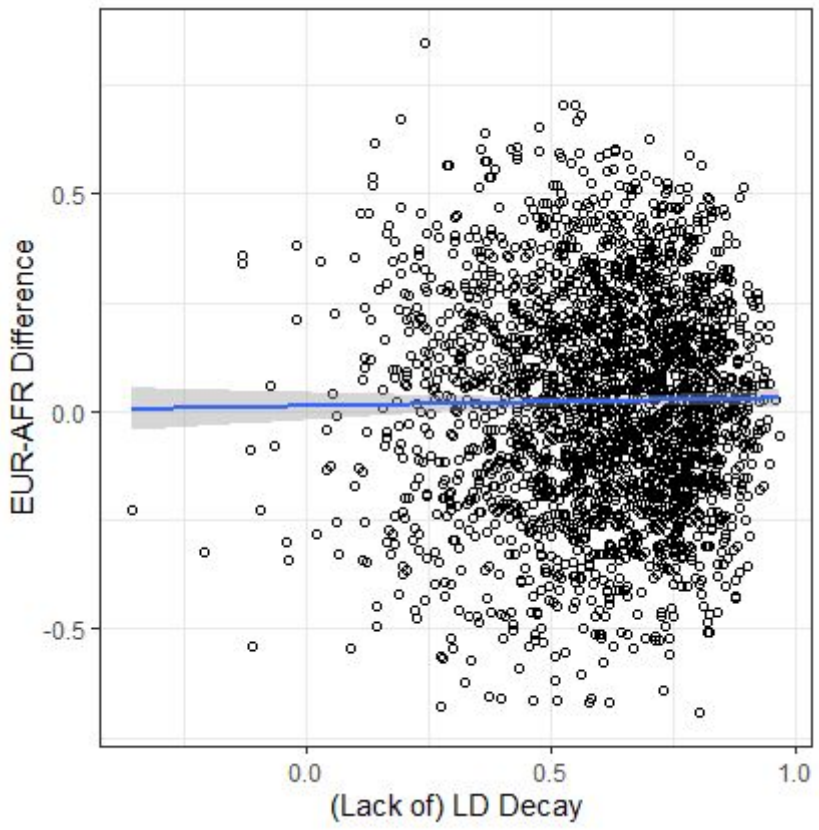
For each SNP, the PGS for CEU and YRI was computed, as well as the pairwise Fst.

The average correlation coefficient between the CEU and YRI R2 values across the 2596 SNPs was r=0.608. This shows the presence of a moderate amount of LD decay.

There was a significant PGS difference between CEU and YRI. Welch Two Sample t-test: means: 50.312% - 47.995% respectively, t= 3.134, 95% C.I 0.008 - 0.037, p= 0.001.

There was no correlation between LD decay and the CEU-YRI PGS difference (r= 0.015, p= 0.451).

Figure 12. Association between LD decay and European-African difference in EA polygenic score.

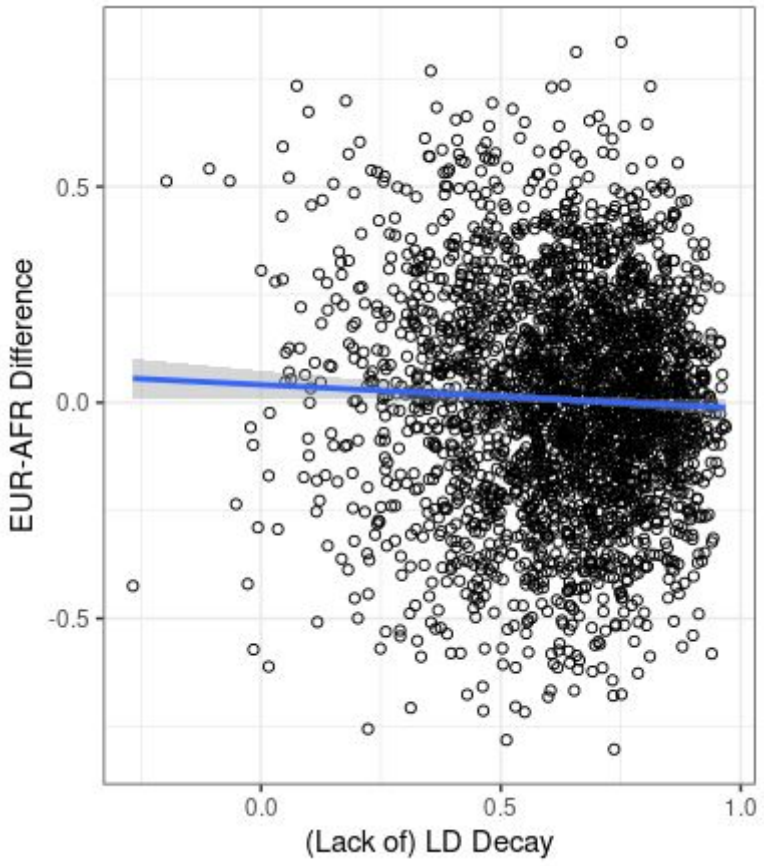


The same analysis was performed on the height significant SNPs. After filtering for MAF (>0.01) there were 2762 SNPs, and 1,693,394 variants in LD within the 500 Kb window.

The average correlation between the pairwise R2 values of CEU and YRI was r= 0.63. The polygenic score difference was 0.67 % (50.02 % vs 49.33%). There was a significantly

negative correlation between (lack of) LD decay and PGS difference (r= -0.0409, p= 0.0315). This can be seen from the scatterplot in figure 13.

Figure 13. Association between LD decay and European-African difference in Height polygenic score.

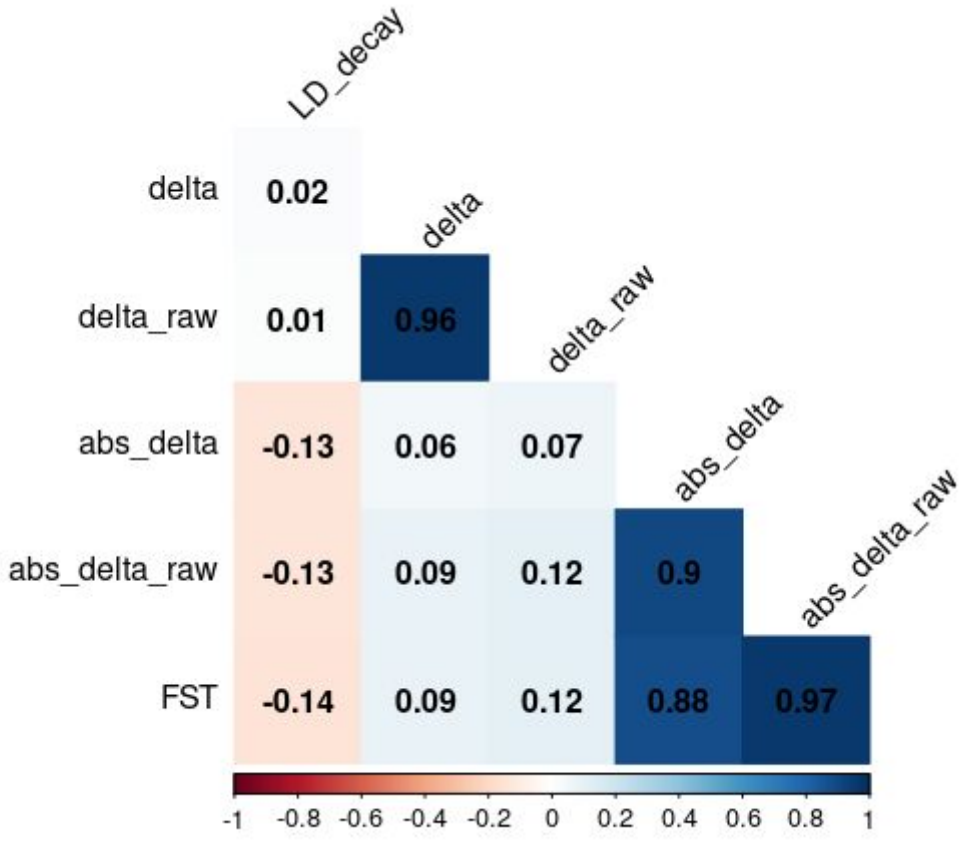


After selecting the SNPs with low amount of LD decay (r>0.8), the PGS difference was reduced to 0.53%.

Correlation between allele LD decay, Fst and allele frequency differences

Fst is a measure of allele frequency differences. However, unlike polygenic scores, it is non-directional, that is, it is "agnostic" about the allele's direction of effect. Hence, Fst suffers from loss of information compared to polygenic scores. Indeed, it was almost perfectly correlated (r= 0.97) to the absolute allele frequency difference (AFD, absolute value of the difference between population frequencies) (Figure 13), but had zero correlation with the polygenic score difference. Fst and AFD were also negatively correlated to (lack of) LD decay, that is SNPs with higher LD decay had higher Fst values.

Figure 13. Correlation matrix



The results were almost identical when using LD decay across Europeans and East Asians (CEU - CHB). However, the extent of LD decay between Europeans and Chinese was lower than between Europeans and Africans (r= 0.727 and 0.608, respectively; t= 22.043, p < 2.2e-16).

PGS difference/Fst as signal of selection

If the polygenic score difference between populations is more sensitive to selection than Fst or AFD, the average ratio of PGS difference to Fst across SNPs should be higher for GWAS SNPs under selection than for less selected traits. Since Fst is nearly equivalent to the absolute allele frequency difference, it is a mixture of allele frequency shifts due to drift and to directional selection but it is not possible to disentangle them. Conversely, the PGS difference is more representative of selection pressure. Hence, the AFD/PGS difference ratio could be a useful indicator of selection pressure on a trait.

Table 2. GWAS significant SNPs (EA)

	Raw PGS delta	**AFD**	**Raw PGS delta/AFD**
CEU-CHB (EA)	-0.0126	0.1759	**0.0715**
CEU-YRI (EA)	0.0231	0.2026	**0.1143**
CEU - CHB (Height)	0.0148	0.1789	**0.082**
CEU-YRI (Height)	0.0067	0.2	**0.0335**

Simulation with quasi-random GWAS SNPs

The EA GWAS SNPs with p value >0.95 (N= 2331) and MAF> 0.01 were used to compute the PGS delta, the AFD and the correlation with LD Decay. A prediction of the polygenic selection model is that the PGS delta and the PGS delta/absolute delta will be lower than in the GWAS significant SNPs.

The polygenic scores were close to the theoretically expected value of 50% (CEU= 0.4965 and YRI= 0.4997) and the difference was 0.3% (table 3). The AFD was almost 2 times lower than in the GWAS significant SNPs, and the raw PGS delta/AFD ratio was ~4.5 x smaller (0.0259). The lower AFD (Fst) difference is due to the MAF being lower in the less GWAS significant SNPs (0.184 vs 0.311). Indeed, Fst is mathematically dependent on MAF, and has lower values with lower MAF (Jakobsson, Edge and Rosenberg, 2013).

Table 3. Quasi-random GWAS SNPs

	Raw PGS delta	**AFD**	**Raw PGS delta/AFD**
CEU-YRI	-0.0032	0.1225	**0.0259**

Difference in correlation coefficient between GWAS significant and quasi-random SNPs

Another metric to represent similarity in allele frequencies between a population pair is the correlation coefficient. Unlike the Fst, the correlation coefficient is “sensitive to the sign” of the difference between each pair of observations. In other worse, it represents not only the strength of the relationship between two variables (or lack thereof) such as Fst or the absolute allele frequency difference; in fact, it is also an expression of the direction of such a relationship because it can acquire positive and negative values.

Therefore, directional (divergent) selection on a population pair should depress the correlation coefficient between the (same) alleles in the two populations. A prediction of this model is that the correlation between the allele frequencies of a pair of populations will be lower for GWAS significant SNPs than for less significant (or random) SNPs.

Indeed, the correlation between the YRI and CEU EA GWAS significant SNPs was r= 0.592, and r= 0.894 for the quasi-random SNPs.

The partial correlation of the population frequencies controlling for LD decay was nearly identical, indicating that LD decay does not mediate the correlation.

The height significant SNPs had similar correlation between CEU and YRI (r= 0.612) and CEU-CHS (r= 0.673).

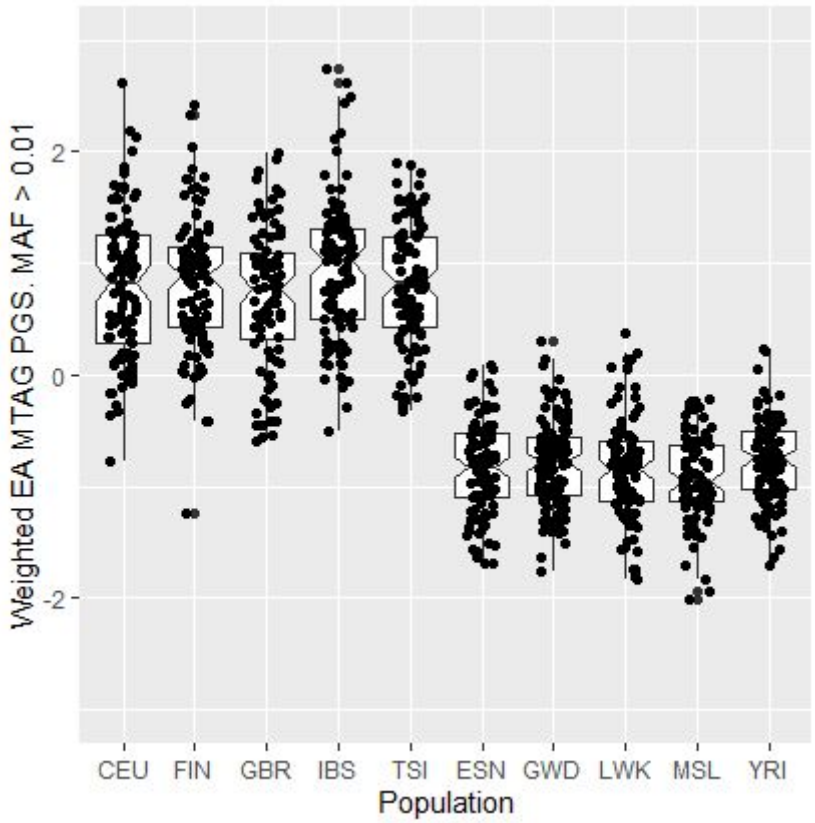
Random SNPs

1000 sets of random SNPs, matched for LD score and MAF, were generated using SNPSNAP. To simulate a GWAS, the status of effect allele was assigned at random for each SNP. The average correlation between the CEU and YRI allele frequencies over 1000 sets was 0.814.

Individual PGS

Polygenic scores were computed for each individual in 1000 Genomes for Europeans and Africans. The individual polygenic scores differed by 1.7 SDs across the two groups ($t = -20.902$, $df = 152.74$, p-value < 2.2e-16). The PGS were calculated for all the populations in the European and African 1000 Genomes groups. Most of the variation was between continents, with little overlap, but considerable overlap among populations from the same continental group (fig. 14).

Figure 14.



Discussion

Height and education-associated SNPs were both highly differentiated across populations, as shown by the global Fst enrichment test and polygenic scores. These differences matched differences in average trait (i.e. height and education), reaching correlations ~ 0.9 with average population IQ and height (figures 3, 4, 6, 7), implying that selection pressure after the out of Africa dispersal acted with different strength on different populations. The results were robust across different datasets (gnomAD, 1000 Genomes and HGDP), yielding more credibility to the findings. The lack of a correlation between LD decay and population differences in polygenic scores (figure 12) suggests that low p value EA GWAS SNPs have a causal effect on the phenotype or they are closely tagging causal variants (i.e. high LD). For height, LD decay had a small effect on the PGS difference, so that the PGS difference computed using SNPs in low LD decay (r> 0.8) was slightly reduced (from 0.67% to 0.53%).
Climate is a potential mechanism that influenced polygenic adaptation for education, via selection for enhanced cognitive ability or life-history traits. Indeed, a positive correlation (r= 0.68) between education PGS and latitude was found (figure 5). A simulation using random SNPs matched for minor allele frequency, showed that this result rarely occurs by chance (p= 0.0009) (fig.6). Remarkably, the height PGS had a much weaker correlation (r= 0.3) with

latitude (figure 1), despite Bergmann's rule predicting cold-climate selection for larger sized animals. However, this mirrors findings of a weak positive relationship between height and latitude in human populations (Gustafsson & Lindenfors, 2009).

Recently, Stern et al. (2021) found evidence for directional selection on EDU PGS. The effect was partly mediated by EDU's correlation to a variable measuring skin pigmentation ("sunburning ability"). The authors found that after accounting for selection pressure on skin pigmentation, the selection signal on EDU was attenuated. Hence, a large share of the selection pressure on EDU was due to correlated response with another trait. In light of the strong correlation with latitude,an alternative explanation to directional selection on EDU being a by-product of selection on pigmentation, is that climatic factors could account for the genetic correlation between EDU and skin pigmentation.

The present study also shows the empirical equivalence of Fst and absolute allele frequency difference (r= 0.97). An advantage of using polygenic scores compared to the Fst or absolute allele frequency difference is that it is directional, that is each allele's effect (whether it is a risk allele or not, or whether it increases or decreases a phenotype) is taken into account. To the contrary, Fst and AFD are non-directional, so the mean Fst or AFD across many genetic variants is independent of alleles with positive effects being overrepresented in a population compared to another one. Hence, Fst or AFD are more representative of drift than selection. Conversely, the polygenic score difference is more indicative of directional selection because it is dependent on the average direction of selection across many genetic variants. Hence, the ratio between the latter and the mean Fst or AFD is a measure of directional selection net of the effects of drift. Accordingly, there was a much stronger reduction in PGS difference than Fst in a set of low significance ($p>0.95$) GWAS SNPs, which putatively contain mostly noise (and very little selection signal). They had lower (2x) Fst, but much lower (7x) PGS difference, resulting in a 4.5-fold reduction in PGS difference/AFD ratio (tables 2,3).

Another way to represent the coefficient of directional selection is to compute the correlation between the frequencies of (GWAS significant) alleles with positive effect among a pair of populations; one can compare them to non-significant (almost random) SNPs, or a set of random SNPs matched for MAF. The advantage of using correlation of allele frequency across population pairs is that it is intuitive and, unlike Fst, it is sensitive to the direction of selection on each genetic variant as well as its strength. Divergent selection will make allele frequencies shift in different directions among populations. Indeed, the GWAS significant SNPs for height and EA had much weaker correlation of allele frequencies ($r\sim 0.6$) compared to non-significant and random SNPs ($r>0.8$).

Allele frequencies computed by group are traditionally used for tests of selection. This allows researchers to identify the genetic variants that have the strongest selection signals.

However, another way to represent allele frequency differences between groups is with individual PGS: this gives a better idea of how much variation is partitioned between individuals and between groups. An in-depth analysis of this topic is not within the scope of this paper, but it can be seen (figure 14) that for polygenic scores of traits under strong polygenic selection, there is much more dispersion between continental groups than between individuals. That is, there is little overlap in the individual polygenic scores across continental groups (Africans and Europeans), as they deviate by more than 1.5 SDs. On the other hand, populations within the same continent have relatively tiny differences.

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