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Evidence for Recent Polygenic Selection on Educational Attainment and Intelligence Inferred from GWAS Hits: A Replication of Previous Findings Using Recent Data

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Abstract:
Background: The genetic variants identified by three large genome-wide association studies (GWAS) of educational attainment and the largest intelligence GWAS were used to test a polygenic selection model. Methods: Average frequencies of alleles with positive effect (polygenic scores or PS) were compared across populations (N=26) using data from 1000 Genomes. Factor analysis was used to extract a signal of polygenic selection. Results: A polygenic selection factor of educational attainment GWAS hits is high among a handful of SNPs within genomic regions replicated across GWAS publications and it is highly correlated to the genetic intelligence factor (r= 0.96). These factors are both highly predictive of average population IQ (r=0.9), and are robust to tests of spatial autocorrelation. Several Monte Carlo simulations yielded highly significant p values. Furthermore, the polygenic selection model shows high replicability, with the EA and intelligence factor scores being virtually identical to those from an older study (r=0.96-0.99). A larger sample of populations (N=53) produced similar results. Conclusion: This study shows robust results after accounting for spatial autocorrelation and Monte Carlo simulation using random SNPs and shows robust reproducibility of results from a previous study.

Keywords: educational attainment; polygenes; polygenic selection; IQ; GWAS

1. Introduction

Over the last decade, population geneticists have recognized that most traits are highly polygenic, and hence have moved away from the study of genetic evolution using the single-gene, Mendelian approach, towards models that examine many genes together (i.e. polygenic models).

Signals of polygenic selection can be identified by various methods, such as correlation of allele frequencies [1-4] and the regression of population average of trait values on polygenic scores (PS) [2,5-7], which have been successfully applied to human stature [5-7] and cognitive abilities [2]. This paper has several aims: to test the presence of a factor among GWAS hits and the predictive power of polygenic scores (average frequencies of GWAS alleles with positive effect), independently of spatial autocorrelation. A prediction is that the polygenic selection model provides a better fit to the data (i.e. average population IQ). A goal of this study is to replicate the effects found by Piffer in 2015 [2], with the evidence from new intelligence and educational attainment GWAS published to date. Piffer [2] factor analyzed educational attainment and intelligence GWAS hits and found a factor that was highly predictive of population IQ.

The factor analytic method is based on the assumption that polygenic selection acts as a latent variable which accounts for commonalities among several genetic variants scattered across the

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genome [1]. The model also includes an error term due to measurement error in the form of limited sample size, imperfect coverage or genetic drift, which all act to increase the noise.
Piffer [8] identified 9 genomic loci (table S1) that were replicated across the three largest GWAS of educational ("EA") attainment published to date [9-11]. The 9 loci contain GWAS significant alleles that were found to be in strong LD (r>0.8). One locus was replicated across three GWAS [9-11] and the same SNP (rs9320913) was found in two of them[9,11]. The population frequencies of the 9 pairs (one member belonging to each GWAS publication) of alleles were highly correlated (r=0.919), hence the SNPs published in [4] were used. Thus, this set of 9 SNPs was considered the best candidate for analysis of natural selection on educational attainment and related phenotypes (e.g. general cognitive ability or gca). In addition, the full sets of 74 and 162 SNPs (respectively, the new hits and those found after pooling together different datasets) from the latest GWAS of educational attainment [11] will be employed. Finally, the results of a recent GWAS of human intelligence [12] will be analyzed with the same method and compared to previous findings for educational attainment.
Average estimated population IQ will be used as the phenotype of interest and main dependent variable in the analyses. This choice can be justified by its privileged status in psychometric research and its robust genetic correlation (r= around 0.7) with educational performance [13] and attainment [14]. Moreover, the GWAS hits identified by the three educational GWAS also predict general cognitive ability in their samples [9-11]. A re-analysis of the Okbay et al. dataset revealed that the polygenic score also predicts general intelligence (3.6%) compared to 2% for the 2013 polygenic score [13]. If educational attainment and intelligence are genetically correlated also at the group level, a prediction is that there will be a population-level genetic correlation between educational attainment and intelligence GWAS polygenic or factor scores.

2. Materials and Methods

Rietveld et al. [9] produced 3 SNPs reaching GWAS significance for educational attainment.
Davies et al. [10] reported 1115 SNPs reaching GWAS significance, of which 15 were independent signals for educational attainment. 942 SNPs were found on 1000 Genomes. Among the 15 independent signals, one (2:48696432_G_A) was missing.
Okbay et al. [11] reported 74 SNPs associated with years of education. 70 were found in 1000 Genomes (the other 4 variants were flagged because they had more than 3 different alleles). In a pooled meta-analysis, 162 SNPs were reported (161 were found in 1000 Genomes).
A set of nine GWAS hits from Okbay et al. [11] that were in close linkage disequilibrium (linkage cut-off r≥.8, 500kb linkage window) with 'hits' predicting educational attainment across two other large GWAS studies [9,10] was identified. Linkage was determined using the NIH LDLink program [14] with the 1000 Genomes Phase3 CEU population as a reference group
The 18 independent (i.e. unlinked) hits for general cognitive ability from the most recent intelligence GWAS were included in the analysis [12]. This study also produced 9 SNPs that were also available in the educational attainment sample, and reached genome-wide significance [12]. This set of SNPs will be called "Int-EA SNPs".

Factor analysis was carried out using the Ordinary Least Squares method ("minres" option in R package "psych").

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Monte Carlo simulations were performed using a random dataset, consisting of a large sample (N=13130) of matched random unlinked SNPs (downloaded from 1000 Genomes, phase 3).
The empirical value p= (r+1)/(n+1) was calculated, where r is the number of runs whose Pearson's correlation coefficient (r x population IQ) was higher than the one found using the actual (GWAS-derived) polygenic score; n= total number of runs. The corrected formula was provided by Davison & Hinkley [16].
Matching was carried out using SNPSNAP[5], by feeding the 9 and the 18 intelligence SNPs and setting LD r^2 <0.1 (for EUR), with maximum allowed deviation for MAF= 5%. Unlinked SNPs were used in order to have a sample with independent observations. Fst distances were obtained from [2], calculated using Vcftools with 1000 Genomes, phase 3 data. Average population IQ estimates were obtained from [8]. Previously published scores were used also to guarantee that the values were not created ad hoc.
Analyses were run using R [18]
SNP frequencies for ALFRED were downloaded from alfred.med.yale.edu. Fst distances for ALFRED/HGDP populations were obtained from [19], and after removal of the non-overlapping samples, 49 matching populations were retained.

3. Results

Correlation between polygenic scores and population IQ

The polygenic score computed using the 9 SNPs was highly correlated (r=0.88) to an estimate [2] of average population IQ (fig. 1). A Monte Carlo simulation was run using 818 PS computed from groups of 9 SNPs taken from the random dataset. The average correlation between population IQ and the random polygenic scores was 0.22 (N=818). The slightly positive correlation can be interpreted as an effect of spatial/phylogenetic autocorrelation [8] A Monte Carlo approach was used: the percentile corresponding to a correlation coefficient r=0.88 was found to be 99% (using the 818 random polygenic scores), implying that the result is highly significant. The corrected (and more conservative) calculation of Monte Carlo p value, where p= r+1/n+1 (see Methods) was used, producing p= 0.011 (n= 819, r= 8).

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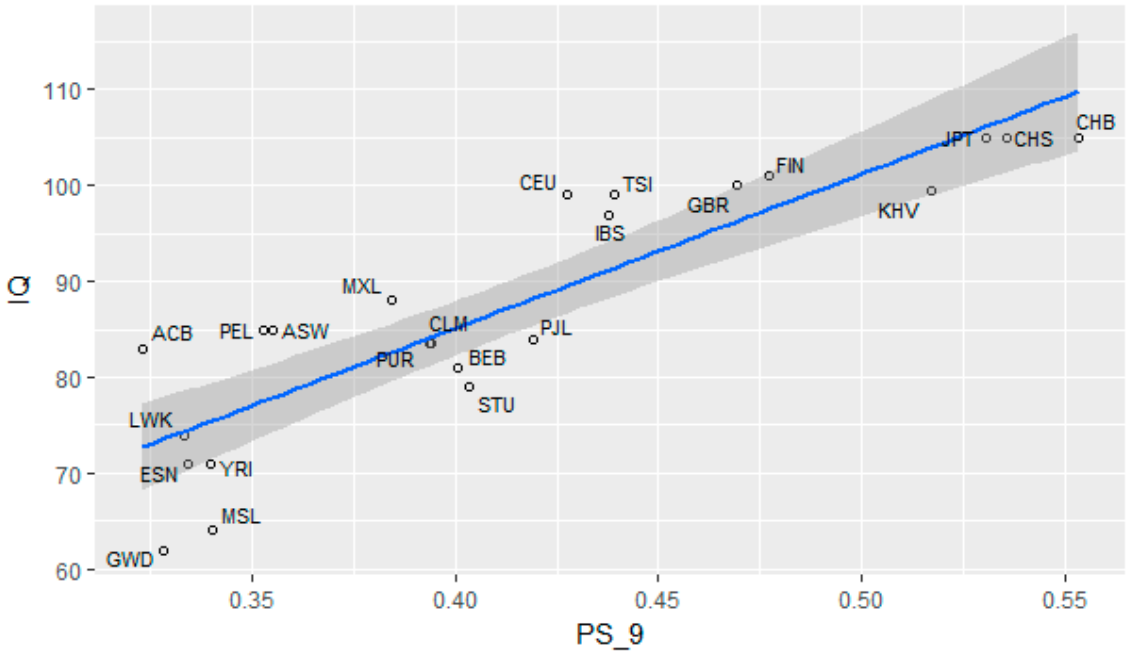
Figure 1. Correlation between population IQ and educational attainment polygenic score.



The correlation between the 161 SNPs polygenic score and population IQ was high (r=0.854), corresponding to the 98th percentile in the simulation (using PS comprising 161 random SNPs each). The 161 SNPs and the 9 SNPs polygenic scores were strongly correlated (r= 0.949). Conversely, the 74 SNPs did not have much predictive power (r=0.655).

A polygenic score for the intelligence GWAS was computed, yielding only a moderate correlation with population IQ (r= 0.496), and a non-significant Monte Carlo p=0.43. The polygenic score had correlations of similar magnitude to the educational attainment polygenic scores, but had poor Monte Carlo significance (p=0.213). Since the population differences in polygenic scores were small, continent-level polygenic scores were computed to identify potential differences at a higher level (i.e. 1000 Genomes “superpopulations”).
These only showed an advantage for East Asians, but were virtually identical for other super-populations (EAS= 49%, EUR= 45.9%, AFR=47.3%, AMR= 45.6%, SAS= 44.2%).
A polygenic score for the intelligence-educational attainment SNPs [12] was computed, yielding high correlations with population IQ (r= 0.876). Weighing by effect size produced almost identical results. Values for super-populations were the following: EAS= 62.98%, EUR= 56.95%, AFR= 50.71%, AMR=55.08%, SAS= 54.08%.
A Monte Carlo simulation for the correlation with population IQ was run, using SNP sets of the same size (9), yielding a highly significant p value= 0.008.
Polygenic scores are reported in table 1.

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Table 1. Polygenic scores

Population	G	EA 9	Int EA 9
ACB	0.475	0.224	0.520
ASW	0.469	0.259	0.524
BEB	0.431	0.353	0.545
CDX	0.493	0.425	0.632
CEU	0.475	0.384	0.581
CHB	0.526	0.481	0.627
CHS	0.507	0.462	0.638
CLM	0.462	0.343	0.556
ESN	0.469	0.227	0.499
FIN	0.462	0.442	0.577
GBR	0.465	0.416	0.569
GIH	0.471	0.389	0.538
GWD	0.472	0.218	0.497
IBS	0.454	0.396	0.560
ITU	0.431	0.365	0.552
JPT	0.532	0.458	0.626
KHV	0.507	0.450	0.627
LWK	0.457	0.231	0.491
MSL	0.489	0.231	0.527
MXL	0.442	0.335	0.544
PEL	0.447	0.299	0.561
PJL	0.443	0.378	0.543
PUR	0.455	0.345	0.542
STU	0.444	0.361	0.529
TSI	0.458	0.396	0.562
YRI	0.470	0.231	0.501

*ACB= African Caribbeans in Barbados; ASW= Americans of African Ancestry in SW USA; BEB= Bengali from Bangladesh; CDX= Chinese Dai in Xishuangbanna, China;CEU= Utah Residents (CEPH) with Northern and Western European Ancestry; CHB= Han Chinese in Bejing, China; CHS= Southern Han Chinese; CLM= Colombians from Medellin, Colombia; ESN= Esan in Nigeria; FIN= Finnish in Finland; GBR= British in England and Scotland; GIH= Gujarati Indian from Houston, Texas; GWD= Gambian in Western Divisions in the Gambia; IBS= Iberian Population in Spain; ITU= Indian Telugu from the UK; JPT= Japanese in Tokyo, Japan; KHV= Kinh in Ho Chi Minh City, Vietnam; LWK= Luhya in Webuye, Kenya; MSL= Mende in Sierra Leone; MXL= Mexican Ancestry from

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Los Angeles USA; PEL= Peruvians from Lima, Peru; PJL= Punjabi from Lahore, Pakistan; PUR= Puerto Ricans from Puerto Rico; STU= Sri Lankan Tamil from the UK; TSI= Toscani in Italia; YRI= Yoruba in Ibadan, Nigeria.

Factor analysis of allele frequencies

Factor analysis was performed on the 9 quasi-replicated educational attainment SNPs, on the 18 intelligence SNPs and on the 9 intelligence-EA SNPs in order to extract a signal of polygenic selection [1,2]. Factor loadings are reported in tables 2a,b.

Factor loadings

Table 2a. Factor loadings (Intelligence SNPs)

SNP	Loading
rs10191758	0
rs10236197	-0.382
rs11138902	0.71
rs12744310	-0.778
rs12928404	-0.329
rs13010010	0.929
rs16954078	-0.396
rs2251499	0.238
rs2490272	0.921
rs36093924	0.568
rs4728302	-0.713
rs6746731	-0.422
rs6779302	0.829
rs7646501	-0.977
rs9320913	0.84
rs66495454	0.726
rs113315451	-0.834
rs41352752	0.31

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Table 2b. Factor loadings (EA SNPs)

SNP	Loading
rs1008078	-0.801
rs11588857	0.831
rs12987662	0.956
rs148734725	-0.492
rs11712056	0.606
rs62263923	0.863
rs13294439	0.91
rs12969294	0.459
rs9320913	0.717

Table 2c. Factor loadings (Intelligence-EA SNPs)

SNP	Loading
rs12928404	-0.358
rs12744310	-0.883
rs13010010	0.994
rs10191758	0.156
rs6801153	0.305
rs6779302	0.875
rs9320913	0.789
rs215601	0.475
rs4728302	0.510

Factor scores are reported in table 3.

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Table 3. Factor scores for educational attainment and intelligence

Population	G factor	EA factor	Int-EA factor
ACB	-1.276	-1.351	-1.063
ASW	-0.961	-1.177	-0.997
BEB	-0.075	-0.209	-0.66
CDX	1.35	1.017	1.251
CEU	0.844	0.471	0.754
CHB	1.109	1.511	1.374
CHS	1.208	1.382	1.635
CLM	0.357	0.010	-0.113
ESN	-1.660	-1.453	-1.255
FIN	0.771	0.702	0.581
GBR	0.797	0.745	0.782
GIH	-0.049	0.271	-0.001
GWD	-1.358	-1.397	-1.186
IBS	0.631	0.350	0.476
ITU	-0.074	0.049	-0.212
JPT	0.878	1.342	1.321
KHV	1.267	1.346	1.925
LWK	-1.599	-1.488	-1.255
MSL	-1.444	-1.403	-1.165
MXL	0.215	0.056	-0.259
PEL	-0.060	0.050	-0.762
PJL	0.066	0.240	0.035
PUR	0.375	-0.004	-0.208
STU	-0.391	0.134	-0.432
TSI	0.764	0.248	0.677
YRI	-1.684	-1.443	-1.243

The correlation between the G and EA factors was r= 0.96. A Monte Carlo simulation was run,

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carrying factor analysis over sets of 18 SNPs and correlating them to the EA 9 factor scores. The MC p value was 0.02. The Int-EA factor was similarly highly correlated to the other two factors (r= 0.93-0.94).

Controlling for spatial autocorrelation

The presence of spatial autocorrelation in a dataset means that the cases are not independent leading to an overestimation of degrees of freedom and, in the case of positive autocorrelation, an inflation in the correlation between two or more variables. The source of spatial autocorrelation in population genetics datasets is the similarity caused by admixture among neighbouring populations, and the differences caused by random drift. Demonstrating that the alleles predict population-level differences in average phenotypic values above and beyond that predicted on the basis of migration, drift etc, provides evidence for a model of polygenic selection.

Fst distances were used to partial out spatial autocorrelation, following the method outlined in [1], similar to Mantel test [21]. The correlation between Fst distances and IQ distances was moderate (r=0.588), pointing out the presence of spatial autocorrelation. Multiple regression was performed with 9 SNPs and Fst as predictors and population IQ as dependent variable. Significant models (respectively for 9 and 161 SNPs) were obtained (Adjusted R-squared: 0.503, F-statistic: 128.5 on 2 and 250 DF, p< 2.2e-16), (Adjusted R-squared: 0.7251,F-statistic: 30.01 on 2 and 20 DF, p= 9.514e-07) (table 4).

Table 4. Multiple regression with random SNPs and GWAS hits

Variable	Beta	t	sig	VIF
PS 9 distances	0.524	9.024	<2e-16	1.713
Fst distances	0.250	4.305	2.4e-05	
PS 161 distances	0.456	7.063	1.61e-11	1.912
Fst dist	0.274	4.241	3.14e-05	
Fa EA dist	0.81	8.864	< 2e-16	4.22
Fst dist	-0.12	1.172	0.189	
Int factor dist	0.837	16.295	< 2e-16	3.42
Fst dist	-0.108	0.964	0.152	

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Replication of scores by Piffer (2015).

Piffer [2] calculated polygenic and factor scores for 1000 Genomes population using the data available at the time. The correlation between the present study's EA and intelligence factors and Piffer's 2015 polygenic score are very high (r=0.96-0.99).

ALFRED

The 9 quasi-replicated EA SNPs and the 18 intelligence hits were searched in ALFRED (52 populations). Four of them were found. Rs9320913 (a hit in Skiekers et al., Davies et al,, Okbay et al.) was not found but it was in LD (r=0.95) with Rs1906252 [2].

A factor analysis was carried out. Factor loadings are reported in table 5.

Table 5. Factor loadings.

SNP	Loading
rs10236197_T	-0.218
rs1906252_T	0.533
rs13010010_T	0.868
rs11588857_A	0.790

Polygenic score and factor scores are reported in table 6. Factor scores broken down by sub-continent are reported in table 7.

Table 6. Factor and polygenic scores for HGDP (ALFRED) populations

	Population	Factor	PS
Africa	Bantu SA	-1.454	0.063
Africa	Bantu Kenya	-1.381	0.168
Africa	San	-1.488	0.188

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Africa	Biaka	-1.369	0.198
Africa	Mbuti	-1.415	0.204
Africa	Yoruba	-1.270	0.168
Africa	Mandenka	-1.153	0.150
N. Africa	Mozabite	-0.768	0.294
Asia	Bedouin	-0.156	0.378
Asia	Druze	0.254	0.416
Asia	Palestinian	-0.071	0.405
Europe	Adygei	0.257	0.360
Europe	Basque	-0.088	0.388
Europe	French	0.217	0.408
Europe	Italians_C	0.404	0.405
Europe	Italians_N	0.437	0.413
Europe	Orcadian	0.753	0.493
Europe	Russians	0.073	0.393
Europe	Sardinian	-0.225	0.315
Asia	Burusho	0.151	0.390

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Asia	Kalash	0.475	0.375
Asia	Pashtun	-0.426	0.345
Asia	Mongolian	1.358	0.488
Asia	Balochi	0.055	0.363
Asia	Brahui	-0.334	0.370
Asia	Hazara	0.506	0.458
Asia	Sindhi	-0.438	0.325
EastAsia	Dai	0.987	0.463
EastAsia	Daur	1.246	0.540
EastAsia	Han	0.936	0.410
EastAsia	Hezhe	0.980	0.488
EastAsia	Japanese	1.018	0.410
EastAsia	Koreans	1.127	0.471
EastAsia	Lahu	0.877	0.388
EastAsia	Miao	1.078	0.525
EastAsia	Naxi	0.113	0.363
Asia	Oroqen	0.445	0.325

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EastAsia	She	0.737	0.488
EastAsia	Tu	0.828	0.450
EastAsia	Tujia	1.507	0.463
EastAsia	Uyghur	0.566	0.475
EastAsia	Xibe	0.802	0.375
EastAsia	Yi	1.190	0.413
EastAsia	Cambodians, Khmer	0.340	0.346
Oceania	Papuan New Guinean	-0.569	0.348
Oceania	Melanesian, Nasioi	-0.533	0.334
Siberia	Yakut	0.311	0.432
NorthAmerica	Pima, Mexico	-1.312	0.320
NorthAmerica	Maya, Yucatan	-1.300	0.204
SouthAmerica	Amerindians	-1.366	0.260
SouthAmerica	Karitiana	-1.530	0.200
SouthAmerica	Surui	-1.382	0.245

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Table 7. Factor scores by continent

Sub-continent	Factor	PGS
Africa	-1.287	0.179
M East	0.009	0.400
Europe*	0.293	0.408
W Asia	-0.002	0.375
E Asia**	0.959	0.450
Oceania	-0.551	0.341
SE Asia	0.340	0.346
America	-1.378	0.246
Siberia	0.311	0.432
North Africa	-0.768	0.294

*Sardinia is not included in the European group due to its status as genetic outlier and higher similarity to Middle Eastern populations. ** Includes Mongolia.

The correlation between factor scores distances and Fst distances was r=0.462 (N=1176). The correlation between geographic distance from Addis Ababa and factor scores was r= - 0.483 (N=49).

4. Discussion

Two methods were used to estimate polygenic selection and related genotypic differences in intelligence and educational attainment between populations.

The calculation of population-level polygenic scores (average allele frequencies with positive GWAS beta) is a promising and quick approach. However, it is a-theoretical relative to

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evolutionary processes. Factor analysis of allele frequencies is another method, whose goal is to detect a hypothetical signal of polygenic selection which accounts for covariance among frequencies of several alleles associated with the same trait. A drawback of this method is it can be performed only on small sets of SNPs, because using large sets would excessively reduce the observations to variable ratio, hence making the results of factor analysis less stable.

The polygenic score obtained from 9 quasi-replicated SNPs is a good candidate for estimating selection strength on educational attainment: it outperforms (in predicting average population phenotypic intelligence) 99% of the polygenic scores obtained from random SNPs (Monte Carlo p= 0.011): that is, over a total of 819 runs, a correlation coefficient equal to or higher than 0.88 occurred 8 times, producing p= 0.011. It is also relatively robust to tests of spatial autocorrelation (table 3).

A recent GWAS produced 18 independent genomic hits for intelligence.

The results produced by the intelligence GWAS were positive only with regards to the factor scores. Monte Carlo simulations with 13,000 random SNPs showed that the intelligence polygenic scores failed to predict population IQ significantly better than random SNPs. However, a subset of 9 SNPs identified by [12] that were significant both in the intelligence GWAS and in the educational attainment GWAS produced high correlation with population IQ (r=0.88), which was robust to Monte Carlo simulation (p=0.008).

Furthermore, factor analysis yielded factor scores that strongly predicted population IQ (r=0.9), both for the intelligence and the intelligence-EA SNPs. The significance of this correlation was ascertained via Monte Carlo simulation, and found to be high (Monte Carlo p= 0.004). Moreover, the factor scores were also highly correlated to the 9 SNPs educational attainment PS (r= 0.89) and to the 161 SNPs PS (r= 0.88). Monte Carlo simulations show that this inter-correlations were significant (p=0.016 and 0.021, respectively).

A factor analysis was carried out on the 9 educational attainment SNPs and the factor scores were found to be almost identical (r=0.96) to the intelligence factor scores. This correlation had MC p= 0.023. Hence, support was found for the hypothesis that educational attainment and intelligence are genetically correlated at the group level.

The EA polygenic and factor scores and the intelligence factor were robust to tests of spatial autocorrelation (table 3). When IQ was regressed on the factor scores and Fst distances, the latter lost all the predictive power, whereas the former had high Beta (0.81-0.84).

More strength to the present findings is given by the high replicability of the same polygenic model from a previous publication [2]. Piffer [2] calculated polygenic and factor scores for 1000 Genomes population using the data available at the time. The correlation between the present study's EA and intelligence factors and Piffer's 2015 polygenic and factors score are very high (all of the 4 correlations range between r=0.96-0.99). This is remarkable, since the present study included 2 new educational attainment GWAS [10,11] and a new intelligence GWAS [12], comprising much larger samples.

The results were replicated using a larger sample of populations (N=52), which showed similar population and continental rankings of factor scores (tables 5,6). A positive correlation with Fst distances was found, but a negative one with distance from Eastern Africa. The latter finding casts doubt on the hypothesis that evolutionary novelty (operationalized as geographic distance from the ancestral African environment) was a force behind the evolution of general intelligence [23].

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A limitation of the present study is its reliance on estimates of population IQ as the phenotypic variable, which are not perfectly accurate, besides reflecting environmental and economic differences between populations.

The low amount of variance explained at the individual level is not a fatal issue. Indeed, predicting group-level variance is different from predicting variance within a group. The present approach maximizes signal by focusing on the average signal produced by each SNPs, rather than the sum of the signal produced by all the SNPs. Using more SNPs would include more noise in the data, as SNPs with lower significance likely carry out too much noise. One could argue that weighting each SNP by its regression coefficient or p value could allow us to assign less weight to the more noisy SNPs, hence getting rid of this issue. A similar approach was used in [23]. However, this approach assumes a linear relationship between population level noise and GWAS significance, which has never been demonstrated. In fact, it is possible that the relationship between GWAS effect/p value and population-level signal is exponential and concentrated among a handful of SNPs.

The effect of LD decay on comparison of risk alleles between populations is still unclear. Since most GWAS hits are actually tag SNPs, decay in LD implies that the causal SNPs will be less efficiently flagged by the tag SNPs until the tag SNPs will resemble a sample of random SNPs.

It is sensitive to coverage and in older studies using low coverage genomic data (e.g. 1000 Genomes phase 1), it was found to reduce the reproducibility of findings [24]. However, contemporary GWAS use higher coverage data (e.g. 1000 Genomes phase 3), hence this issue is less important.

Moreover, simulations found that the effect of LD decay on true causal variants was null to negligible [24]. The present study, by focusing only on the most significant hits, increased the likelihood of hitting on or very close to causal variants, hence reducing the artifact of LD decay.

Furthermore, LD decay is expected to create noise and not to produce a bias necessarily in a direction that favours the hypothesis of this study.

Since the frequency of the average SNP allele is 50%, the tag SNPs will tend to converge towards an average frequency of 50%, with increasing LD decay. The implication of this for our analysis is that when the European polygenic scores are below 50%, our estimates of non-European polygenic scores will be inflated, and vice-versa for the polygenic scores which are above 50% in Europeans, because LD decay pushes the polygenic scores up (or down) towards the background frequency of 0.5 in the other groups.

Future GWAS studies should be carried out on non-European populations and if the present findings are an accurate prediction of polygenic selection, they should be strong predictors of polygenic or factor scores computed from non-European GWAS hits.

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Supplementary files: https://osf.io/5yhf4/

R code: http://rpubs.com/Daxide/279148

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