A Polygenic Resilience Score Moderates the Genetic Risk for Schizophrenia: Replication in 18,090 Cases and 28,114 Controls from the Psychiatric Genomics Consortium

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Keywords: genome-wide association study, high risk, polygenic score, schizophrenia, resilience

ABSTRACT (181 words)

Identifying heritable factors that moderate the genetic risk for schizophrenia (SCZ) could help clarify why some individuals remain unaffected despite having relatively high genetic liability. Previously, we developed a framework to mine genome-wide association (GWAS) data for common genetic variants that protect high-risk unaffected individuals from SCZ, leading to derivation of the first-ever "polygenic resilience score" for SCZ (resilient controls n = 3,786; polygenic risk score-matched SCZ cases n = 18,619). Here, we performed a replication study to verify the moderating effect of our polygenic resilience score on SCZ risk (OR = 1.09, p = $4.03x10^{-5}$) using newly released GWAS data from 23 independent case-control studies collated by the Psychiatric Genomics Consortium (PGC) (resilient controls n = 2,821; polygenic risk score-matched SCZ cases n = 5,150). Additionally, we sought to optimize our polygenic resilience-scoring formula to improve subsequent modeling of resilience to SCZ and other complex disorders. We found significant replication of the polygenic resilience score, and found that strict pruning of SNPs based on linkage disequilibrium to known risk SNPs and their linked loci optimizes the performance of the polygenic resilience score.

INTRODUCTION (2,561 words)

Over the past decade, scientists have accelerated efforts to understand schizophrenia (SCZ) by studying genetic variation from hundreds of thousands of individuals to identify genes associated with the disorder. This effort has produced an extraordinary amount of genomic data that is available for further analyses. Much has been learned about the biology and genetics of

risk for SCZ, but it is virtually unknown which alleles (if any) help to mitigate predisposition to SCZ, thereby shielding a person from psychosis. The term "*genetic resilience"* is conceptualized as genes that *dampen effects of risk factors* to promote *resistance to disease onset.* We published a proof-of-concept study describing an analytic methodology for mining genome-wide association study (GWAS) data for common variants that confer resistance to genetic risk for SCZ among unaffected individuals.[1] Our study introduced the first-known "*polygenic resilience score*" for a complex disorder, unveiling opportunities to generate new knowledge about the biology and genetics of SCZ. Subsequently, other investigators have worked to validate and evaluate the characteristics of, and phenotypic associations with, this polygenic resilience score. For example, an imaging-genomics study by Hettwer *et al.*[2] identified a significant association between resilience scores and increased volume of brain regions, including the fusiform gyrus, which is involved in ventral visual pathways in the brain contributing to object recognition and categorization; this is consistent with opposing evidence in schizophrenia itself where reduced fusiform gyrus volume has been shown, and volumetric reductions that correlate with severity of negative symptoms.[3–5] He *et al.*[6] subsequently tested the relationship between resilience scores and cognition in a cohort of ultra-high-risk converters and non-converters to psychosis, finding that SCZ resilience scores were significantly positively correlated with cognitive performance on several metrics (full-scale IQ, verbal IQ, performance IQ, and working memory). In addition, they found that risk scores for schizophrenia showed negative correlation with full-scale IQ and working memory, suggesting that risk and resilience scores may influence certain phenotypes in opposing manners. Collectively, such findings suggest that resilience genes potentially buffer against the effects of risk loci by contributing to neural and cognitive reserve, offering valuable mechanistic insights into genetic resilience for SCZ.

Building upon this body of prior work, we leveraged a newly released collection of GWAS data in the Psychiatric Genomics Consortium (PGC), comprising data from 46,204

individuals,[7] to evaluate the protective association of our polygenic resilience score for SCZ. Furthermore, we tested the correlation between risk and resilience scores for SCZ within groups defined in this independent replication sample based on diagnostic status and level of genetic risk, and we assessed the impact of specific model parameters on the performance of our SCZ resilience scores. By excluding risk SNPs and their linked loci from the resilience score, we ensured that resilience scores capture protective effects of SNPs that are independent of risk SNPs. The findings from this study raise confidence in the protective capacity of our polygenic resilience score and offer a useful guide for future applications of our resilience-scoring approach to SCZ and to other complex disorders.

METHODS

Samples and Imputed Genotypes

We obtained access to a new set of GWAS samples, none of which were included in our first study[1] wherein we previously derived a resilience score for SCZ. Our analysis was performed on quality-controlled, hard-called imputed genome-wide genotypes from 18,090 SCZ cases and 28,114 controls from 23 case-control cohorts predominantly of European descent that were collated by the Schizophrenia Working Group of the PGC (PGC-SCZ), hereafter referred to as the new Wave-3 dataset (**Table 1**). Genotyping data had been uniformly processed and imputed by the PGC *via* the Ricopili pipeline (for details see [7]). All data were accessed on the centralized PGC server with permission from the PGC-SCZ.

Identifying Resilient Controls and Matched-Risk Cases

Following our previously described framework,[1] we used the summary statistics from a GWAS meta-analysis of 51 studies from the Wave-2 release from the PGC-SCZ (SCZ

n=32,838, controls *n*=44,357)[8] to compute PRSs for each individual in the non-overlapping set of samples from the PGC-SCZ dataset (*n*=46,204) using the software *Plink* (v1.9). In the PRS calculations, we included 24,166 linkage disequilibrium (LD)-independent SNPs associated with SCZ at $p \leq 0.05$, the significance threshold that was found to maximize the proportion of phenotypic-variance explained in SCZ.[7,8] PRSs were standardized across individuals *per* cohort by centering to a mean of 0 and standard deviation of 1. Within each cohort, controls ranked in the top 10th percentile of the PRS were selected as "resilient" controls (*n*=2,821), and SCZ cases within the top 10th percentile were selected as PRS-matched cases (*n*=5,150). We excluded SCZ cases from our analysis whose PRS exceeded the highest PRS observed in controls (*i.e.,* ultra-high-risk cases, *n*=106), leaving 17,984 SCZ cases for our downstream analyses.

Polygenic Resilience Scores

We used our published summary statistics for a GWAS of resilience to SCZ[1] to compute polygenic resilience scores for each of the 46,204 individuals in the new PGC-SCZ dataset. In our prior study, we performed a GWAS including data from 45 cohorts that had been collated by the PGC Schizophrenia Working Group, which included data from up to 3,786 resilient controls that were in the top 10th percentile of PRS for SCZ and 18,619 SCZ cases within the same range of PRS as resilient controls. The SNPs used in the PRS calculations in our prior study were associated with SCZ at a *p*-value ≤ 0.05, which maximized the proportion of variance in SCZ explained by the PRS. For our prior study and current analysis, we excluded SNPs if they were previously associated with SCZ at $p \leq 0.05$ (based on the results from the GWAS meta-analysis of 32,838 SCZ cases and 44,357 controls performed by the PGC-SCZ[8]) *or* were in LD with SCZ-associated SNPs at a $R^2 \geq 0.2$. We also excluded variants in regions of long-range LD, including the extended major histocompatibility locus located on chromosome 6:25 MB–35 MB

and SNPs located in the inversion region of chromosome 8:7 – 14 MB. Hence, our resilience scores were designed to capture effects of common SNPs that moderate risk for SCZ independent of the protective alleles of SCZ-associated SNPs. We calculated resilience scores across 14 *p*-value thresholds using SNPs from the HapMap3 reference panel: $p \leq 1x10^{-5}$, $1x10^{-4}$, $1x10^{-3}$, 0.01, 0.1, 0.2, 0.3, 0.4, 0.5, 0.6, 0.7, 0.8, 0.9, 1.0. Retaining only SNPs that are part of HapMap3 is a recommended procedure among current polygenic-scoring algorithms because HapMap3 variants are well-imputed, provide excellent coverage of the genome, and yield accurate measures of SNP-based heritability.[9,10] In addition to replicating associations with our existing resilience score, another key aim of this study was to optimize our resilience-scoring method, as it could improve our modeling of resilience to SCZ and its related phenotypes. In service of this effort, we tested how varying the LD-filtering criteria for pruning SNPs impacted the performance of the resilience score. Strict pruning avoids sub-threshold risk SNPs from "leaking" into our resilience score, which would risk misclassifying a mild risk variant as a resilience variant. On the other hand, lessening the stringency of our LD-pruning may permit incorporation of more SNPs into our resilience score, thus improving the overall variance explained in resilience to SCZ (but at the expense of possibly including risk-associated variants). Thus, to evaluate the performance of resilience scores under such filtering scenarios, we constructed five additional resilience scores by applying varying thresholds of LD-pruning to our GWAS summary statistics: while our original model removed SNPs with R^2 values to risk SNPs of ≥ 0.2, these new models additionally removed SNPs with R^2 values ≥ 0.05, 0.1, 0.4, 0.5, or 0.9. We then recomputed polygenic resilience scores in the 23 replication cohorts and evaluated the performance of the scores on two critical metrics: 1) the proportion of phenotypic variance-explained in resilience (*i.e.,* diagnostic status); and 2) the correlation between risk scores and each of the resilience scores among controls and cases, including individuals stratified by low and high polygenic risk score (PRS) for SCZ.

Statistical Analysis

We tested the association between resilience scores for SCZ and resilience status (resilient controls coded 1, PRS-matched cases coded 0) in the 23 new case-control GWAS cohorts[7] (**Table 1**) using logistic regression models. We included the first five principal components of ancestry previously generated by PGC-SCZ as covariates to adjust for population stratification[11,12]. However, no other principal components were associated with resilience at a $p<0.1$ from logistic regression analyses, so were not included as covariates. Separately, we examined the association between our existing resilience score (calculated using a *p*-value threshold ≤ 0.2) and the top five principal components related to ancestry among the full Wave-3 dataset (excluding ultra-high-risk cases) using a multiple linear regression model wherein study ID was included as a covariate. To determine the proportion of variance (measured by Nagelkerke's R^2) in resilience status explained by resilience scores, the total variance explained by a model that included only covariates was subtracted from the total variance attributed to a second model that included resilience scores *and* covariates. The procedure of Lee *et al.*[13] was used to convert phenotypic variance explained from the observed to liability-threshold scale. In addition, we investigated the covariation of resilience scores and PRSs for SCZ by performing Pearson's correlation tests within four groups: resilient controls, PRS-matched cases, low-PRS controls (PRSs below those of the resilient controls; *i.e.*, those in the bottom 90th percentile of PRS), and low-PRS cases (PRSs below those of resilient controls). The highest-risk SCZ cases with PRSs above the resilient-control PRS range (*i.e.*, ultra-high-risk cases, $n=106$) were excluded from all statistical analyses. We adjusted *p*-values using the Benjamini-Hochberg false-discovery rate (FDR) procedure to correct for multiple testing, which was applied to all logistic regression analyses testing the association of resilience scores with resilience status. Associations that reached a FDR$p<0.05$ were declared significant.

In addition, we examined the direction of effect of the top resilience-associated SNP (rs66718632) identified in our prior GWAS among the 23 replication studies. We used a logistic regression model to test the association of the resilience-increasing T-allele on diagnostic status between resilient controls and PRS-matched cases while covarying for the top five principal components related to ancestry.

RESULTS

We found that our existing polygenic resilience score for SCZ was significantly associated with the first (p=0.0012), second (p=0.0005), and fifth (p=0.0003) principal components, suggesting that the resilience scores we derived in our previously published GWAS may be slightly biased by variation in allele frequencies due to differences in ancestry. To mitigate this bias, we included principal components as covariates in our replication analyses. We replicated the protective effect of our published polygenic resilience score among unaffected individuals in the top 10th percentile of PRS for SCZ (**Figure 1**) on the basis of the following parameters: LD-pruning threshold of R^2<0.2 and p-value threshold for resilience SNPs of p<0.3. A one-standardized-unit increase in the resilience score was associated with a 10% increase in the odds of being a resilient control (Odds Ratio [OR] = 1.096, 95% CI = 1.05 – 1.14, p=4.03×10^{-5}, FDRp=9.8×10^{-5}, Nagelkerke's R^2=0.0029 [liability-scale adjusted R^2=0.0031]). The replication was significant even after imposing relatively stringent selection criteria by including only those SNPs with very weak LD (R^2<0.05) with known risk SNPs (OR=1.07, 95% CI = 1.02 – 1.11, p=0.0043, FDRp=0.0058, Nagelkerke's R^2=0.0013 [liability-scale adjusted R^2=0.0014]). Permitting into our resilience score SNPs that showed moderate or even strong LD with known risk SNPs (LD cutoff R^2<0.9) for SCZ allowed the resilience score to achieve a stronger protective effect against SCZ (OR=1.13, 95% CI = 1.08 – 1.18, p=2.4×10^{-8}, FDRp=6.4×10^{-7}, Nagelkerke's pseudo-R^2=0.0053 [liability-scale adjusted R^2=0.0057]), though these effects may be driven in part by the protective alleles of sub-threshold risk SNPs. The increase in phenotypic

variance explained in diagnostic status by the resilience scores defined using the most permissive (R^2<0.9) *vs*. most stringent (R^2<0.05) LD-selection criteria represented a 4-fold increase. In addition, the resilience scores defined using the most permissive LD-pruning threshold (R^2<0.9) yielded a 1.8-fold increase in phenotypic variance-explained in diagnostic status relative to the resilience score derived using our previously published resilience score formula (R^2<0.2).

Small but significantly positive correlations between risk and resilience scores were found across all six resilience scores (**Table 2** and **Figure 2**). However, correlations between risk and resilience scores differed by diagnostic status as well as the degree of SCZ risk within diagnostic groups defined by PRS (**Figure 3**). As hypothesized, controls in the top 10^{th} percentile of PRS for SCZ showed the strongest correlation between risk and resilience scores among all groups tested (LD R^2<0.05: Pearson's r=0.094, p=3.7x10^{-7}), corroborating evidence from our previous study that resilience scores increase commensurate with increasing risk scores in order for at-risk individuals to remain unaffected.[1] In cases with high PRS, resilience and risk scores were not significantly correlated provided that the resilience scores were derived using relatively restrictive LD filtering criteria, such as LD R^2<0.05 (Pearson's r = 0.0025, p=0.86) or LD R^2<0.1 (Pearson's r=0.013, p=0.35) (**Figure 3**).

Correlations between risk and resilience scores were found to be a function of our LD-pruning criteria. Relaxing the LD-pruning criteria increased the slope and significance of the correlation between risk and resilience scores among all groups, indicating greater leakage of mild risk SNPs into resilience scores derived using relaxed LD-pruning thresholds. This increase in correlation between risk and resilience scores reached an inflection point at a LD-pruning threshold of R^2<0.2 **(Figure 2**)**,** beyond which the slope and significance of the correlations between risk and resilience diminished; thus, the function relating LD-filtering threshold and the correlation of risk and resilience scores does not appear to be strictly linear.

We examined the direction of effect for the most significant SNP associated with resilience from our prior GWAS (rs66718632) in the replication studies. We observed a consistent direction of effect for the resilience-increasing T-allele in 16 out of the 23 replication studies, lending support to the evidence that this SNP may contribute to resilience to SCZ.

DISCUSSION

We previously developed a generalizable pipeline to derive the first-known multivariate measure of genetic resilience to a complex disorder among unaffected individuals at high risk based on PRS.[1] Our prior study showed that this multivariate measure, the polygenic resilience score, moderates the genetic risk for SCZ, hence protecting unaffected individuals at relatively high PRS. Furthermore, we previously showed that resilience and risk scores follow an expected pattern of correlations (or lack thereof) within the GWAS data used to construct our resilience scores, but these findings warranted replication in external cohorts. In this study, we replicated the finding that unaffected individuals who had high polygenic resilience scores are significantly protected against SCZ despite high PRS for SCZ. In addition, we extended our approach for constructing polygenic resilience scores by assessing the impact of LD-based filtering criteria on the performance of resilience scores, finding this parameter has a discernable effect on the amount of phenotypic variance explained, as well as on the strength and significance of correlations between PRS and resilience scores.

Using more stringent LD-filtering criteria slightly reduced the proportion of phenotypic variance that could be explained by resilience scores, but also yielded correlations between risk and resilience scores that were consistent with our training data. We posit that a good LD-filtering criterion for deriving resilience scores for SCZ is a R^2<0.05 because it optimizes performance of the resilience score while maintaining orthogonality with risk scores (as originally postulated) among high-PRS cases. These findings may hold practical and scientific

importance for future studies, including efforts to model the joint effect of risk and resilience scores on SCZ.

In order to operationalize resilience, we studied individuals in the highest decile of PRS for SCZ whose risk for SCZ is similar to someone who has an affected first-degree relative (when compared to individuals in the lowest decile of PRS).[8] Our findings showed that polygenic resilience generally increases as PRS increases, hence resilience likely is not constrained to a specific PRS threshold. Using an alternative approach that models resilience as a continuous outcome would improve the statistical power required to detect resilience genes with small effect sizes.

Various conceptualizations of resilience have been described, including several field-specific paradigms; *i.e.*, psychological resilience referring to personality or behavioral traits that help individuals cope with adversity; cognitive resilience referring to reduced rates of cognitive decline over time despite elevated risk for or diagnosis of dementia. Conceptualizations of resilience have been synthesized into a model that defines resilience as three interrelated components: *capacity*, *process*, and *outcome*.[14] Our conceptualization of genetic resilience links, in some ways, to each of these. We effectively treated resilience as an *outcome* measure in order to identify genetic variants that protect individuals despite having high PRS. Genes that comprise the polygenic resilience score are hypothesized to instill a general *capacity* that buffers the brain against vulnerabilities posed by genetic risk.[14] Resilience *processes* may unfold over time providing adaptive protection to vulnerabilities instilled by risk factors. Our conceptualization of genetic resilience could benefit from future studies determining the timing and mechanism by which resilience genes promote protection against risk factors.

One limitation of our study is the reliance on data that overwhelmingly represent the genetic variation among individuals of European descent (~93%) with a relatively small percentage of individuals from East-Asian descent included (~7%). The replication samples that

we leveraged to test the performance of the resilience scores were also of European descent. This raises potential concerns about the portability of polygenic resilience scores to non-European individuals, and the possibility of the flip-flop phenomenon causing diminished performance of resilience scores due to variation in allele frequencies and across populations.[15] As GWAS data from non-Europeans increases, opportunities will present to include currently underrepresented populations in the derivation and replication of resilience scores. In addition to protective effects of genetic variants, environmental factors (*e.g.,* access to nature, social activity, exercise, diet, sleep), could potentially contribute further resilience to individuals who are susceptible to SCZ. However, due to limitations in the dataset utilized for our analysis, we were unable to investigate the impact of environmental factors on resilience. Furthermore, investigating differences in the penetrance of resilience scores on SCZ due to sex represents a possible avenue for future research.

In summary, we have validated that resilience scores moderate against elevated genetic risk for SCZ among unaffected individuals, and provide data on the performance of various criteria for deriving them. We will continue to experiment with techniques to optimize resilience scores in order to improve their performance for future applications. Evaluating the portability of resilience scores across populations is a foremost priority.

Data availability

We were granted access to imputed genome-wide SNP genotypes by PGC. The data sets from the PGC remained on the Genetic Cluster Computer where statistical analyses were performed. Other investigators can request access to these data *via* application to PGC.

Code availability

Custom-written scripts used for analysis are available upon request made to the corresponding author.

Disclosures

In the past year, Dr. Faraone received income, potential income, travel expenses continuing education support and/or research support from Aardvark, Akili, Genomind, Ironshore, KemPharm/Corium, Noven, Ondosis, Otsuka, Rhodes, Supernus, Takeda, Tris and Vallon. With his institution, he has US patent US20130217707 A1 for the use of sodium-hydrogen exchange inhibitors in the treatment of ADHD. In previous years, he received support from: Alcobra, Arbor, Aveksham, CogCubed, Eli Lilly, Enzymotec, Impact, Janssen, Lundbeck/Takeda, McNeil, NeuroLifeSciences, Neurovance, Novartis, Pfizer, Shire, and Sunovion. Dr. Faraone also receives royalties from books published by Guilford Press: *Straight Talk about Your Child's Mental Health*; Oxford University Press: *Schizophrenia: The Facts;* and Elsevier: *ADHD: Non-Pharmacologic Interventions.* He is also Program Director of www.adhdinadults.com. In the past year, Dr. Glatt has received royalties from a book published by Oxford University Press: *Schizophrenia: The Facts*. Dr. Cairns is supported by NHMRC project grants (1147644 and 1188493) and an NHMRC Senior Research Fellowship (1121474), and a University of Newcastle College of Health Medicine and Wellbeing, Gladys M Brawn Senior Fellowship.

Acknowledgements

Dr. Hess is supported by grants from the U.S. National Institute of Mental Health (R21MH126494), the U.S. National Institute of Neurological Disorders and Stroke (R01NS128535), and NARSAD: The Brain & Behavior Research Foundation. Dr. Faraone is supported by the European Union's Seventh Framework Programme for research, technological development and demonstration under grant agreement no 602805, the European Union's Horizon 2020 research and innovation programme under grant agreements No 667302 & 728018 and NIMH grants 5R01MH101519, U01 MH109536-01, and R21MH126494-01. Dr.

Glatt is supported by grants from the U.S. National Institutes of Health (R01MH101519,

R01AG054002, R01AG064955, and R21MH126494), the Sidney R. Baer, Jr. Foundation, and

NARSAD: The Brain & Behavior Research Foundation.

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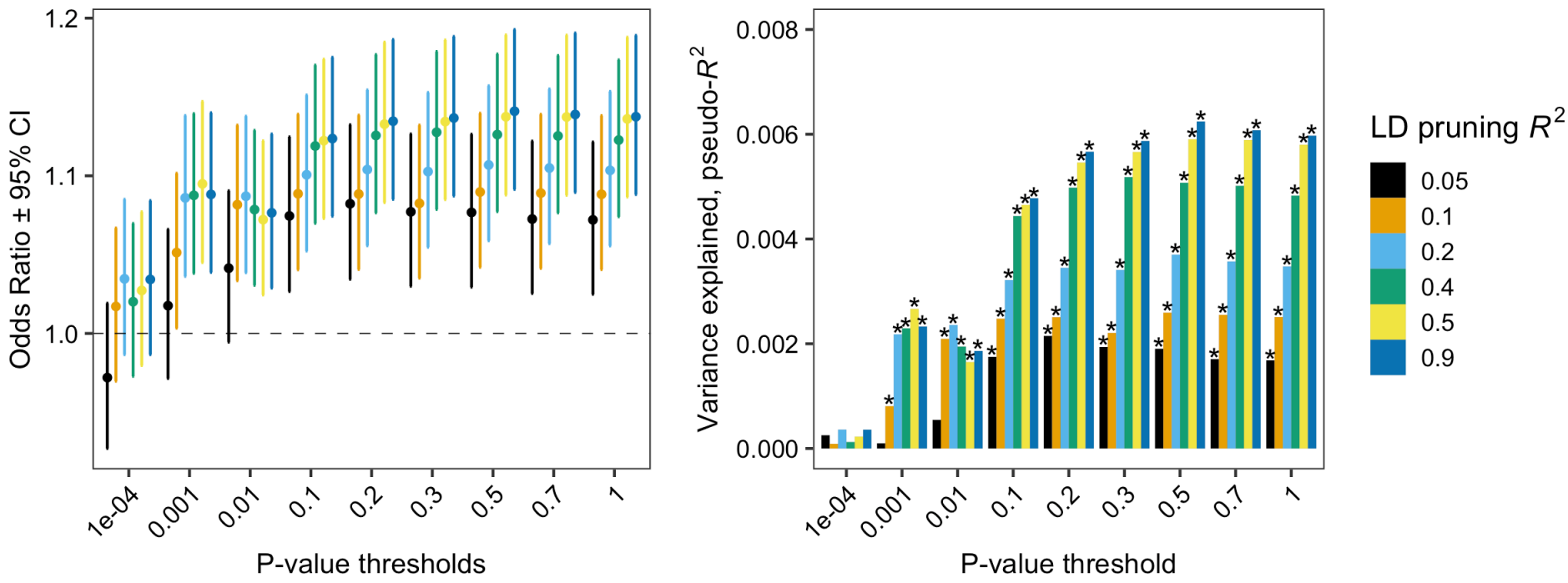

Figure 1. Resilience scores are associated with increased protection from schizophrenia (SCZ) among controls at relatively high genetic risk (*n* high-PRS controls=2,812, *n* PRS-matched cases=5,150). We derived six different resilience-scoring formulae that differed according to the amount of filtering imposed on resilience SNPs based on observed linkage disequilibrium (**LD**, measured by R^2) with known risk SNPs for SCZ. We specified our LD-filtering criteria, which ranged from relatively stringent (*i.e.,* resilience SNPs show virtually no LD with known risk SNPs; R^2<0.05) to relatively permissive (*i.e.,* resilience SNPs allowed to be in strong LD to known risk SNPs; R^2<0.9) criteria, using a color code. The left panel shows the change in odds of being a "resilient" control (*i.e.,* high-PRS control) per standardized unit increase in the polygenic resilience score. Bars denote the 95% confidence interval of the Odds Ratio (OR). Resilience scores were computed for nine *p*-value thresholds that successively permitted more SNPs with weaker effects on resilience into the scoring calculation. An OR > 1 (*i.e.,* above the horizontal dotted line) is interpreted as an increased odds of being a high-PRS control per standard unit increase in the resilience score, hence the polygenic resilience score had a moderating effect on the risk for SCZ among those controls at relatively high risk for the disorder. In the right panel, we provided the pseudo-R^2 values measuring the proportion of phenotypic variance-explained in "resilience" as a phenotype. Asterisks above the bars denote statistical significance after correction for multiple comparisons across all tests (false discovery rate-adjusted *p*-values < 0.05).

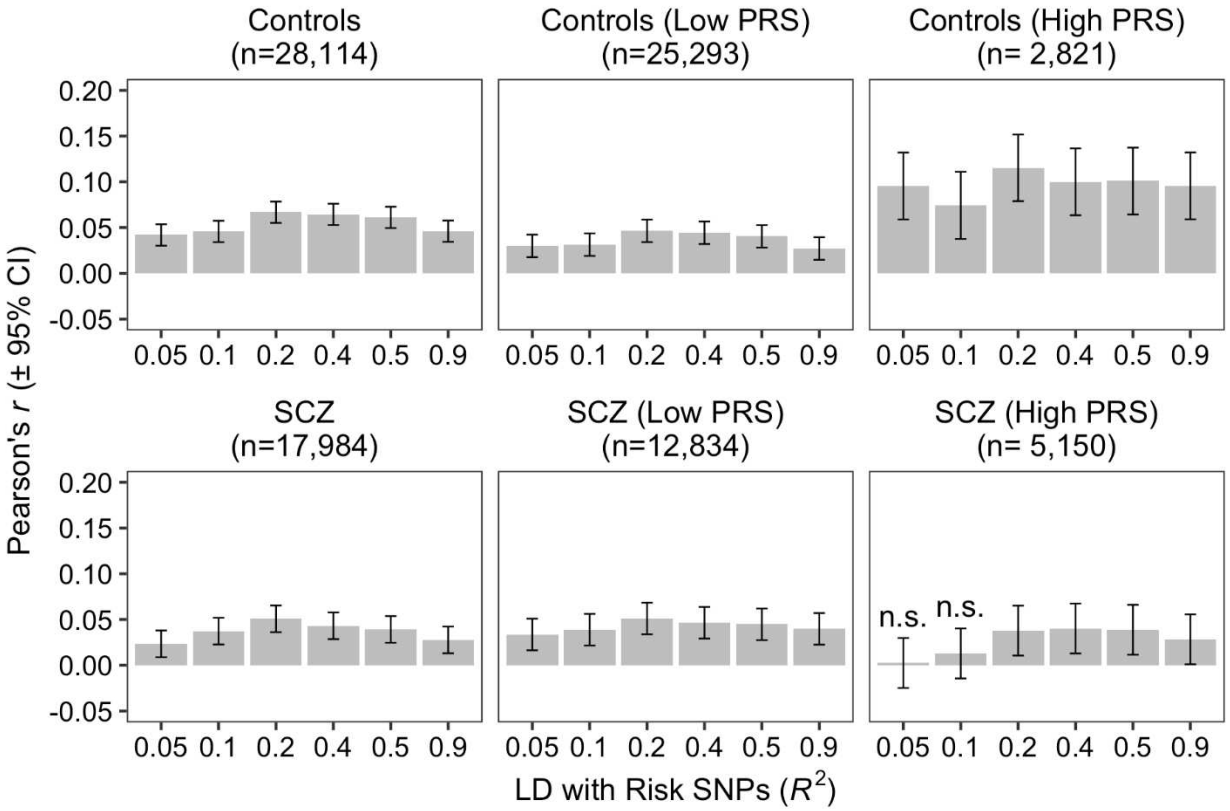

Figure 2. Bar plots present the correlation between risk and resilience scores among study participants included in the 23 new GWAS cohorts from the Psychiatric Genomics Consortium. Plotted on the x-axis are the six resilience scoring formulae that differed according to the filtering imposed on resilience SNPs based on observed linkage disequilibrium (**LD**, measured by R^2) with known risk SNPs for SCZ. Plotted on the y-axis are the Pearson's *r* correlation coefficients measuring the correlation between risk and resilience scores. Error bars denote the 95% confidence intervals. The number of samples analyzed per group is indicated in the panel titles. Controls in the top 10th percentile of PRS and PRS-matched cases are denoted as "High PRS"; controls and SCZ cases that fell below the same risk-score threshold are labeled "Low PRS". The highest-risk SCZ cases (i.e., ultra-high-risk cases) with PRSs above the resilient control PRS-range were excluded (*n*=106), leaving 17,984 cases for our statistical analyses. Asterisks (*) denotes correlations that were statistically significant after correction for multiple comparisons (false-discovery rate-adjusted $p<0.05$).

Figure 3A. Correlation of polygenic risk scores and polygenic resilience scores (LD R^2 threshold ≤ 0.05, *p*-value threshold ≤ 0.2) in controls and schizophrenia cases.

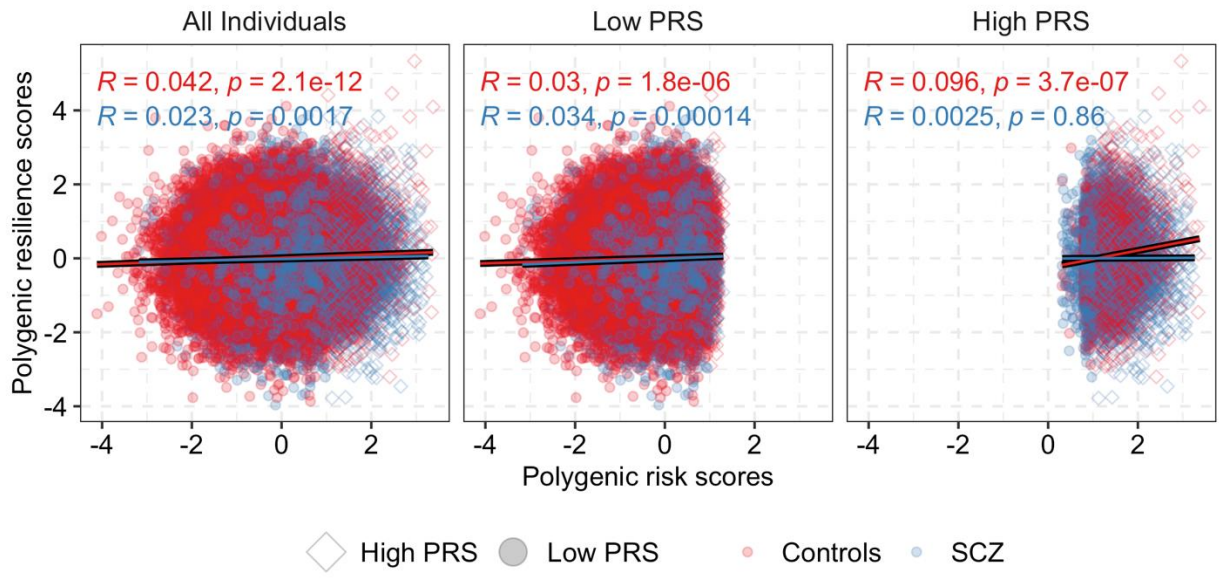

Figure 3B. Correlation of polygenic risk scores and polygenic resilience scores (LD R^2 threshold ≤ 0.1, *p*-value threshold ≤ 0.01) in controls and schizophrenia cases.

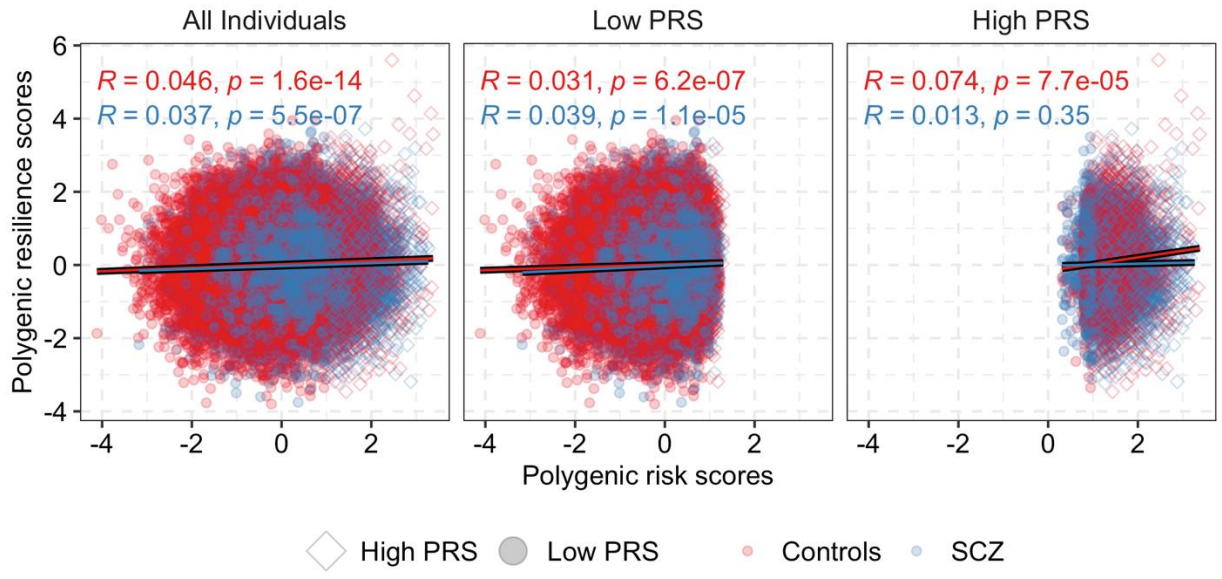

Figure 3. Scatterplots showing the relationship between polygenic risk and resilience scores in control and schizophrenia (SCZ) cases. We removed ultra-high-risk SCZ cases whose risk score exceeded the upper limit of the control range for this analysis. Correlations are shown for all controls and cases in the 23 new cohorts from the Wave-3 dataset from the Psychiatric Genomics Consortium (PGC) SCZ Working Group, in addition to controls and cases stratified by PRS (low PRS: below the top 10th percentile of PRS; high PRS: in the top 10th percentile of PRS). A *p*-value threshold for SNPs at ≤ 0.05 was used to compute the PRS for SCZ. SNPs showing a *p*-value in association with resilience at ≤ 0.2 (Panel A) and ≤ 0.01 (Panel B) were used to compute the resilience score. SNPs included in the polygenic resilience score formulae showed very low LD with known risk SNPs for SCZ (R^2<0.05 for Panel A, R^2≤0.1 for Panel B).

Pearson's *r* correlation coefficients are provided in each panel separately for controls and SCZ cases.

Table 1. Number of individuals from the 23 cohorts comprising the latest release of PGC Wave-3 dataset from the Schizophrenia Working Group included in our replication analysis.

Cohort	*n* controls	*n* cases	n total	*n* resilient controls	*n* PRS-matched cases	*n* total	Diagnostic criteria	Screened controls?
bep1b	573	294	867	58	60	118	ICD-10	Yes
braz2	334	110	444	34	21	55	ICD-10	Yes
celso	1,517	2,030	3,547	152	557	709	ICD-10	Yes
cgs1c	3,115	518	3,633	312	140	452	DSM-IV	No
clz2a	6,940	5,368	12,308	694	1874	2,568	DSM-IV	Mixed
cogs1	469	427	896	47	90	137	DSM-IV	Yes
du2aa	245	345	590	25	140	165	DSM-IV	?
enric	574	699	1,273	58	150	208	DSM-IV-TR	Yes
eu5me	615	182	797	62	33	95	ICD-10	Yes
eusp2	490	338	828	49	91	140	ICD-10	Yes
eutu2	690	392	1,082	69	84	153	DSM-IV-TR	Yes
gap1a	179	151	330	18	39	57	ICD-10	Yes
geba1	703	393	1,096	71	117	188	DSM-IV	?
gpc2a	2,059	1,950	4,009	206	470	676	DSM-IV/DSM-5/ICD-10	Yes
gro2a	277	328	605	28	168	196	DSM-IV	Yes
mcqul	1,301	1,349	2,650	131	459	590	ICD-10	Yes
mosc2	433	409	842	44	90	134	ICD-10	Yes
price	727	841	1,568	73	151	224	ICD-10	Yes
rive1	1,202	331	1,533	121	70	191	DSM-IV	Yes
rouin	185	204	389	19	54	73	DSM-III/DSM-IV	Yes
sb2aa	237	250	487	24	22	46	DSM-IV	Yes
serri	238	217	455	24	61	85	DSM-IV-TR	Yes
to10c	5,011	964	5,975	502	209	711	DSM-IV-TR	Yes
Total	28,114	18,090	46,204	2,821	5,150	7,971		

Note: The column labeled "Screen controls?" denotes whether the control group was screened for schizophrenia and/or a DSM Axis 1 disorder. A question mark (?) symbolizes whether a study did not explicitly report whether controls were screened. Studies that included both screened and un-screened controls are are denoted as "Mixed".
Abbreviations: polygenic risk score (PRS), International Classification for Disease (ICD), Diagnostic and Statistical Manual for Mental Disorders (DSM), text revision (TR), fourth edition (IV). Information about cohort abbreviations are provided in the Supplementary documents published by Trubetskoy *et al.,* 2022.[7]

Table 2. Correlation of polygenic resilience scores and PRS among controls and cases collated from the 23 replication cohorts from the PGC Schizophrenia working Group.

Groups	LD filtering R^2	*p*-value threshold	Pearson's r	*t*-statistic	*p*-value	*df*	95% CI Lower	95% CI Upper
Controls (High PRS)	0.05	0.2	0.096	5.10	3.66E-07	2,819	0.06	0.13
Controls (Low PRS)	0.05	0.2	0.030	4.77	1.83E-06	25,291	0.02	0.04
SCZ (High PRS)	0.05	0.2	0.002	0.18	0.86	5,148	-0.02	0.03
SCZ (Low PRS)	0.05	0.2	0.034	3.81	1.37E-04	12,832	0.02	0.05
Controls	0.05	0.2	0.042	7.03	2.08E-12	28,112	0.03	0.05
SCZ	0.05	0.2	0.023	3.14	1.68E-03	17,982	0.01	0.04
Controls (High PRS)	0.1	0.01	0.074	3.96	7.69E-05	2,819	0.04	0.11
Controls (Low PRS)	0.1	0.01	0.031	4.99	6.20E-07	25,291	0.02	0.04
SCZ (High PRS)	0.1	0.01	0.013	0.93	0.35	5,148	-0.01	0.04
SCZ (Low PRS)	0.1	0.01	0.039	4.41	1.05E-05	12,832	0.02	0.06
Controls	0.1	0.01	0.046	7.68	1.64E-14	28,112	0.03	0.06
SCZ	0.1	0.01	0.037	5.01	5.52E-07	17,982	0.02	0.05
Controls (High PRS)	0.2	0.5	0.115	6.17	7.74E-10	2,819	0.08	0.15
Controls (Low PRS)	0.2	0.5	0.046	7.39	1.51E-13	25,291	0.03	0.06
SCZ (High PRS)	0.2	0.5	0.038	2.72	6.53E-03	5,148	0.01	0.07
SCZ (Low PRS)	0.2	0.5	0.051	5.80	6.85E-09	12,832	0.03	0.07
Controls	0.2	0.5	0.067	11.22	3.87E-29	28,112	0.06	0.08
SCZ	0.2	0.5	0.051	6.81	9.73E-12	17,982	0.04	0.07
Controls (High PRS)	0.4	0.7	0.100	5.34	9.85E-08	2,819	0.06	0.14
Controls (Low PRS)	0.4	0.7	0.044	7.06	1.75E-12	25,291	0.03	0.06
SCZ (High PRS)	0.4	0.7	0.040	2.89	3.92E-03	5,148	0.01	0.07
SCZ (Low PRS)	0.4	0.7	0.046	5.27	1.37E-07	12,832	0.03	0.06
Controls	0.4	0.7	0.064	10.83	2.91E-27	28,112	0.05	0.08
SCZ	0.4	0.7	0.043	5.79	6.95E-09	17,982	0.03	0.06
Controls (High PRS)	0.5	0.7	0.101	5.39	7.72E-08	2,819	0.06	0.14
Controls (Low PRS)	0.5	0.7	0.040	6.43	1.26E-10	25,291	0.03	0.05
SCZ (High PRS)	0.5	0.7	0.039	2.79	5.32E-03	5,148	0.01	0.07
SCZ (Low PRS)	0.5	0.7	0.045	5.07	3.96E-07	12,832	0.03	0.06
Controls	0.5	0.7	0.061	10.27	1.08E-24	28,112	0.05	0.07
SCZ	0.5	0.7	0.039	5.26	1.47E-07	17,982	0.02	0.05
Controls (High PRS)	0.9	0.5	0.096	5.10	3.53E-07	2,819	0.06	0.13
Controls (Low PRS)	0.9	0.5	0.027	4.32	1.56E-05	25,291	0.01	0.04
SCZ (High PRS)	0.9	0.5	0.028	2.04	0.04	5,148	0.00	0.06
SCZ (Low PRS)	0.9	0.5	0.040	4.51	6.45E-06	12,832	0.02	0.06
Controls	0.9	0.5	0.046	7.73	1.09E-14	28,112	0.03	0.06
SCZ	0.9	0.5	0.028	3.72	2.01E-04	17,982	0.01	0.04