

Measuring Genetic Heterogeneity in Psychiatric Phenotypes: A Scoping Review

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Abstract—An improved understanding of genetic etiological heterogeneity in a psychiatric condition may help us (A) isolate a neurophysiological “final common pathway” by identifying its upstream genetic origins and (B) facilitate characterization of the condition’s phenotypic variation. This review aims to characterize existing genetic heterogeneity measurements in the psychiatric literature.

Method. The Scopus database was searched for studies that quantified genetic heterogeneity or correlation of psychiatric phenotypes with human genetic data.

Results. Ninety studies were included. Eighty-seven reports quantified genetic correlation, five applied genomic structural equation modelling, three evaluated departure from the Hardy-Weinberg equilibrium at one or more loci, and two applied a novel approach known as MiXeR.

Discussion. We found no study that rigorously measured genetic etiological heterogeneity across a large number of markers. Developing such approaches may help better characterize the biological diversity of psychopathology.

Index Terms—genetic heterogeneity, psychiatric disorder, psychiatric phenotypes, biological diversity, pleiotropy, genetic correlation, genomic structural equation modelling

I. INTRODUCTION

Psychiatric research often considers the genetics of phenotypic heterogeneity, which has led to a growing appreciation of the low dimensional genetic structure of many psychiatric disorders, including the description of a unidimensional “p-factor” of psychiatric vulnerability [1]. The genetics of phenotypic heterogeneity has also proven relevant for advancing the understanding of psychiatric pharmacogenetics. For example, we have shown that limiting phenotypic heterogeneity in a clinical sample can dramatically improve the accuracy of genetic prediction of lithium response [2], [3].

The psychiatric genetics literature has ostensibly focused largely on quantifying pleiotropy: the degree to which phenotypic heterogeneity can arise from common genetic underpinnings. Conversely, in the neuroimaging literature, there has been a growing effort to quantify *etiological heterogeneity* (or equivalently *etiological diversity*), in which we have tried to measure the degree to which distinct underlying biological states can yield the same clinical phenotype [2], [4].

There are several reasons to believe that genetic etiological diversity may exist in psychiatric disorders. First, it is possible that multiple genes can have the same downstream functional

consequence, such as the Dopa-responsive dystonias of childhood that can be caused by mutations in *TH*, *SPR*, or *GCH1* [5], [6], or the *Cornelia de Lange* syndrome, which can be caused by mutations in seven different genes involved in the cohesin complex [7]. This has traditionally been considered *moreso* in the domain of monogenic disorders, and less in the context of unique polygenic combinations. Although most polygenic psychiatric conditions are found to have low effect sizes across many alleles, these represent averages across large samples. It is possible that subpopulations contain distinct genetic combinations that, as an ensemble, carry higher effect size. Second, if these variations segregate geographically, one might observe regional differences in genetic etiologies. Third, the prevalence of many major psychiatric disorders, such as bipolar disorder or schizophrenia, show only minor overall variations across the world [8]–[10]. Yet, it is well-known that genetic diversity in a population declines as a function of land migratory distance from East Africa [11]. If a disorder is caused by a restricted or stereotyped genetic profile, one should expect that the greater number of alleles in a genetically diverse population would lead to a “dilution” of the disease genotype, and consequently a lower population prevalence. However, if a disease can be caused by multiple routes to a “final common pathway,” then its prevalence might be less affected by population genetic diversity.

Understanding the degree to which distinct genotypes can cause a given psychiatric disorder may (A) help us to isolate a neurophysiological “final common pathway” by identifying its upstream genetic basis, or (B) facilitate characterization of the condition’s phenotypic variation. To do this, we must first develop an operational framework to quantify this genetic etiological heterogeneity. The objective of this review is therefore to characterize measurement approaches to quantify genetic heterogeneity that have been undertaken in psychiatric genomics.

II. METHODS

A. Scoping Review

The Scopus database (which has 100% MEDLINE coverage) was searched from inception until April 27, 2021, with the search query provided in Supplementary Materials. Studies were independently screened by two researchers and included if they (A) were concerned with psychiatric phenotypes, (B)

analyzed genetic data in humans, and (C) clearly reported at least one measure of genetic heterogeneity, diversity, or correlation. Data were abstracted by one reviewer and subsequently verified by a second reviewer. For each study, we characterized the representation upon which heterogeneity is measured, the scientific question(s) of interest, and the heterogeneity measurement method(s) employed.

B. Role of the funding source

The funding body had no role in study design, data collection, data analysis, data interpretation, or writing of the report.

III. RESULTS

A PRISMA diagram describing the results of our search procedure is included as Supplementary Figure 1. A total of ninety studies were included. Three of these evaluated departure from Hardy-Weinberg equilibrium at one or more loci [12]–[14]. Eighty-seven studies quantified genetic correlation [1], [15]–[100] and five studies extended genetic correlation into genomic structural equation modelling (genomic SEM) [17], [33], [40], [82], [91]. Finally, two studies employed the *MiXeR* method [31], [87] to estimate the number of loci contributing to two phenotypes together and individually, respectively. A list of these studies is provided in Supplementary Table 1.

In the remainder of this section, we discuss genetic correlation, genomic SEM, and *MiXeR*, since departure from Hardy-Weinberg equilibrium is a well known standard aspect of genetic analysis. We ultimately show that none of these methods can quantify genetic etiological heterogeneity.

A. Genetic Correlation as a Contraction in the Sample Space of Additive Effect Sizes

Let M be the number of genotyped autosomal single-nucleotide polymorphisms (SNPs) deemed common variants. Let \mathbf{X} be an $1 \times M$ random genotype for a subject, including all genotyped alleles, where $\mathbf{X}_j \in \{0, 1, 2\}$ is the number of minor alleles at SNP $j \in \{1, 2, \dots, M\}$. Let Y_1 and Y_2 be two quantitative phenotypes. We model the relationships between \mathbf{X} , Y_1 , and Y_2 as

$$Y_1 = \mathbf{X}\mathbf{W}_1 + \epsilon_1, \quad (1)$$

$$Y_2 = \mathbf{X}\mathbf{W}_2 + \epsilon_2, \quad (2)$$

where \mathbf{W}_i is an $M \times 1$ vector of additive genetic effect sizes and $(\epsilon_1, \epsilon_2)^\top$ is a Gaussian random variable representing non-additive effects on phenotypes Y_1 and Y_2 . The common variant heritability of the i th phenotype, denoted h_i^2 , is the amount of variance in Y_i that can be explained by an optimal model consisting only of the additive effects of common autosomal SNPs. The genetic correlation between phenotypes Y_1 and Y_2 is defined as the correlation between the optimal parameters of their respective additive predictors, denoted r_g [74], [101]. Let \mathbf{W} be the concatenation of \mathbf{W}_1 and \mathbf{W}_2 into a $2M \times 1$ vector

$(W_{11}, W_{12}, \dots, W_{1M}, W_{21}, W_{22}, \dots, W_{2M})^\top$. This model is specified as

$$\mathbf{W} \sim \mathcal{N}\left(\mathbf{0}, \begin{pmatrix} \frac{h_1^2}{M} \mathbf{I}_M & \frac{\rho_g}{M} \mathbf{I}_M \\ \frac{\rho_g}{M} \mathbf{I}_M & \frac{h_2^2}{M} \mathbf{I}_M \end{pmatrix}\right), \quad (3)$$

where $\mathbf{0}$ is a $2M \times 1$ vector of zeros, \mathbf{I}_M is the $M \times M$ identity matrix, and $\rho_g = r_g \sqrt{h_1^2 h_2^2}$ is the genetic covariance between phenotypes Y_1 and Y_2 . The non-additive effects are similarly modelled as follows, where $\sigma_{e,i}^2 = (1 - h_i^2)$:

$$(\epsilon_1, \epsilon_2)^\top \sim \mathcal{N}\left(\mathbf{0}, \begin{pmatrix} \sigma_{e,1}^2 & \rho_e \\ \rho_e & \sigma_{e,2}^2 \end{pmatrix}\right), \quad (4)$$

where $\mathbf{0}$ is in this case a 2×1 vector of zeros. Common genetic correlation estimation methods, such as LDSC [102], GNOVA [103], HDL [104], and REML [105] are all based on the general model shown in Equations 1-4 [101].

Clearly, genetic correlation is an index of genetic *homogeneity*, insofar as a sample of individuals with two correlated phenotypes must be less heterogeneous than a sample of individuals whose phenotypes are independent. In fact, one can show that the effective hypervolume of the sample space of \mathbf{W} is always maximized at $\rho_g = 0$. Intuitively, greater genetic correlation reduces the size of the space of genetic effects, making it more likely that a given genotype X can yield both phenotypes Y_1 and Y_2 . Furthermore, one can show that the genetic correlation r_g contracts the effective size of \mathbf{W} 's sample space (i.e. the total range of available effect size values) by a factor of $(1 - r_g^2)^{-M/2}$. Put differently, \mathbf{W} 's sample space has contracted by a factor of K at a correlation of $r_g = (1 - K^{-2/M})^{1/2}$. For constant h_1^2 and h_2^2 , a contraction in the domain of the distribution over \mathbf{W} will result in a greater mutual information between \mathbf{W}_1 and \mathbf{W}_2 . Proofs of these statements are provided in the supplementary materials.

B. Measurement of Heterogeneity through Genomic Structural Equation Modeling

Grotzinger et al. [33] developed genomic structural equation modelling (GenomicSEM) to estimate a lower dimensional factor structure for genetic correlations. On a high level, their analysis proceeds by generalizing the empirical genomic covariance matrix to scenarios with $K > 2$ phenotypes, where the entries can be obtained using methods such as LDSC:

$$\hat{\Sigma} = \begin{pmatrix} h_1^2 & \cdots & \sigma_{1K} \\ \vdots & \ddots & \vdots \\ \sigma_{1K} & \cdots & h_K^2 \end{pmatrix}, \quad (5)$$

where σ_{ij} is the genetic covariance between phenotypes i and j . For a factor model with L multivariate Gaussian latent variables with $L \times L$ covariance matrix Q , one learns a matrix of $K \times L$ factor loadings A and a $K \times K$ diagonal covariance matrix B over residuals such that

$$\hat{\Sigma} \approx \Sigma(A, Q, B) = AQA^\top + B. \quad (6)$$

In other words, B represents the covariance unique to each phenotype, while AQA^\top is the covariance determined by the latent factor structure.

Since GenomicSEM represents a mapping from observable phenotypes onto a latent space of underlying factors, we can quantify the heterogeneity of the set of phenotypes as the effective size of the latent space [106]. Many options here are possible, with the specific measure being determined by the question at hand. For example, the effective number of underlying factors is an immediate candidate, insofar as a genetically homogenous set of K phenotypes might plausibly be modelled using few (or even one) latent factors. It may also be of interest to measure the effective hypervolume of the latent space, which can be done with the latent variable covariance matrix Q [106], [107].

C. Quantifying Polygenic Overlap with MiXeR

Frei et al. [31] noted that genetic correlation captures the overall degree of positive or negative correlation among all additive variants between two phenotypes, but it fails to capture scenarios in which there are mixtures of effect directions between causal variants affecting two traits. They thus devised an approach to quantify *polygenic overlap* between two conditions, which they called *MiXeR*. This approach models the pair of effects for locus j on traits 1 and 2, respectively (W_{1j}, W_{2j}) , as distributed according to the following mixture model:

$$(W_{1j}, W_{2j}) \sim a_0 F_\delta(0) + a_1 F_{\mathcal{N}\delta}(\sigma_1^2, 0) + a_2 F_{\delta\mathcal{N}}(0, \sigma_2^2) + a_{12} \mathcal{N}(0, \Sigma_{12}), \quad (7)$$

where a_0 is the probability that both effects (W_{1j}, W_{2j}) are drawn from a point-mass distribution centred at 0. We have that a_1 is the probability that SNP j is causative for phenotype 1 but not phenotype 2 (represented by a Gaussian-point mass mixture $F_{\mathcal{N}\delta}(\sigma_1^2, 0)$). Similarly, a_2 is the probability that SNP j is causative for phenotype 2 but not phenotype 1 (represented by the point mass-Gaussian mixture $F_{\delta\mathcal{N}}(0, \sigma_2^2)$), and a_{12} is the probability that SNP j has a causal effect on both phenotypes (modeled by the bivariate Gaussian $\mathcal{N}(0, \Sigma_{12})$). The covariance matrix for the bivariate Gaussian is

$$\Sigma_{12} = \begin{pmatrix} \sigma_1^2 & \rho_{12}\sigma_1\sigma_2 \\ \rho_{12}\sigma_1\sigma_2 & \sigma_2^2 \end{pmatrix}, \quad (8)$$

where σ_1^2 and σ_2^2 are the proportions of variance in phenotypes 1 and 2 accounted for by additive effects of common variants, and ρ_{12} is the genetic covariance between phenotypes.

By multiplying the total number of alleles considered in an analysis, M , with the proportions (a_1, a_2, a_{12}) , one can obtain an estimate of the number of alleles that contribute distinctly to phenotypes 1 and 2, as well as an estimate of the number of alleles that contribute to both phenotypes. One can also compute similarity coefficients such as the Sørensen-Dice index, $2a_{12}/(a_1 + a_2 + 2a_{12})$, as was undertaken in the most recent Psychiatric Genomics Consortium (PGC) genome-wide association study (GWAS) on bipolar disorder [87].

IV. DISCUSSION

There are no studies in psychiatric genetics that evaluate the effective number of etiological genotypes for a given condition. We showed this via a review of the literature in which we found an overwhelming majority of studies focusing on genetic correlation-based evaluation of pleiotropy.

The sole exception may be the MiXeR method, which quantifies the number of loci that may contribute to two phenotypes, together or individually [31], [87]. However, this approach does not quantify the effective number of distinct genetic profiles that may be associated with a given single condition. Rather, it estimates the number of loci that, given sufficient power, may be discovered as contributing exclusively to each of two phenotypes, and the number that will contribute to both phenotypes in an overlapping fashion. In future studies, it will be useful to extend MiXeR to a larger number of phenotypes, since a proportion of alleles that are estimated to exclusively contribute to phenotype A (in comparison to phenotype B) may actually overlap with some phenotype C, thereby having an initial overestimate of the number of distinct loci contributing to phenotype A. Notwithstanding, MiXeR is at present the only method in psychiatric genetics being used to evaluate the degree of genetic uniqueness of various conditions.

Discovery of genetic etiological diversity may be a useful step towards identifying a “final common pathway” upon which multiple genetic differences converge downstream. For instance, the TH, SPR, and GCH1 mutations converge on the dopamine synthesis pathway as integral to the physiology of dopa responsive dystonias [5], [6], and mutations in *NIPBL*, *SMC1A*, *SMC3*, *RAD21*, *BRD4*, *HDAC8*, and *ANKRD11* can all result in the Cornelia de Lange syndrome [7]. For bipolar disorder, it could be interesting to ascertain whether multiple genetic profiles may converge on the Wnt beta-catenin signalling pathway, which may differ in function at different points depending on whether the individual is a lithium responder or nonresponder [108]. In such cases, quantifying genetic etiological heterogeneity may also provide evidence of unresolved phenotypic heterogeneity.

One promising approach to quantifying genetic etiological heterogeneity can be found in the neuroimaging literature, in the form of normative modelling [2], [4]. Here, one is given a set of M biological features $\mathbf{Y} = (y_{ij})_{i=1\dots N}^{j=1\dots M}$ for a “healthy,” “control,” or “normative” population with N subjects, and an accompanying set of K covariates $\mathbf{X} = (x_{ij})_{i=1\dots N}^{j=1\dots K}$ (such as neuropsychological or demographic features, age, site of origin, etc.). The first step is to learn a model of normative variation $g(\mathbf{X}) \mapsto \mathcal{P}(\mathbf{Y})$, where $\mathcal{P}(\mathbf{Y})$ refers to the space of probability distributions over the biological features. Given the set of covariates $\mathbf{X}_i = (x_{i1}, \dots, x_{iK})$ for the i th subject, we can predict his or her biological data as $\mu_g(\mathbf{X}_i)$, where μ_g is a function computing the expectation of the biological features under the model of normative variation, g . If the i th subject is drawn from the normative cohort, then his or her true biological features \mathbf{Y}_i will be closely approximated by

$\mu_g(\mathbf{X}_i)$. However, if he or she is drawn from a different cohort, such as a group of individuals with a psychiatric disorder, then \mathbf{Y}_i will deviate strongly from $\mu_g(\mathbf{X}_i)$ along some specific features. Given a larger set of data from a target cohort of individuals with psychiatric disorders, we can then identify the biological features, here genetic loci, at which the target cohort deviates most substantially from the normative model's predictions. We have previously shown that this approach can be used to estimate the effective number of deviation patterns in neuroimaging data and binary images, using various model architectures [2]. Indeed, there is a growing precedent for our ability to quantify etiological heterogeneity rigorously using various forms of data [109].

Unfortunately, the challenge in applying normative modelling to genetic data are twofold. First, we must develop a more rigorous understanding of measuring the normative model prediction error for non-Gaussian distributions. For genomic data drawn from micro-arrays, this amounts to developing a rigorous deviation metric for binomially distributed data that is sensitive to extreme deviations. This is difficult because of the bounded nature of a binomial distribution. Only recently has normative modelling with non-Gaussian distributions been tackled more intently [2], [109]. Second, we must develop normative modelling architectures that are sufficiently complex to model genomic data well, yet can efficiently handle the massive scale inherent in modern genomics. This, too, is an ongoing area of work [109].

In conclusion, we have shown that there are currently no methods employed in the psychiatric genomics literature to quantify genetic etiological heterogeneity in a rigorous fashion across a large number of markers. Developing such methods may help us to steer biological research toward identifying (A) common molecular pathways that lead to psychiatric disorders, or (B) phenotypic substrata that are biologically motivated. An open area for methodological research in this vein is the generalization of normative modelling to the genomic sphere.

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Supplementary Materials for *Measuring Genetic Heterogeneity in Psychiatric Phenotypes: A Scoping Review*

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I. SEARCH QUERY

TITLE-ABS-KEY (psychiatr*)
AND TITLE-ABS (

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  (
    gene* OR genomic OR allele*
    OR SNP OR nucleotide
  ) PRE/1 (
    heterogeneity OR diversity
    OR similarity OR correlation
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OR (
  "population structure"
  OR "population stratification"
  OR "band informativeness"
  OR "hardy-weinberg equilibrium"
  OR "average number of alleles"
  OR "effective number of alleles"
  OR "shannon's information index"
  OR "shannon information index"
  OR "effective population size"
  OR "minimum viable population"
  OR "f-statistics"
  OR "fixation index"
  OR "fixation indices"
  OR "gene flow"
  OR "shannon's evenness measure"
  OR "shannon evenness"
  OR "heip's evenness index"
  OR "heip evenness"
  OR "spatial gene diversity"
  OR "phylogenetic diversity"
  OR "hierarchical gene diversity"
  OR "analysis of molecular variance"
  OR "hill numbers"
  OR "species richness"
  OR "shannon entropy"
  OR "shannon-wiener"
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OR "shannon-weaver"
OR "simpson index"
OR "simpson concentration"
OR berger-parker
OR "freeman index"
OR modvr
OR avdev
OR "lincoln index"
OR "petersen index"
OR "birthday paradox"
OR "heip index"
OR "herfindahl index"
OR "herfindahl coefficient"
OR "herfindahl-hirschman"
OR "renyi entropy"
OR "tsallis entropy"
OR lempel-ziv
OR "huffman code"
OR "huffman coding"
OR "statistical evenness"
OR "gini index"
OR "gini coefficient"
OR "gini-simpson index"
OR "gini-simpson coefficient"
OR "lorenz curve"
OR "theil index"
OR "theil coefficient"
OR "atkinson index"
OR "atkinson coefficient"
OR "generalized entropy index"
OR "pietra index"
OR "robin hood index"
OR "schutz index"
OR ( pielou AND evenness )
OR "functional diversity"
OR "quadratic entropy"
OR "jaccard index"
OR "jaccard coefficient"
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II. PRISMA DIAGRAM

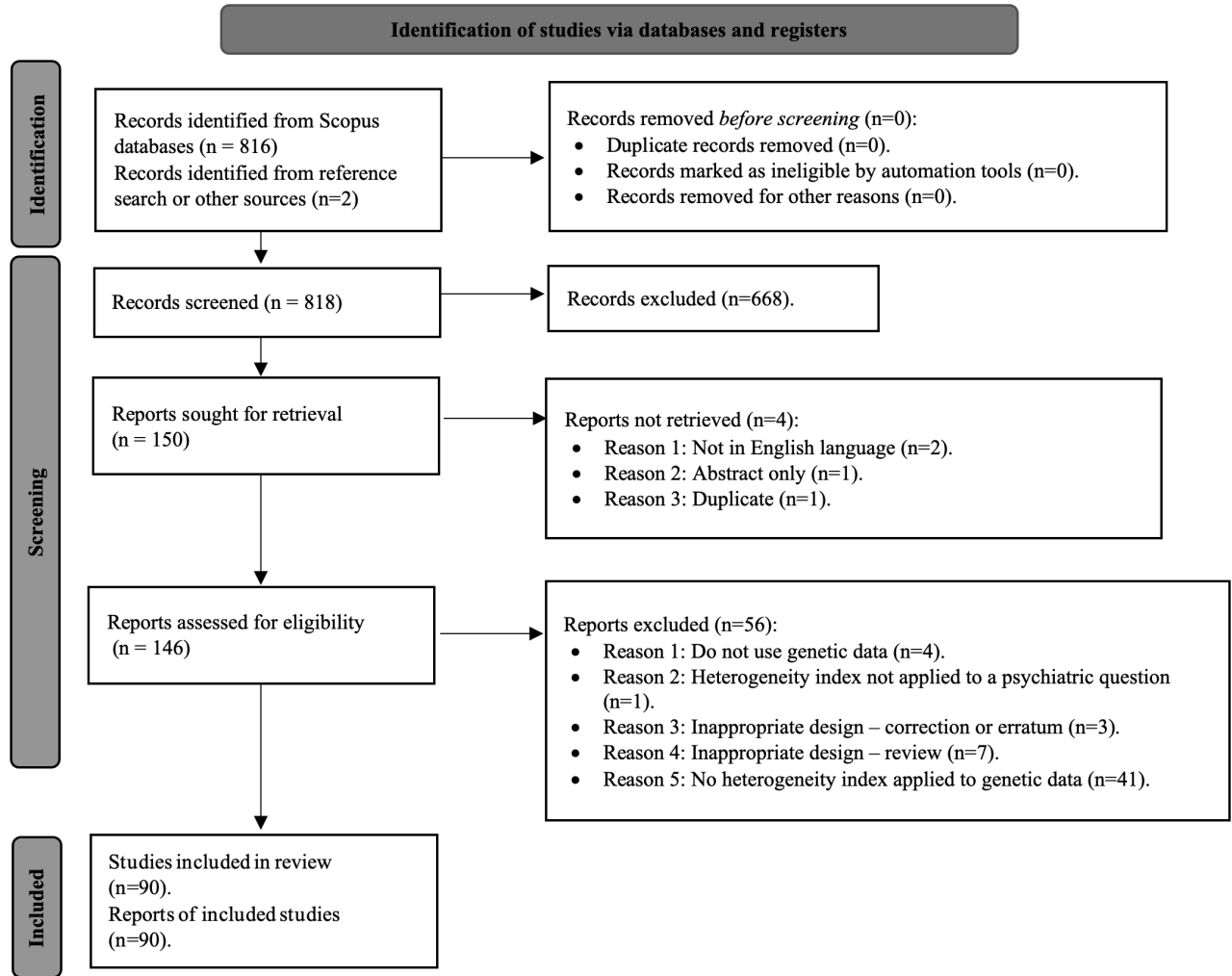


Fig. 1. PRISMA flow diagram.

III. STUDY SUMMARY TABLE

Paper	Conditions(s)	Data	Index
[1]	SCZ	Single locus	Homozygosity
[2]	SCZ	Single locus	Homozygosity
[3]	ADHD across sites	GWAS Binomial(2,p) microarray data	Chi-square heterogeneity test
[4]	SCZ, BD	GWAS Binomial(2,p) microarray data	Genetic correlation (similar to GREML)
[5]	ADHD, BD, SCZ, MDD, ASD	GWAS Binomial(2,p) microarray data	Genetic correlation (REML)
[6]	Tobacco use disorder, empirically identified set of other conditions	Gene2MeSH associations	Jaccard index
[7]	Educational attainment, MDD	GWAS Binomial(2,p) microarray data	Genetic correlation (REML)
[8]	Cognitive function, educational attainment, SCZ, BD, MDD, ADHD, ASD, AN, Alzheimer's disease	GWAS Summary statistics	Genetic correlation
[9]	Schizophrenia, Cognition	GWAS Binomial(2,p) microarray data	Genetic correlation (GREML)
[10]	Neuroticism across cohorts, SCZ, BD, MDD	GWAS Summary statistics	Genetic correlation
[11]	PTSD, SCZ, ADHD, MDD, ASD, Cross-disorder phenotype, Immune related disorders	GWAS Summary statistics	Genetic correlation
[12]	Depressive symptoms	GWAS Summary statistics	Genetic correlation
[13]	Alzheimer's, MDD	GWAS Summary statistics	Genetic correlation
[14]	BD subtypes	GWAS Binomial(2,p) microarray data	Genetic correlation (REML)
[15]	MDD Subgroups, BMI	GWAS Binomial(2,p) microarray data	Genetic correlation (GREML)
[16]	Big-5 personality traits, SCZ, BD, MDD, ADHD, ASD, AN	GWAS Summary statistics	Genetic correlation
[17]	Mood instability, MDD, Anxiety Disorders, SCZ, BD, ADHD, PTSD	GWAS Summary statistics	Genetic correlation
[18]	4 Sleep-related traits	GWAS Summary statistics	Genetic correlation
[19]	Insomnia, 6 other sleep-related phenotypes and 29 other traits	GWAS Summary statistics	Genetic correlation
[20]	ADHD and ASD Symptoms	GWAS Binomial(2,p) microarray data	Genetic correlation (GREML)
[21]	AN, other psychiatric, medical, educational, and personality phenotypes	GWAS Summary statistics	Genetic correlation
[22]	BD	GWAS Summary statistics	Genetic correlation
[23]	SCZ, BD, MDD, ADHD, ASD, ANX, OCD, AN, PTSD, Substance use, Alcohol use, Crime	GWAS SNP	Genetic correlation (PCA applied to correlation matrices)
[24]	Many	GWAS Summary statistics	Genetic correlation

[25]	SCZ, Psychiatric, personality, substance related, immune, anthropometric, and biochemical phenotypes	GWAS Summary statistics	Genetic correlation
[26]	Psychiatric and immune-related phenotypes	GWAS Summary statistics	Genetic correlation
[27]	Risk-taking, psychiatric, cognitive, and behavioural traits	GWAS Summary statistics	Genetic correlation
[28]	Empathy, SCZ, BD, MDD, depressive symptoms, educational attainment, personality features, subjective well-being, neuroticism, AN, ADHD, ASD	GWAS Summary statistics	Genetic correlation
[29]	Risk-taking, ADHD, SCZ, BD, MDD, Anxiety, PTSD, Smoking status, lifetime cannabis use, fluid intelligence, years of education, obesity, alcohol use disorder	GWAS Summary statistics	Genetic correlation
[30]	Intelligence, 38 other phenotypes	GWAS Summary statistics	Genetic correlation
[31]	Risk-taking, 12 other traits	GWAS Summary statistics	Genetic correlation
[32]	Cannabis use, Various other psychiatric, psychological phenotypes, BMI	GWAS Summary statistics	Genetic correlation
[33]	PTSD (stratified by sex), SCZ, BD, MDD	GWAS Summary statistics	Genetic correlation
[34]	Various psychiatric disorders and psychological traits	GWAS Summary statistics	Genetic correlation
[35]	MDD (stratified by adversity)	GWAS Binomial(2,p) microarray data	Genetic correlation (GREML)
[36]	ADHD, Educational attainment	GWAS Summary statistics	Genetic correlation
[37]	(Cross-population) SCZ, BD, MDD	GWAS Summary statistics	Genetic correlation
[38]	AD (Cross-population)	GWAS Summary statistics	Genetic correlation
[39]	Psychiatric diagnosis, Infection risk	GWAS Binomial(2,p) microarray data	Genetic correlation (GREML)
[40]	(Cross-population) SCZ, MDD, BD, AN, Neuroticism, Subjective well-being, ASD, ADHD, Educational attainment, General intelligence, Fluid intelligence	GWAS Summary statistics	Genetic correlation
[41]	SCZ, BD, ASD, MDD, ADHD	GWAS eQTL-weighted summary statistics	Genetic correlation
[42]	Various psychiatric, glycemic, and anthropometric traits	GWAS Summary statistics	Genetic correlation
[43]	Anxiety & stress-related disorders, 824 other phenotypes and traits	GWAS Summary statistics	Genetic correlation
[44]	Insomnia, 6 Sleep-related traits, 28 Other Traits	GWAS Summary statistics	Genetic correlation

[45]	Cocaine dependence, SCZ, ADHD, MDD, Childhood aggressive behaviour, Antisocial behaviour, Risk-taking behaviour, Vitamin D levels (Control)	GWAS Summary statistics	Genetic correlation
[46]	SCZ, BD, MDD	GWAS Summary statistics	Genetic correlation
[47]	AN, OCD, TS, SCZ, BD, MDD, ADHD, ASD	GWAS Summary statistics	Genetic correlation (also used GenomicSEM)
[48]	Various psychiatric disorders and psychological traits	GWAS Summary statistics	Genetic correlation (also used GenomicSEM)
[49]	Suicidality, Deliberate self-harm, Suicidal ideation or attempt, Attempted suicide, MDD, Neuroticism, Mood instability, SCZ, BD, Risk-taking behaviour, Anxiety disorder, ADHD, PTSD	GWAS Summary statistics	Genetic correlation
[50]	Anhedonia, MDD, SCZ, BD, OCD, Parkinson's Disease	GWAS Summary statistics	Genetic correlation
[51]	Suicidal ideation, Cognitive functioning	GWAS Binomial(2,p) microarray data	Genetic correlation (GREML)
[52]	ADHD, ASD, 8 Other Psychiatric disorders/traits	GWAS Summary statistics	Genetic correlation
[53]	Loneliness, 61 other psychiatric, cognitive, and physical traits	GWAS Summary statistics	Genetic correlation
[54]	PTSD, MDD, Depression, Anxiety, Insomnia, SCZ, BD, Alcohol use, Verbal-numeric reasoning, Years of education, Antisocial behaviour	GWAS Summary statistics	Genetic correlation
[55]	MDD	GWAS Summary statistics	Genetic correlation
[56]	OCD (across sex), 31 phenotypes	GWAS Summary statistics	Genetic correlation
[57]	Asthma, Psychiatric disorders	GWAS Summary statistics	Genetic correlation
[58]	Female reproductive traits, ADHD, MDD, ASD, ED, SCZ, BD	GWAS Summary statistics	Genetic correlation
[59]	Anxiety disorders + 251 phenotypes	GWAS Summary statistics	Genetic correlation
[60]	ADHD, ASD, BD, SCZ, MDD, 3283 Plasma Proteins	GWAS Summary statistics	Genetic correlation
[61]	Broad depression, recurrent MDD, self-reported MDD, BD, SCZ	GWAS Summary statistics	Genetic correlation (LDSC and bivariate meta-GWAS)
[62]	BD, 8 Psychiatric disorders, 8 Other traits	GWAS Summary statistics	Genetic correlation
[63]	AN, OCD	GWAS Summary statistics	Genetic correlation
[64]	Gout, ADHD, ASD, BD, MDD, SCZ	GWAS Summary statistics	Genetic correlation
[65]	Substance use phenotypes, ADHD, AN, MDD, BD, and SCZ	GWAS Summary statistics	Genetic correlation (also used GenomicSEM)

[66]	Cortical thickness, surface area, volume across 34 regions, Physical traits, Psychiatric and neurological disorders	GWAS Summary statistics	Genetic correlation
[67]	Pain phenotypes, Depressive symptoms, MDD, Neuroticism	GWAS Summary statistics	Genetic correlation
[68]	SCZ, BD, MDD, ASD, ADHD, Subcortical brain volumes	GWAS Summary statistics	Genetic correlation
[69]	Depressive symptoms, Multiple other traits	GWAS Summary statistics	Genetic correlation (also used GenomicSEM)
[70]	OCD symptoms, OCD	GWAS Summary statistics	Genetic correlation
[71]	Psychotic symptoms in adolescence, Psychotic symptoms in adulthood, SCZ, BD, MDD	GWAS Summary statistics	Genetic correlation
[72]	MDD, Neuroticism	GWAS Summary statistics	Genetic correlation (also used GenomicSEM)
[73]	Problematic alcohol use and 715 other conditions/traits	GWAS Summary statistics	Genetic correlation
[74]	ADHD, MDD, Anxiety disorder, Antisocial behaviour, SCZ, BD, ASD, AN	GWAS Summary statistics	Genetic correlation
[75]	PTSD and 4 Sleep phenotypes	GWAS Summary statistics	Genetic correlation
[76]	Alcohol use, 8 SUD traits, 11 psychiatric traits, 9 SES measures	GWAS Summary statistics	Genetic correlation
[77]	Anxiety/Disorder, all traits in LDHub	GWAS Summary statistics	Genetic correlation
[78]	ADHD, ASD, Externalizing symptoms, Internalizing symptoms, Neurodevelopmental symptoms	SR-MA Published r_g values	Genetic correlation
[79]	Anxiety disorders, 8 other psychiatric disorders, 7 subcortical brain regions, childhood cognition, general cognitive ability, subjective well-being, loneliness, neuroticism, extraversion	GWAS Summary statistics	Genetic correlation
[80]	SCZ, BD, MDD, BMI	GWAS Summary statistics	Genetic correlation
[81]	Alcohol dependence, PTSD	GWAS Summary statistics	Genetic correlation
[82]	Suicide attempt and 7 psychiatric phenotypes	GWAS Summary statistics	Genetic correlation
[83]	BD1, BD2, SZA-BD, rMDD, sMDD, subMDD	GWAS Summary statistics	Genetic correlation
[84]	Mood instability, MDD, Anxiety, PTSD, SCZ, BD	GWAS Summary statistics	Genetic correlation
[85]	9 Psychiatric disorders, 7 substance abuse traits, three indicators of SES	GWAS Summary statistics	Genetic correlation
[86]	11 Psychiatric disorders	GWAS Summary statistics	Genetic correlation

[87]	BD in Han Chinese and Europeans; BD vs. SCZ, MDD, cognitive performance, intelligence, educational attainment	GWAS Summary statistics	Genetic correlation
[88]	p-Factor, subcortical brain volumes	GWAS Summary statistics	Genetic correlation, Pleiotropy, Concordance
[89]	Data-driven psychiatric profiles, SCZ, BD, MDD, ADHD,PTSD, ANX, IQ, EDU	GWAS Summary statistics	Genetic correlation
[90]	BD, 255 other phenotypes from LDHub	GWAS Summary statistics	Genetic correlation, MiXeR

TABLE I: Table 1: Summary of studies found in literature search. Abbreviations: Attention deficit hyperactivity disorder (ADHD), anorexia nervosa (AN), autism spectrum disorder (ASD), bipolar disorder (BD), schizophrenia (SCZ), schizoaffective disorder (SZA)

IV. RELATIONSHIP BETWEEN RÉNYI HETEROGENEITY AND GENETIC CORRELATION

Heterogeneity is the degree to which a system diverges from perfect conformity [91]. Its units, known as numbers equivalent, is the effective number of distinct elements (discrete case) in or the effective hypervolume (continuous case) of an event space. One family of heterogeneity indices satisfies this definition, as well as relevant axioms of heterogeneity measurement encountered across the literature; we call this family the Rényi heterogeneity, as it is the exponential of Rényi's generalized entropy, which is a generalization of the Shannon entropy [91], [92]. It is also known as the generalized inverse participation ratio in physics [93], Hill numbers in ecology [94], and the Hannah-Kay indices in economics [95]. To derive Rényi heterogeneity, we closely follow the presentation given by Nunes et al [96] and Eliazar and Sokolov [93]. Consider a discrete system X , with event space $X = \{1, 2, \dots, n\}$ and probability distribution $p = (p_i)_{i=1,2,\dots,n}$. The probability that $q \in N_{>1}$ independent and identically distributed (i.i.d.) realizations of X , sampled with replacement, will be identical is

$$\mathbb{P}_X(x_1 = x_2 = \dots = x_q) = \sum_{i=1}^n p_i^q. \quad (1)$$

Let X^* be an idealized reference system, whose heterogeneity is equal to that of X , with a uniform probability distribution $p^* = (\frac{1}{n^*})_{i=1,2,\dots,n^*}$ over n^* categorical states. Let $(x_1^*, x_2^*, \dots, x_q^*)$ be a sample of q i.i.d. realizations of X^* such that

$$\begin{aligned} \mathbb{P}(x_1 = x_2 = \dots = x_q) &= \mathbb{P}(x_1^* = x_2^* = \dots = x_q^*) \\ &= \sum_{i=1}^{n^*} (n^*)^{-q}. \end{aligned} \quad (2)$$

Substituting Equation 2 into 1 and solving for n^* yields the Rényi heterogeneity,

$$\Pi_q(\mathbf{p}) = \left(\sum_{i=1}^n p_i^q \right)^{\frac{1}{1-q}} = n^*. \quad (3)$$

System X^* is “idealized” because of its uniform probability distribution, and it is a “reference” system for X in that the probability of drawing homogenous samples of q observations from both systems is identical. Such reference system gives an intuitive interpretation for the units of Rényi heterogeneity, known as numbers equivalent: The number of partitions in “equivalent” system X^* serves to measure the heterogeneity of X . Numbers equivalent allows the inequality in the abundance distribution to be taken into account, while retaining the units of set size.

One important axiom of heterogeneity that Equation 3 satisfies is the axiom of replication, which states that if k unique and disjoint systems with equal amount of heterogeneity h are pooled together, then the heterogeneity of the combined

system should be $k \times h$. Entropy-based measures such as the Gini-Simpson index (GSI) and Shannon entropy do not satisfy this axiom.

Equation 3 also satisfies the axiom of decomposability. This axiom states that the overall heterogeneity (known as the γ -heterogeneity) of a system composed of k pooled groups, must be decomposable into within- and between- components, known respectively as the α - and β -heterogeneity.

Yet another interesting property of the Rényi heterogeneity is that it can generalize or be transformed into several heterogeneity indices that are commonly employed across scientific disciplines [91], such as the perplexity [97] and the inverse Simpson concentration [98].

Finally, the Rényi heterogeneity of an n -dimensional Gaussian random variable \mathbf{X} with covariance matrix Σ is [96], [99]

$$\Pi_q(X) = \begin{cases} \text{Undefined} & q = 0 \\ (2\pi e)^{\frac{n}{2}} |\Sigma|^{\frac{1}{2}} & q = 1 \\ (2\pi)^{\frac{n}{2}} |\Sigma|^{\frac{1}{2}} & q = \infty \\ (2\pi)^{\frac{n}{2}} q^{\frac{n}{2(q-1)}} |\Sigma|^{\frac{1}{2}} & \text{Otherwise} \end{cases}. \quad (4)$$

Lemma 1. *The Rényi heterogeneity of the genetic covariance matrix (Equation 3 in main text) is*

$$\begin{aligned} \Pi_q(\mathbf{W}) &= (2\pi)^M q^{\frac{2M}{2(q-1)}} \sqrt{\det \begin{pmatrix} \frac{h_1^2}{M} \mathbf{I}_M & \frac{\rho_g}{M} \mathbf{I}_M \\ \frac{\rho_g}{M} \mathbf{I}_M & \frac{h_2^2}{M} \mathbf{I}_M \end{pmatrix}} \\ &= (2\pi q^{\frac{1}{q-1}} M^{-1})^M (h_1^2 h_2^2 - \rho_g^2)^{\frac{M}{2}}, \\ & \quad q \notin \{0, 1, \infty\}. \end{aligned} \quad (5)$$

Proof. The proof follows from substituting the genetic covariance matrix into the derivation of the Rényi heterogeneity of a multivariate Gaussian provided by Nunes et al [96]. \square

Proposition 1. *The Rényi heterogeneity of the genetic covariance matrix is maximized at $\rho_g = 0$.*

Proof. Intuitively, we can see from Equation 5 that ρ_g^2 is inversely proportional to the Rényi heterogeneity of the genetic covariance matrix, $\Pi_q(\mathbf{W})$. Since ρ_g^2 is minimized at 0, $\Pi_q(\mathbf{W})$ must be maximized at $\rho_g = 0$.

Formally, we can see this by taking the first derivative of $\Pi_q(\mathbf{W})$ with respect to ρ_g ,

$$\begin{aligned} \frac{\partial}{\partial \rho_g} \Pi_q(\mathbf{W}) &= -M \rho_g \left(2\pi q^{\frac{1}{q-1}} M^{-1} \right)^M \\ & \quad [(h_1 h_2 + \rho_g)(h_1 h_2 - \rho_g)]^{\frac{M}{2}-1}, \end{aligned} \quad (6)$$

and obtain critical points at $\rho_g = 0$ and $\pm h_1 h_2$. Evaluating $\Pi_q(\mathbf{W})$ at these points yields

$$\Pi_q(\mathbf{W})_{\rho_g=0} = \left(2\pi q^{\frac{1}{q-1}} M^{-1} \right)^M (h_1 h_2)^{\frac{M}{2}} \geq 0, \quad (7)$$

$$\Pi_q(\mathbf{W})_{\rho_g=h_1 h_2} = \Pi_q(\mathbf{W})_{\rho_g=-h_1 h_2} = 0, \quad (8)$$

showing that the critical point $\rho_g = 0$ maximizes Π_q .

Evaluating the second derivative of $\Pi_q(\mathbf{W})$ with respect to

ρ_g ,

$$\frac{\partial^2}{\partial \rho_g^2} \Pi_q(\mathbf{W}) = M \left(2\pi q^{\frac{1}{q-1}} M^{-1} \right)^M \left\{ 2\rho_g^2 \left(\frac{M}{2} - 1 \right) \left[(h_1 h_2)^2 - \rho_g^2 \right]^{\frac{M}{2}-2} - \left[(h_1 h_2)^2 - \rho_g^2 \right]^{\frac{M}{2}-1} \right\}, \quad (9)$$

gives

$$\left[\frac{\partial^2}{\partial \rho_g^2} \Pi_q(\mathbf{W}) \right]_{\rho_g=0} = -M \left(2\pi q^{\frac{1}{q-1}} M^{-1} \right)^M (h_1 h_2)^{M-2} \leq 0, \quad (10)$$

showing that $\Pi_q(\mathbf{W})$ is indeed maximized at $\rho_g = 0$. \square

Proposition 2. Genetic correlation r_g contracts the effective size of \mathbf{W} 's sample space by a factor of $K = (1 - r_g^2)^{-M/2}$.

Proof. Substituting $\rho_g = r_g \sqrt{h_1^2 h_2^2}$ into Equation 5, we have

$$\Pi_q(\mathbf{W}) = (2\pi q^{\frac{1}{q-1}} M^{-1})^M (h_1 h_2)^M (1 - r_g^2)^{\frac{M}{2}}, \quad (11)$$

$q \notin \{0, 1, \infty\}$.

Dividing this by $\Pi_q(\mathbf{W})_{\rho_g=0}$, which is the maximal effective size of the sample space for \mathbf{W} , we have

$$\frac{\Pi_q(\mathbf{W})_{\rho_g=0}}{\Pi_q(\mathbf{W})} = \frac{(2\pi q^{\frac{1}{q-1}} M^{-1})^M (h_1 h_2)^M}{(2\pi q^{\frac{1}{q-1}} M^{-1})^M (h_1 h_2)^M (1 - r_g^2)^{\frac{M}{2}}} = (1 - r_g^2)^{-\frac{M}{2}}$$

\square

Corollary 1. \mathbf{W} 's sample space has contracted by a factor of K at a correlation of $r_g = (1 - K^{-2/M})^{1/2}$.

Proof. Simply rearrange $K = (1 - r_g^2)^{-M/2}$ to solve for r_g . \square

Proposition 3. For constant h_1^2 and h_2^2 , a contraction in the domain of the distribution over \mathbf{W} will result in a greater mutual information between \mathbf{W}_1 and \mathbf{W}_2 .

Proof. For constant h_1^2 and h_2^2 , a contraction in the domain of the distribution over \mathbf{W} is possible only by an increase in the magnitude of ρ_g . The mutual information between \mathbf{W}_1 and \mathbf{W}_2 is

$$\mathbb{I}[\mathbf{W}_1; \mathbf{W}_2] = \log(h_1 h_2) - \frac{1}{2} \log(-\rho_g^2 + h_1^2 h_2^2). \quad (12)$$

The derivative with respect to ρ_g is

$$\frac{d}{d\rho_g} \mathbb{I}[\mathbf{W}_1; \mathbf{W}_2] = \frac{\rho_g}{-\rho_g^2 + h_1^2 h_2^2}, \quad (13)$$

which has a critical point at $\rho_g = 0$. Finally, since

$$\left(\frac{d^2}{d\rho_g^2} \mathbb{I}[\mathbf{W}_1; \mathbf{W}_2] \right)_{\rho_g=0} = \frac{1}{h_1^2 h_2^2} > 0, \quad (14)$$

we see that $\mathbb{I}[\mathbf{W}_1; \mathbf{W}_2]$ is concave in ρ_g , with a minimum at $\rho_g = 0$. \square

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