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Heritability enrichment of specifically expressed genes identifies disease-relevant tissues and cell types

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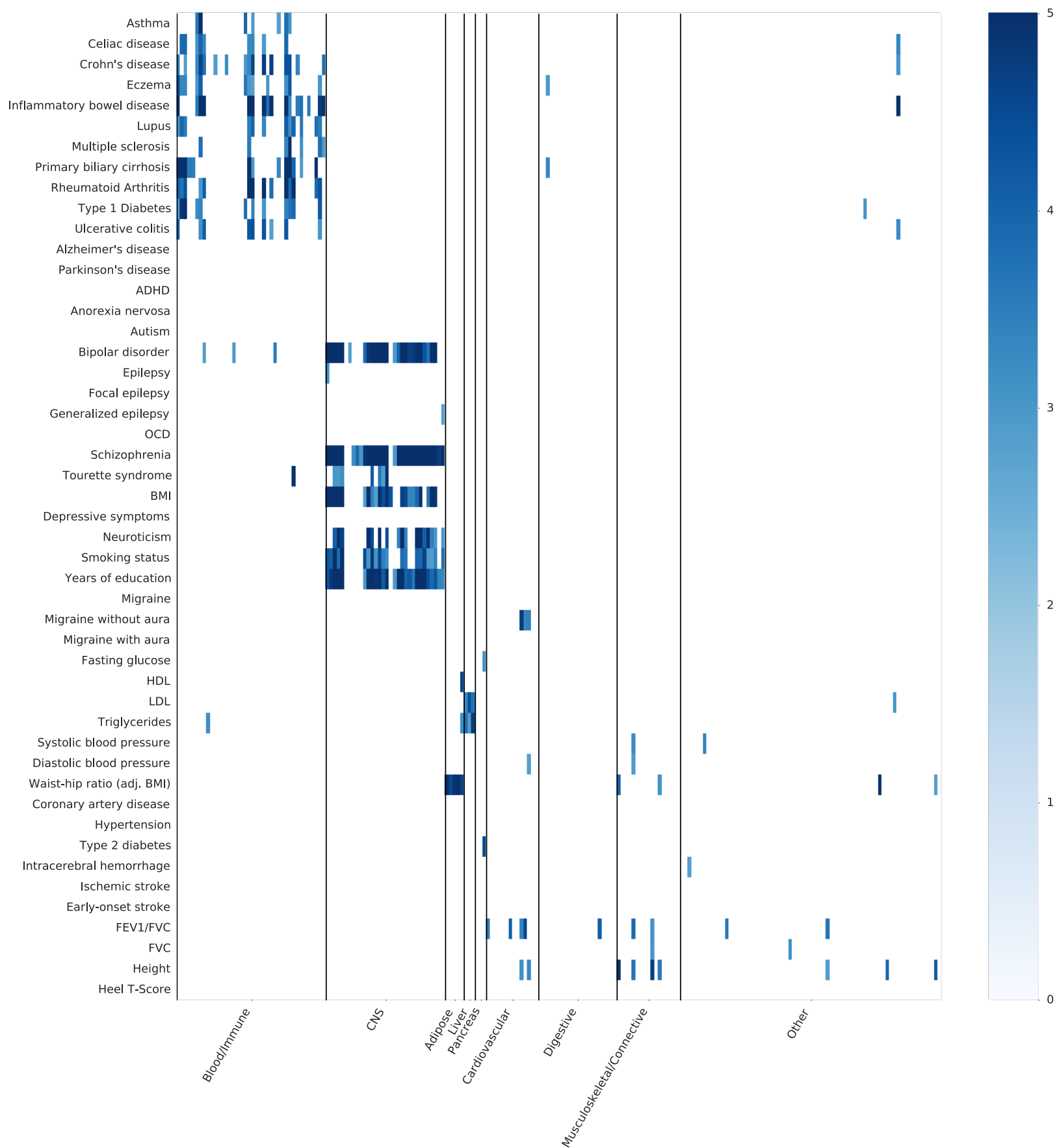
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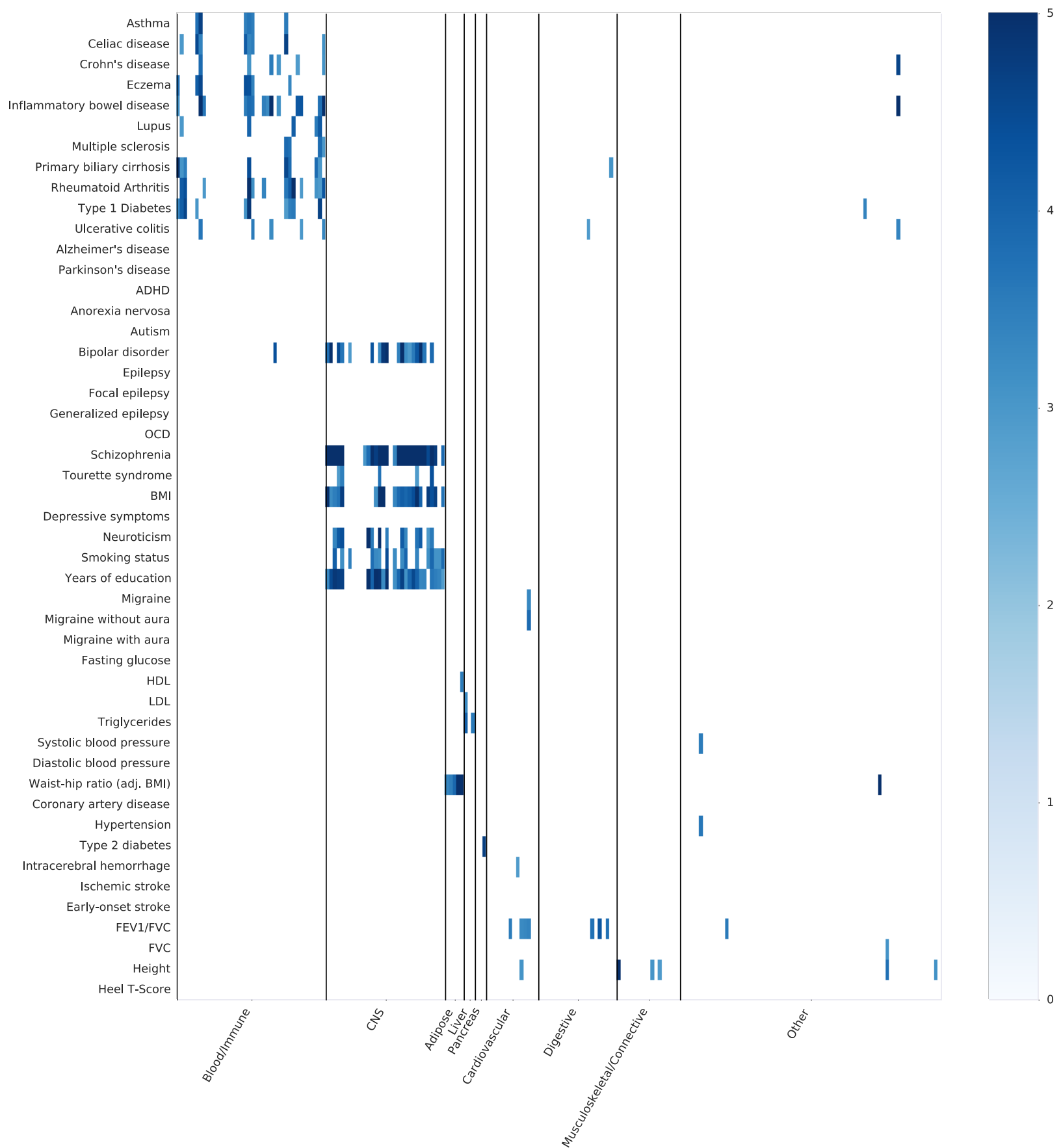
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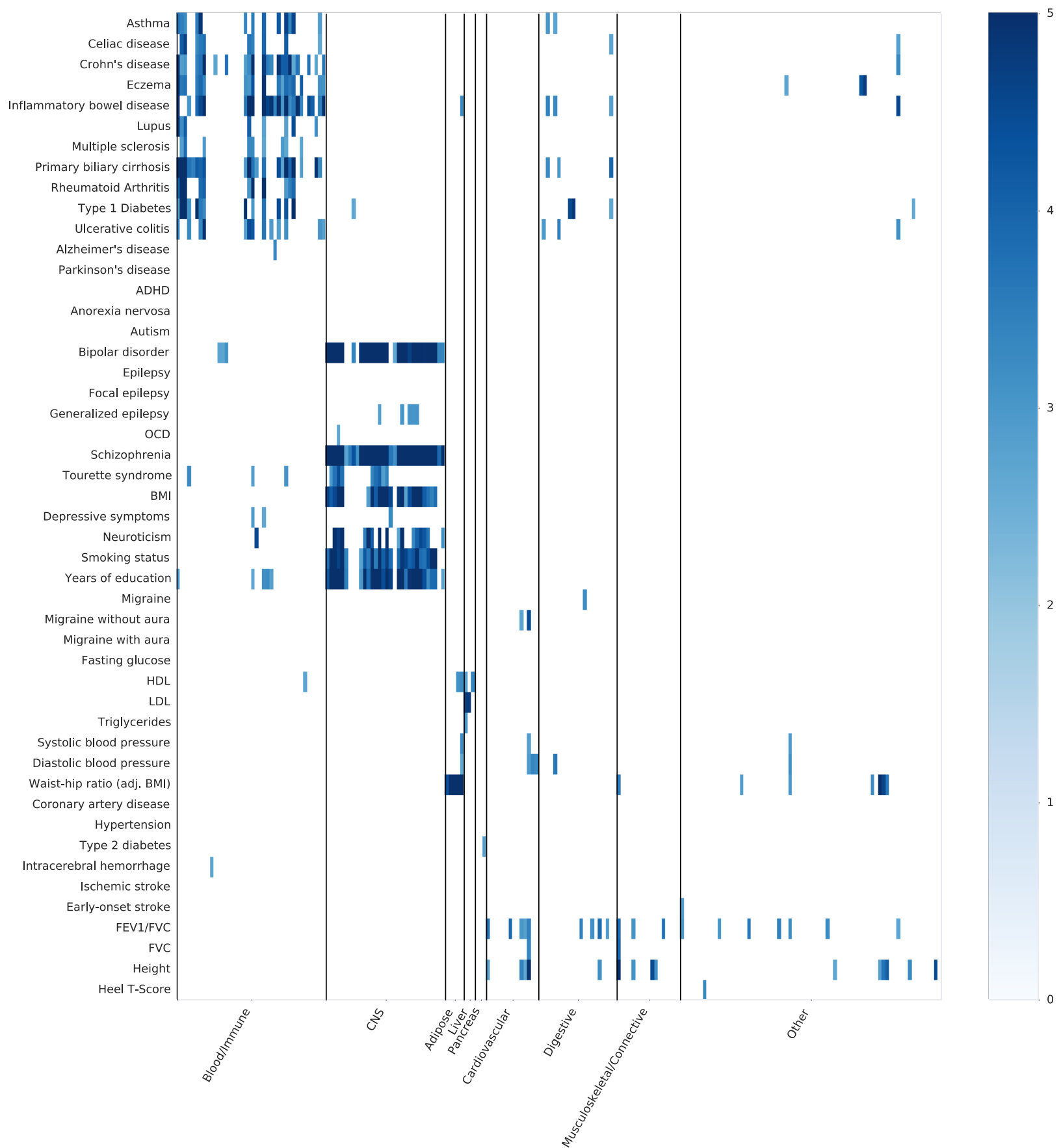
Supplementary Fig. 1. Results of the multiple-tissue analysis for traits with at least one tissue/cell type passing $FDR < 5\%$ that are not displayed in **Figure 2**. Each point represents a tissue/cell type from either the GTEx data set or the Franke lab data set. Large points pass the $FDR < 5\%$ cutoff, $-\log_{10}(P) = 2.75$. GWAS data is described in **Supplementary Table 4**, gene expression data is described in the Online Methods and **Supplementary Tables 2-3**, and the statistical method is described in the Overview of Methods and the Online Methods. Numerical results are reported in **Supplementary Table 6**.



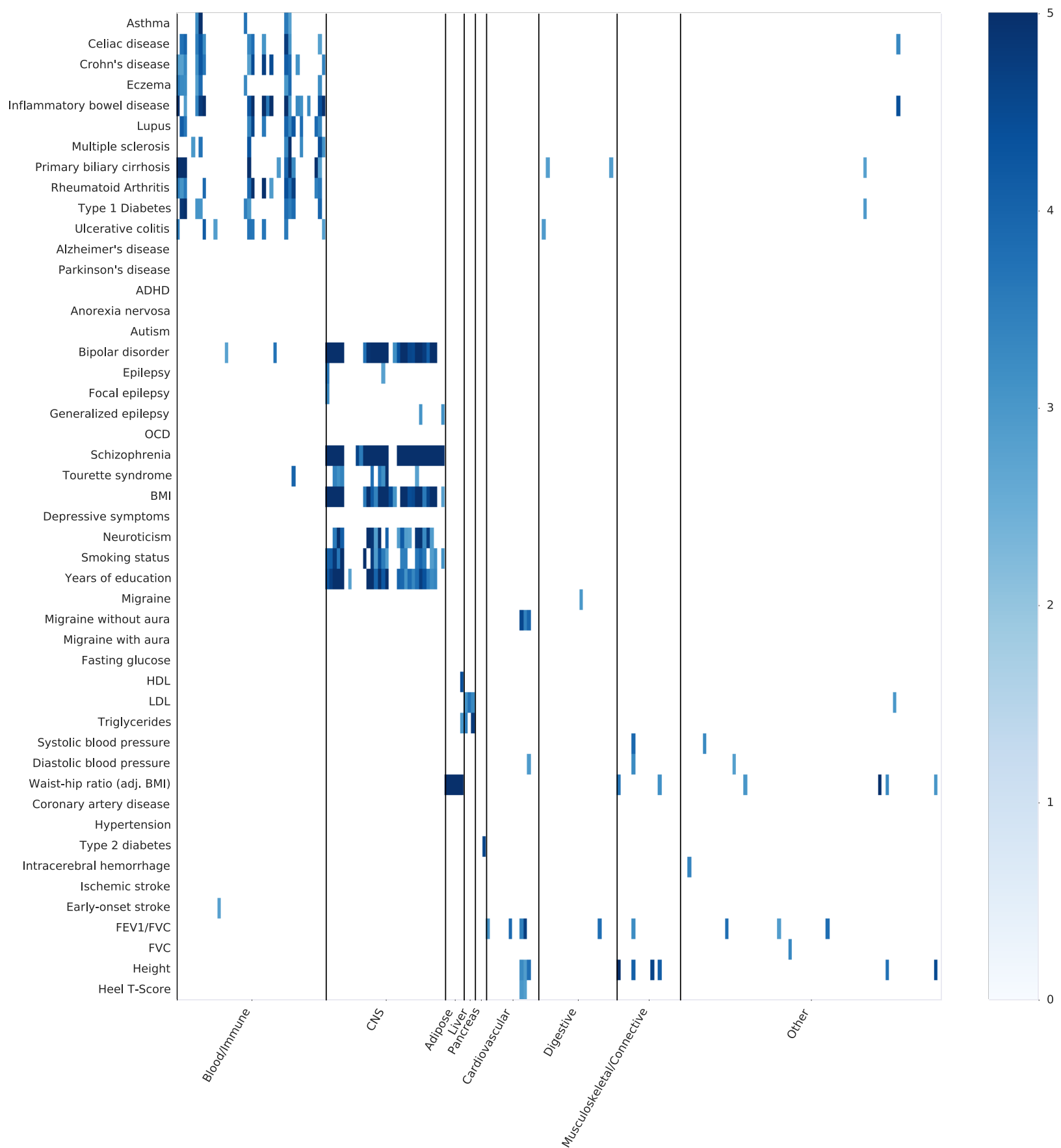
Supplementary Fig. 2a. Results of the multiple-tissue analysis for all traits, for comparison with **Figures S2b-e** and **Figures S12-S15**. $-\log_{10}(P)$ is displayed, truncated at 5, for results that pass the $FDR < 5\%$ threshold of $-\log_{10}(P)=2.75$. GWAS data is described in **Supplementary Table 4**, gene expression data is described in the Online Methods and **Supplementary Tables 2-3**, and the statistical method is described in the Overview of Methods and the Online Methods. Numerical results are reported in **Supplementary Table 6**.



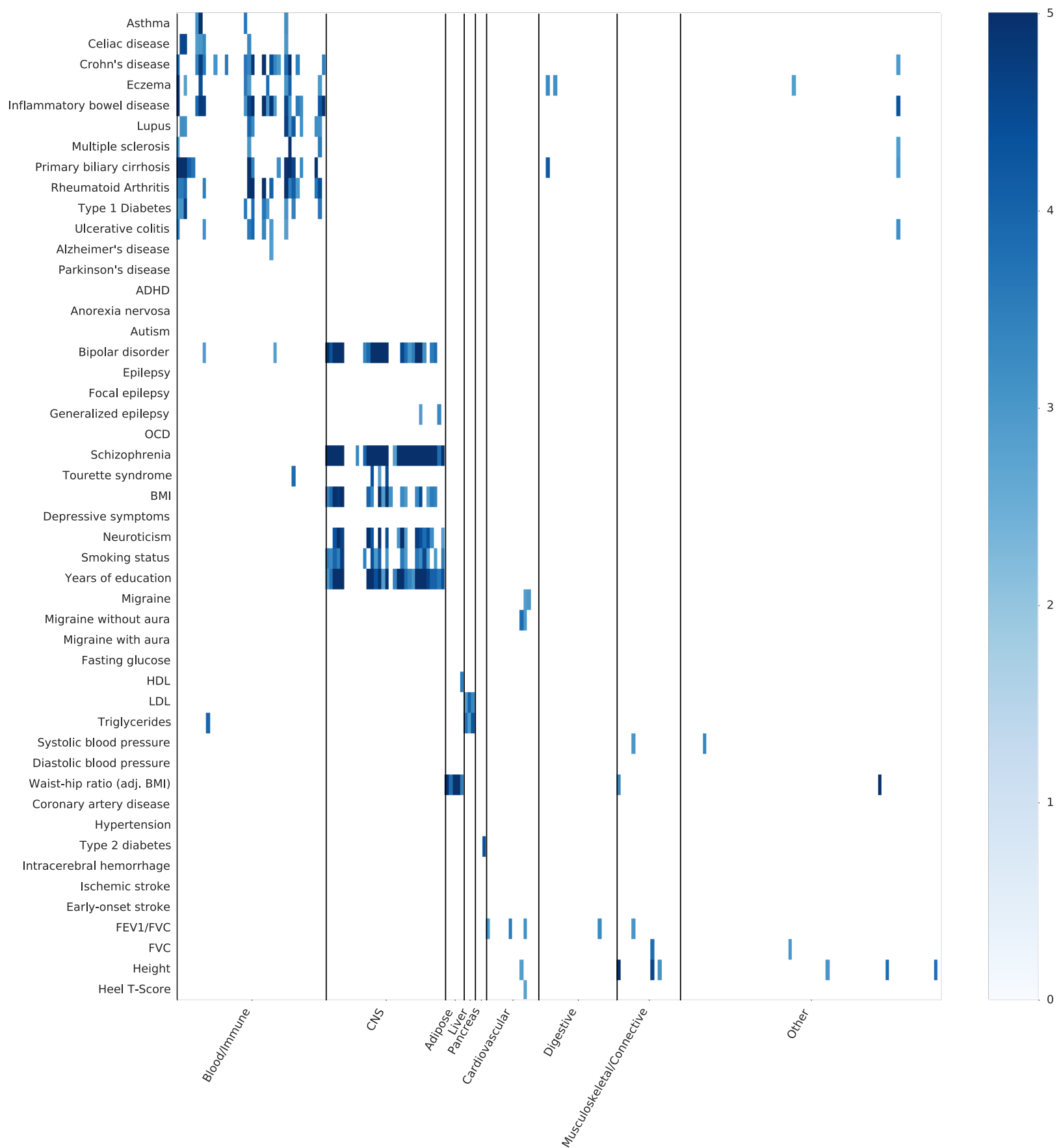
Supplementary Fig. 2b. Results of the multiple-tissue analysis with proportion of genes changed from 10% to 5%. $-\log_{10}(P)$ is displayed, truncated at 5, for results that pass the FDR < 5% threshold of $-\log_{10}(P)=2.91$. GWAS data is described in **Supplementary Table 4**, gene expression data is described in the Online Methods and **Supplementary Tables 2-3**, and the statistical method is described in the Overview of Methods and the Online Methods.



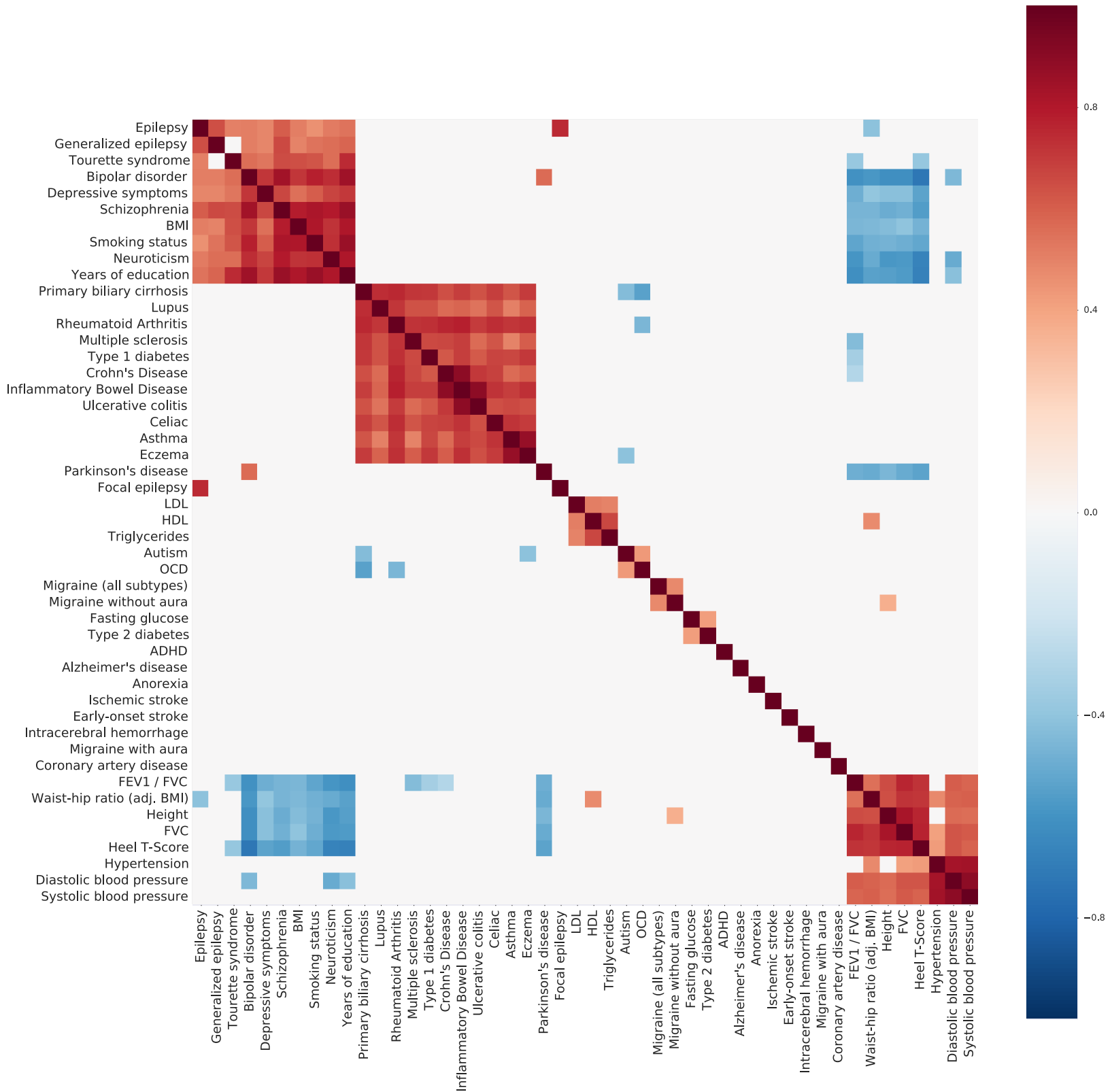
Supplementary Fig. 2c. Results of the multiple-tissue analysis with proportion of genes changed from 10% to 20%. $-\log_{10}(P)$ is displayed, truncated at 5, for results that pass the FDR < 5% threshold of $-\log_{10}(P)=2.84$. GWAS data is described in **Supplementary Table 4**, gene expression data is described in the Online Methods and **Supplementary Tables 2-3**, and the statistical method is described in the Overview of Methods and the Online Methods.



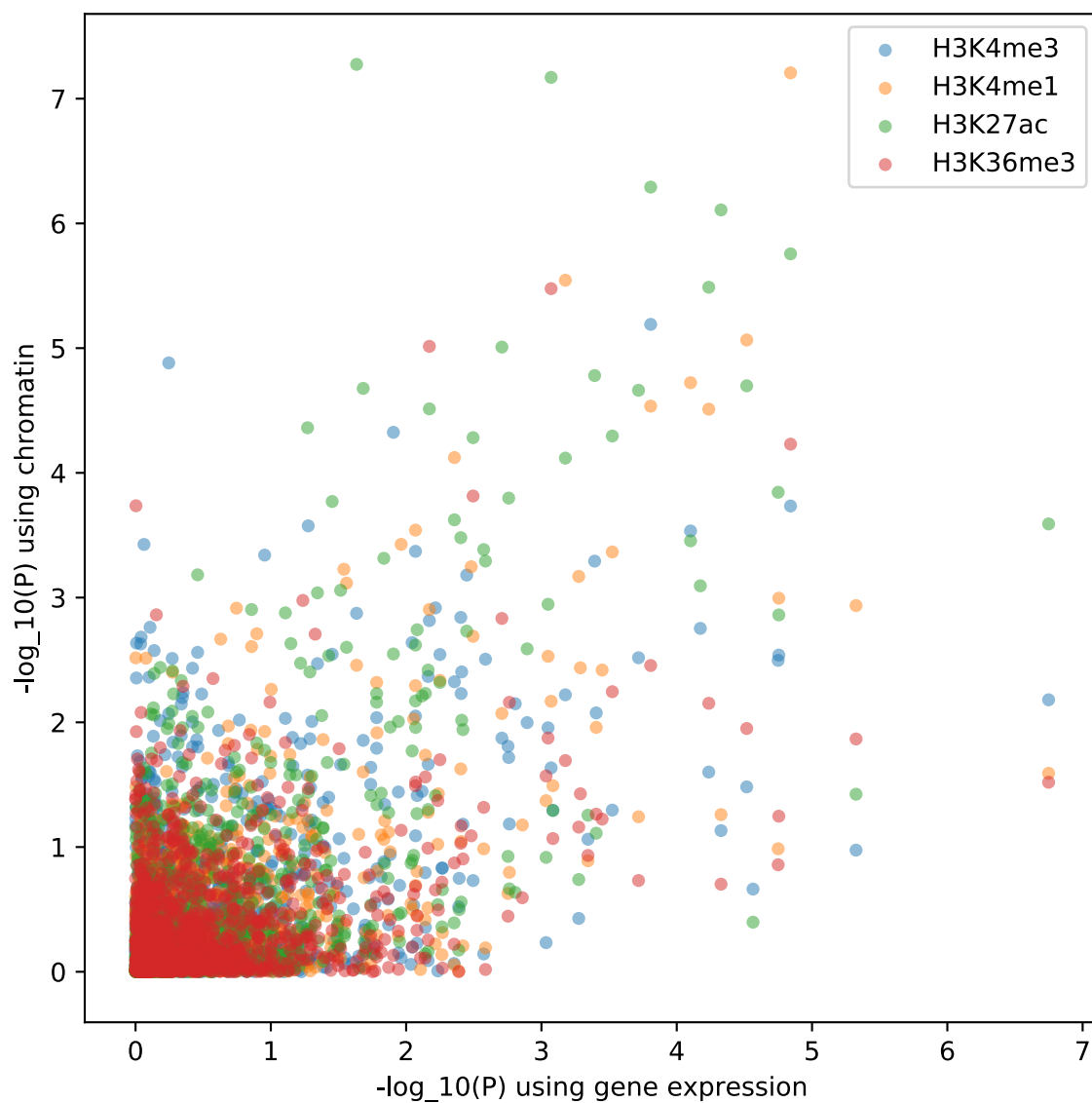
Supplementary Fig. 2d. Results of the multiple-tissue analysis with the window size changed from 100kb to 50kb. $-\log_{10}(P)$ is displayed, truncated at 5, for results that pass the FDR < 5% threshold of $-\log_{10}(P)=2.78$. GWAS data is described in **Supplementary Table 4**, gene expression data is described in the Online Methods and **Supplementary Tables 2-3**, and the statistical method is described in the Overview of Methods and the Online Methods.



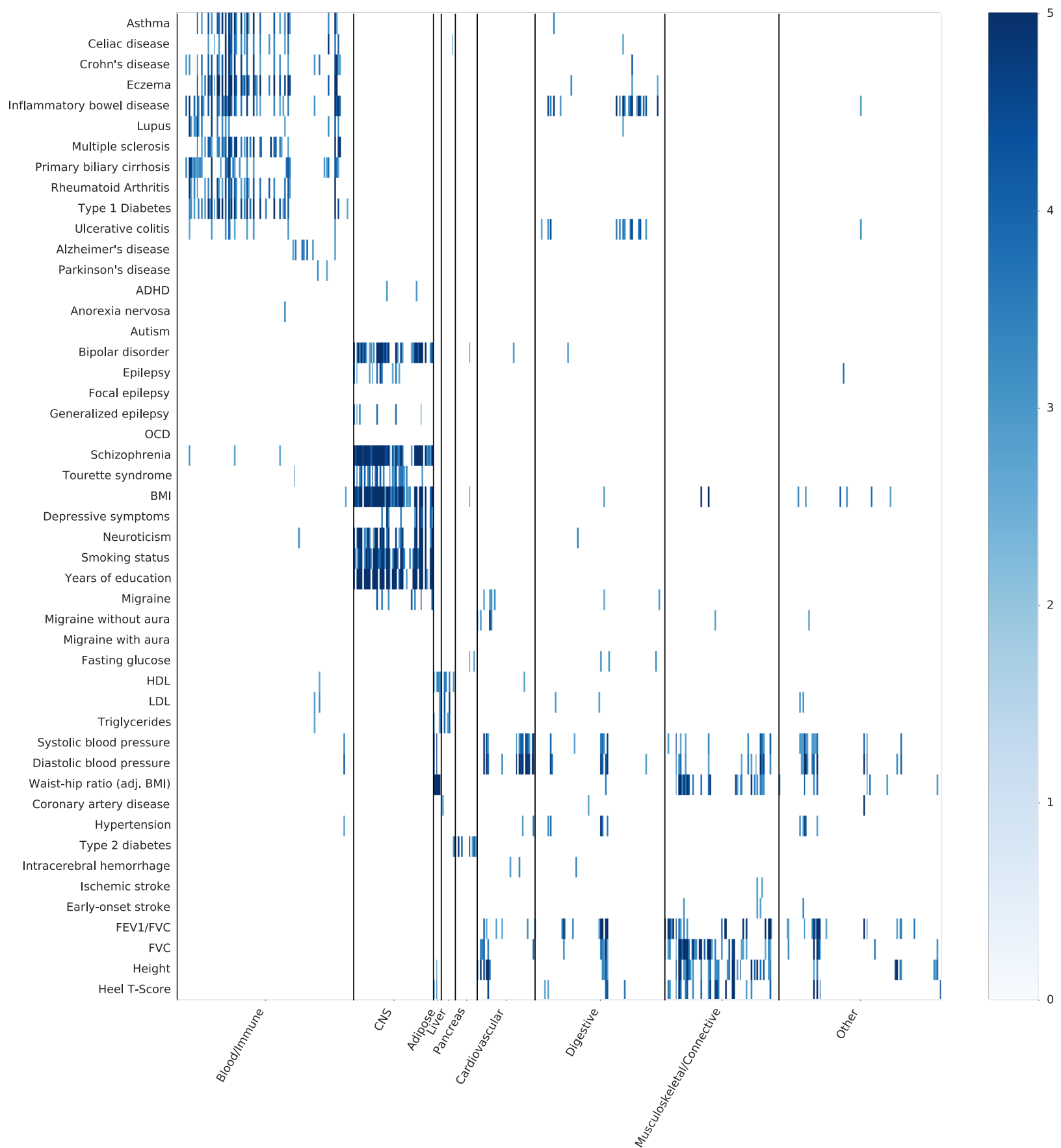
Supplementary Fig. 2e. Results of the multiple-tissue analysis with the window size changed from 100kb to 200kb. $-\log_{10}(P)$ is displayed, truncated at 5, for results that pass the FDR < 5% threshold of $-\log_{10}(P)=2.83$. GWAS data is described in **Supplementary Table 4**, gene expression data is described in the Online Methods and **Supplementary Tables 2-3**, and the statistical method is described in the Overview of Methods and the Online Methods.



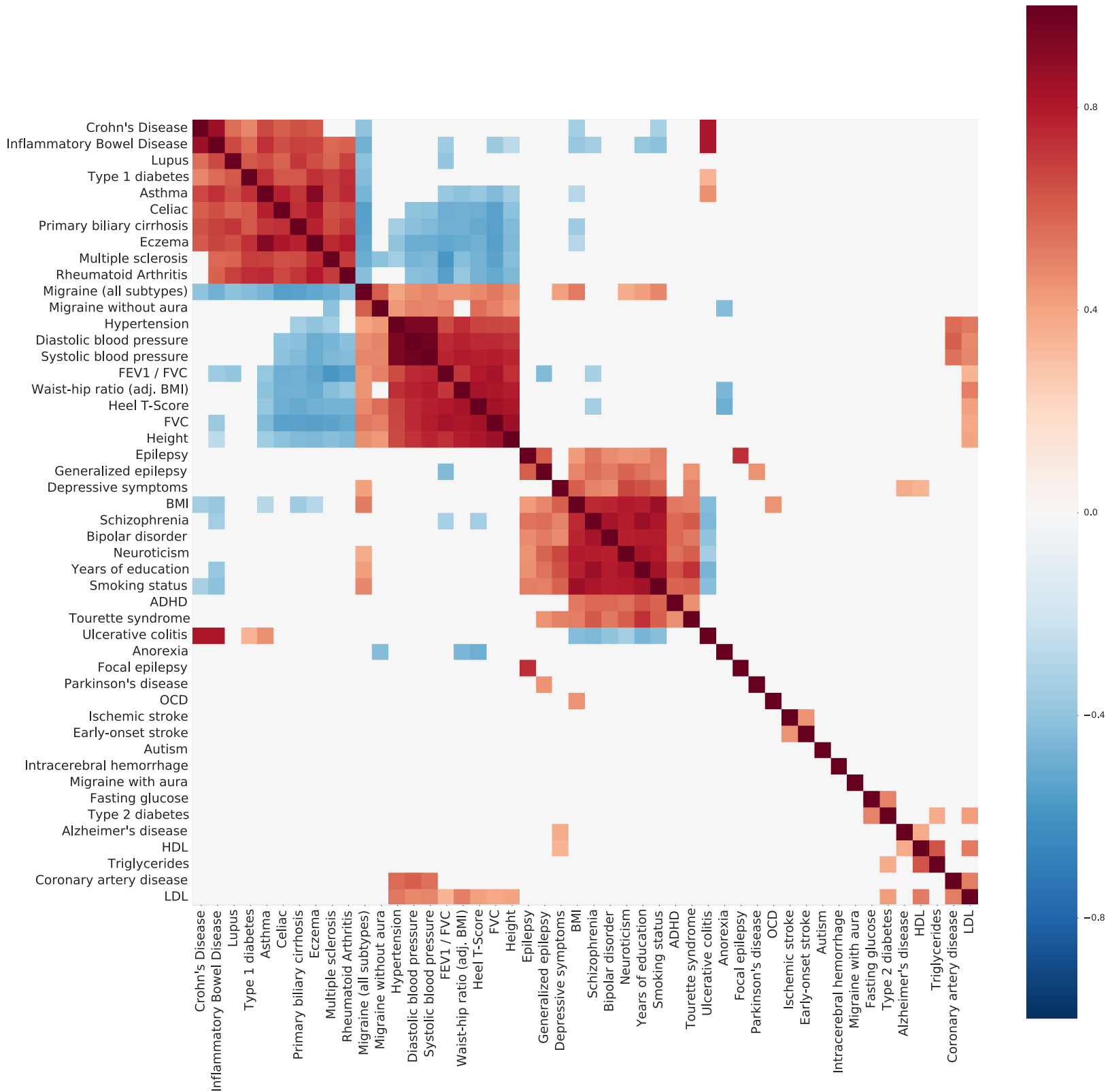
Supplementary Fig. 3. Estimates of enrichment correlations from the multiple-tissue analysis. Enrichment correlation estimates that pass the $FDR < 5\%$ cutoff (two-sided test for difference from 0) are displayed. GWAS data is described in **Supplementary Table 4**, gene expression data is described in the Online Methods and **Supplementary Tables 2-3**, and the statistical method is described in the Online Methods.



Supplementary Fig. 4. Comparison of GTEx and EN-TEG P-values. For each of 48 phenotypes, for each of 24 tissues shared between GTEx and EN-TEG, significance levels from the analysis using gene expression-based annotations are plotted against significance levels from the analysis using chromatin peaks.

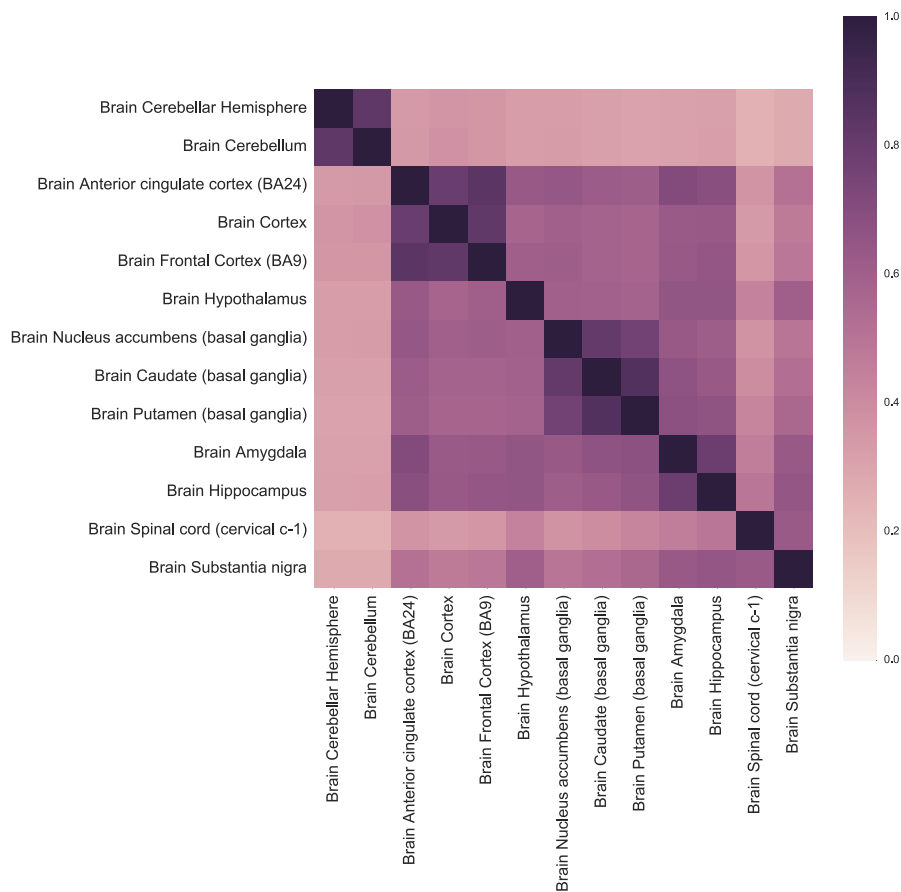


Supplementary Fig. 5. A heatmap of results from the analysis of 48 traits using chromatin data from the Roadmap Epigenomics project and ENCODE. $-\log_{10}(P)$ is displayed, truncated at 5, for results that pass the FDR < 5% threshold of $-\log_{10}(P) = 2.66$. Numerical results are reported in **Supplementary Table 7**. GWAS data is described in **Supplementary Table 4**, chromatin data is described in the Online Methods and **Supplementary Table 7**, and the statistical method is described in the Online Methods.

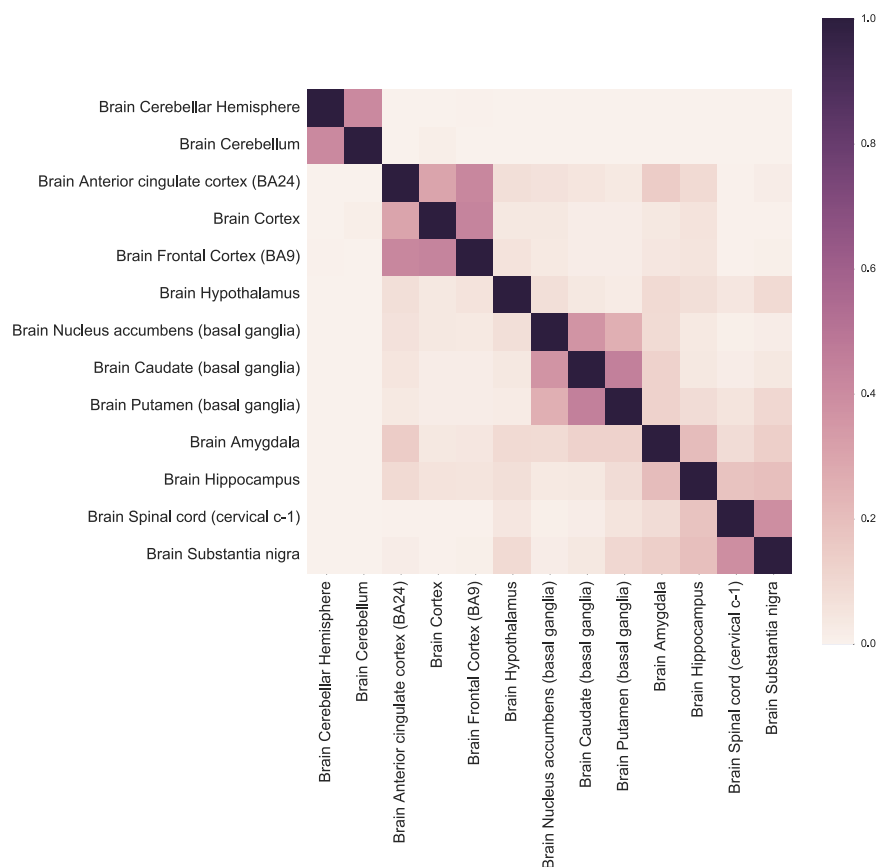


Supplementary Fig. 6. Estimates of enrichment correlations from the chromatin analysis. Enrichment correlation estimates that pass the FDR<5% cutoff (two-sided test for difference from 0) are displayed. GWAS data is described in **Supplementary Table 4**, chromatin data is described in the Online Methods and **Supplementary Table 7**, and the statistical method is described in the Online Methods.

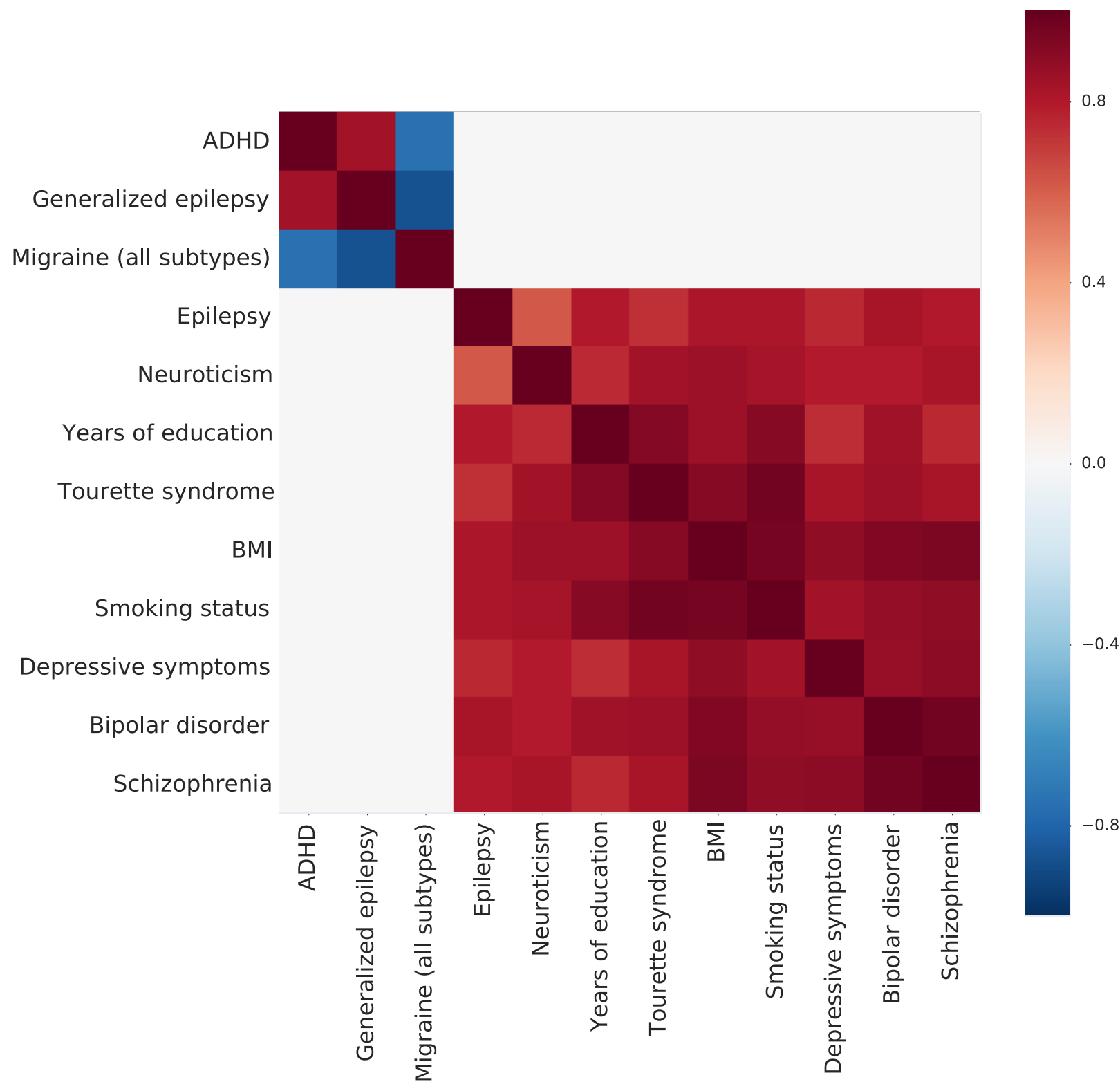
(a)



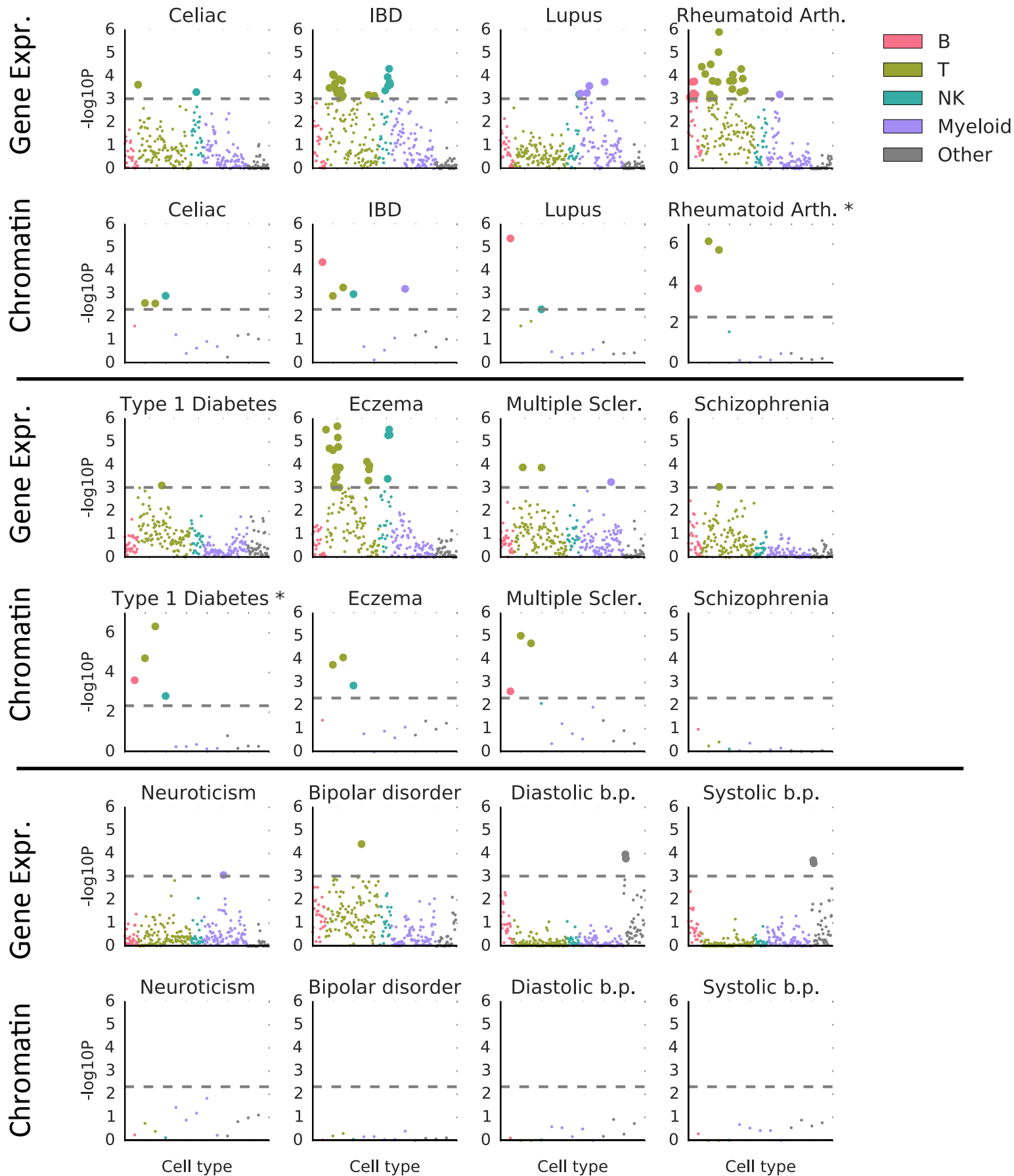
(b)



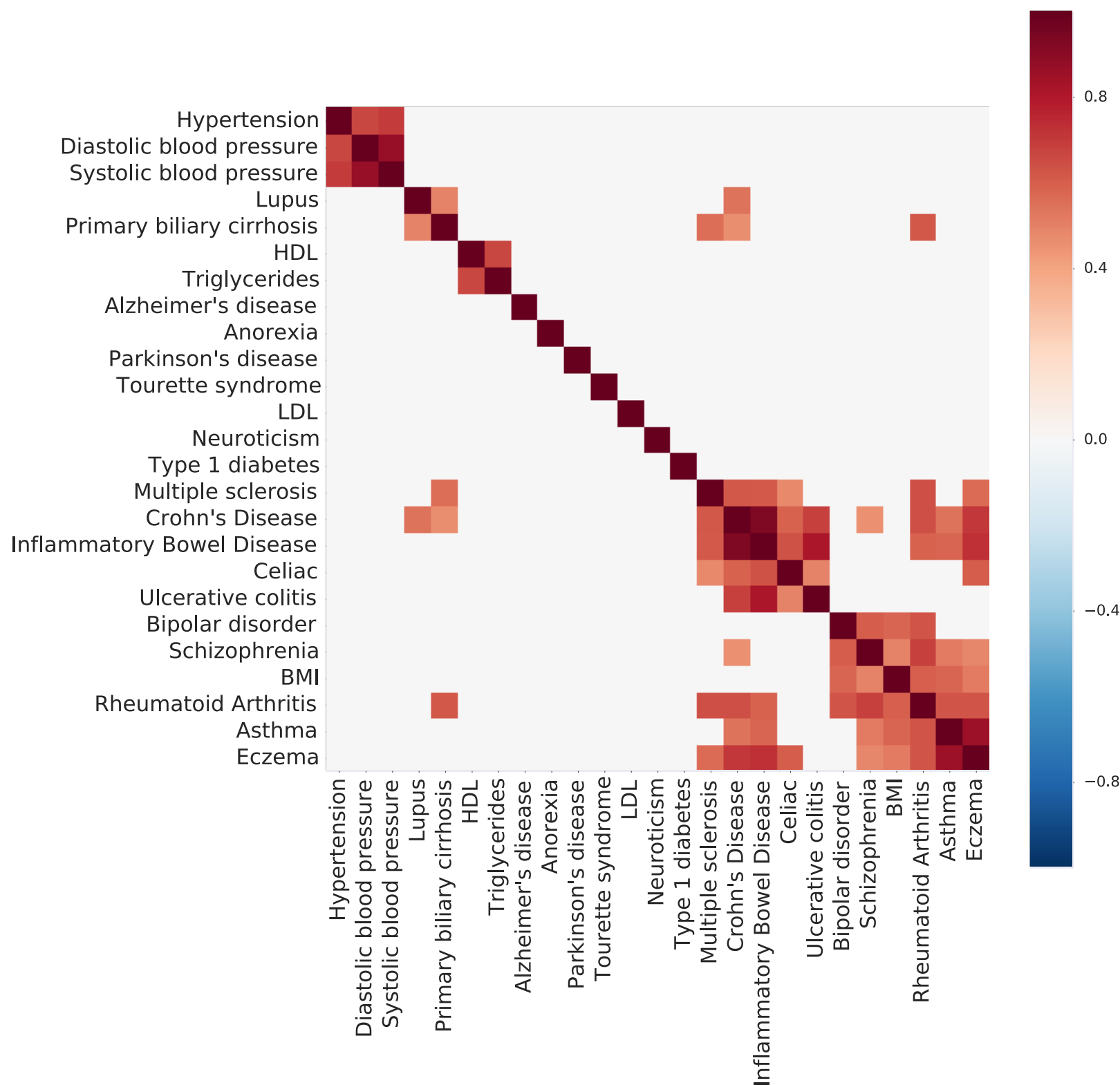
Supplementary Fig. 7. (a) A heatmap of Jaccard indices among gene sets for the 13 brain regions in GTEx, in the multiple-tissue analysis. **(b)** A heatmap of Jaccard indices among gene sets for the 13 brain regions in GTEx, in the analysis of GTEx brain regions only. The data is described in the Online Methods and **Supplementary Table 2** and the statistical method is described in the Overview of Methods and Online Methods.



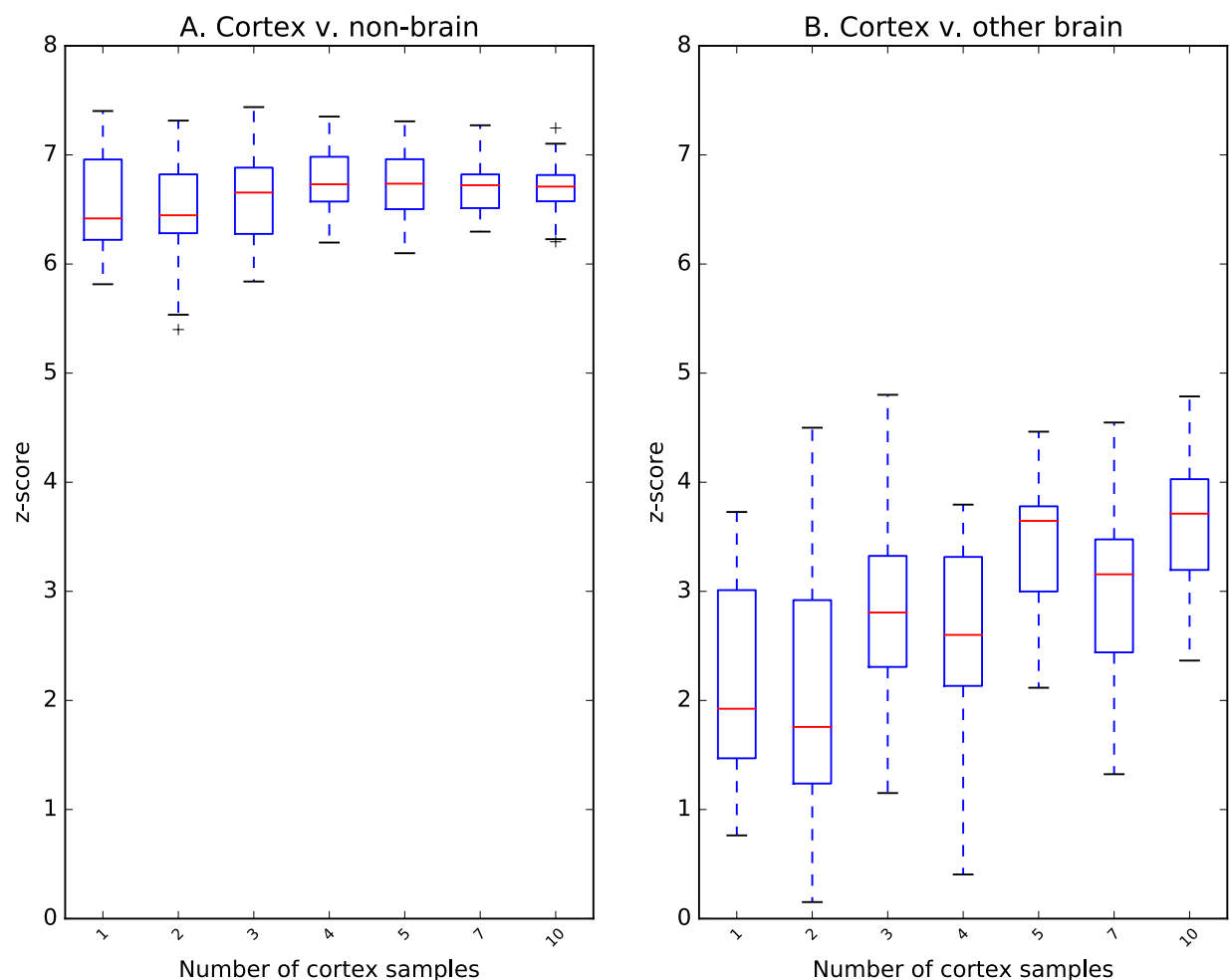
Supplementary Fig. 8. Estimates of enrichment correlations from the analysis of brain regions. Enrichment correlation estimates that pass the $FDR < 5\%$ cutoff (two-sided test for difference from 0) are displayed. GWAS data is described in **Supplementary Table 4**, gene expression data is described in the Online Methods and **Supplementary Tables 2**, and the statistical method is described in the Online Methods.



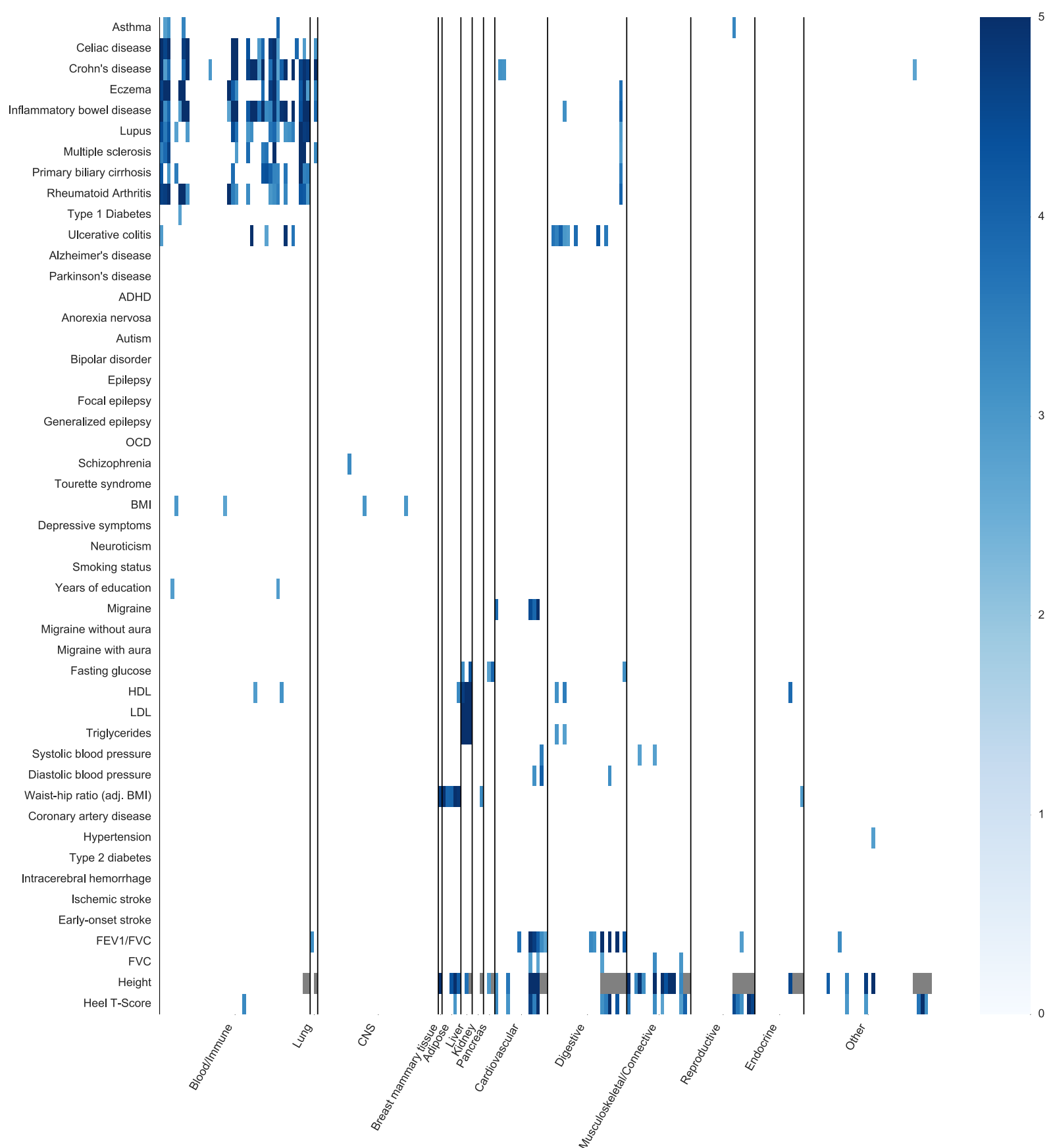
Supplementary Fig. 9. Results of the analysis of ImmGen gene expression data and hematopoiesis ATAC-seq data for traits with at least one ImmGen cell type passing $FDR < 5\%$ not appearing in Figure 5. Large points passed the $FDR < 5\%$ cutoff, $-\log_{10}(P) = 3.03$ (ImmGen) or $-\log_{10}(P) = 2.32$ (hematopoiesis). GWAS data is described in **Supp. Table 4**, gene expression and chromatin data is described in the Online Methods and **Supp. Table 10**, and the statistical method is described in the Overview of Methods and the Online Methods. Numerical results for all traits are reported in **Supp. Table 10**.



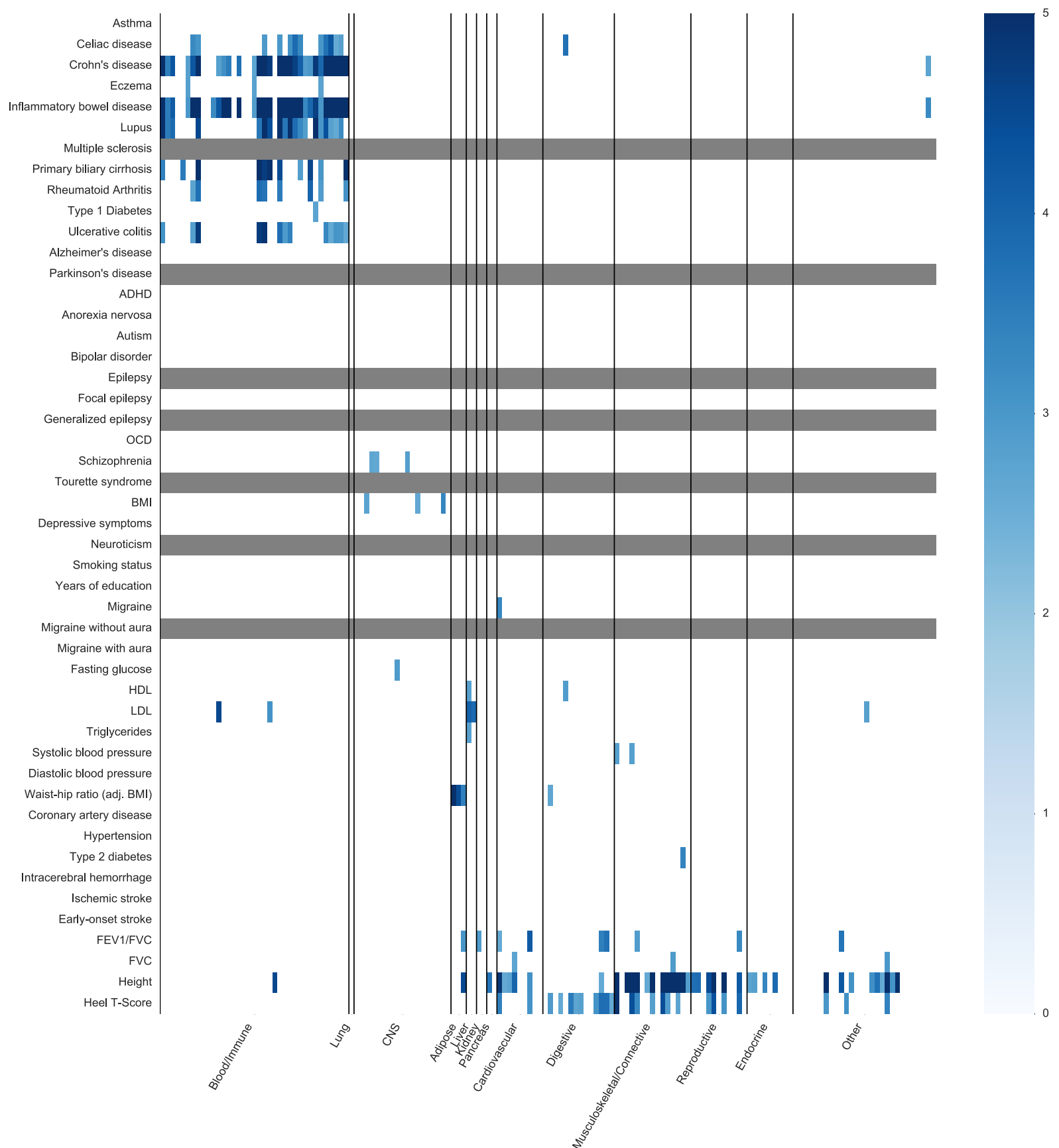
Supplementary Fig. 10. Estimates of enrichment correlations from the analysis of ImmGen data. Enrichment correlation estimates that pass the FDR<5% cutoff (two-sided test for difference from 0) are displayed. GWAS data is described in **Supplementary Table 4**, gene expression and chromatin data is described in the Online Methods and **Supplementary Table 10**, and the statistical method is described in the Online Methods.



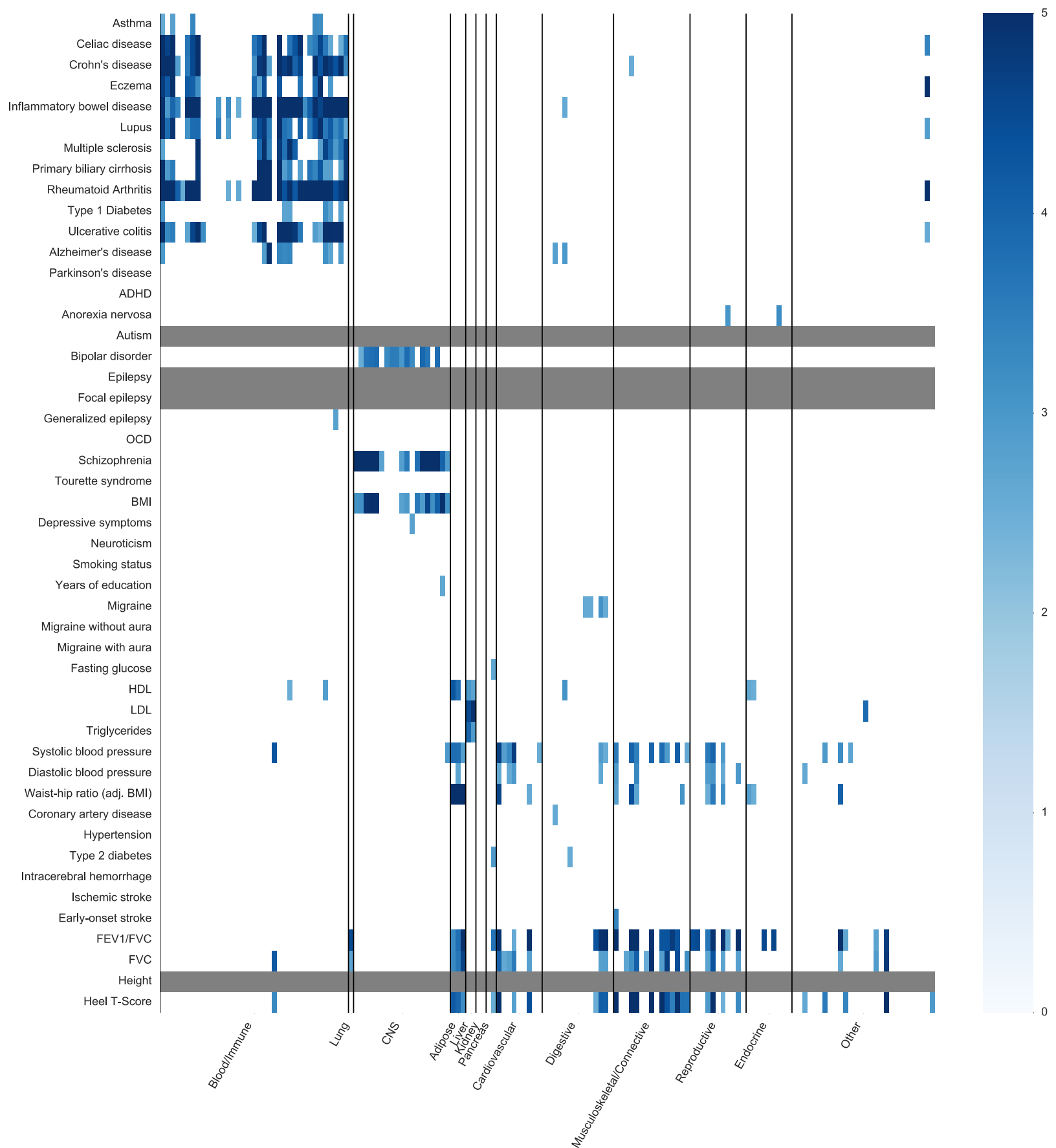
Supplementary Fig. 11. We repeatedly sub-sampled our dataset to a variety of sample sizes and ran our approach on the sub-sampled dataset. Each box plot represents the z-scores of 25 randomly sub-sampled datasets (center line, median; box limits, upper and lower quartiles; whiskers, max and min or 1.5x interquartile range; pluses, outliers). **(A)** We assessed cortex enrichment for schizophrenia in the multiple-tissue analysis, in which cortex was compared to all non-brain samples. We kept the ratio of cortex samples to non-brain samples constant as we downsampled. **(B)** We assessed cortex enrichment for schizophrenia in the analysis of GTEx brain regions, in which cortex was compared to all other brain samples. We kept the ratio of cortex samples to other brain samples constant as we downsampled.



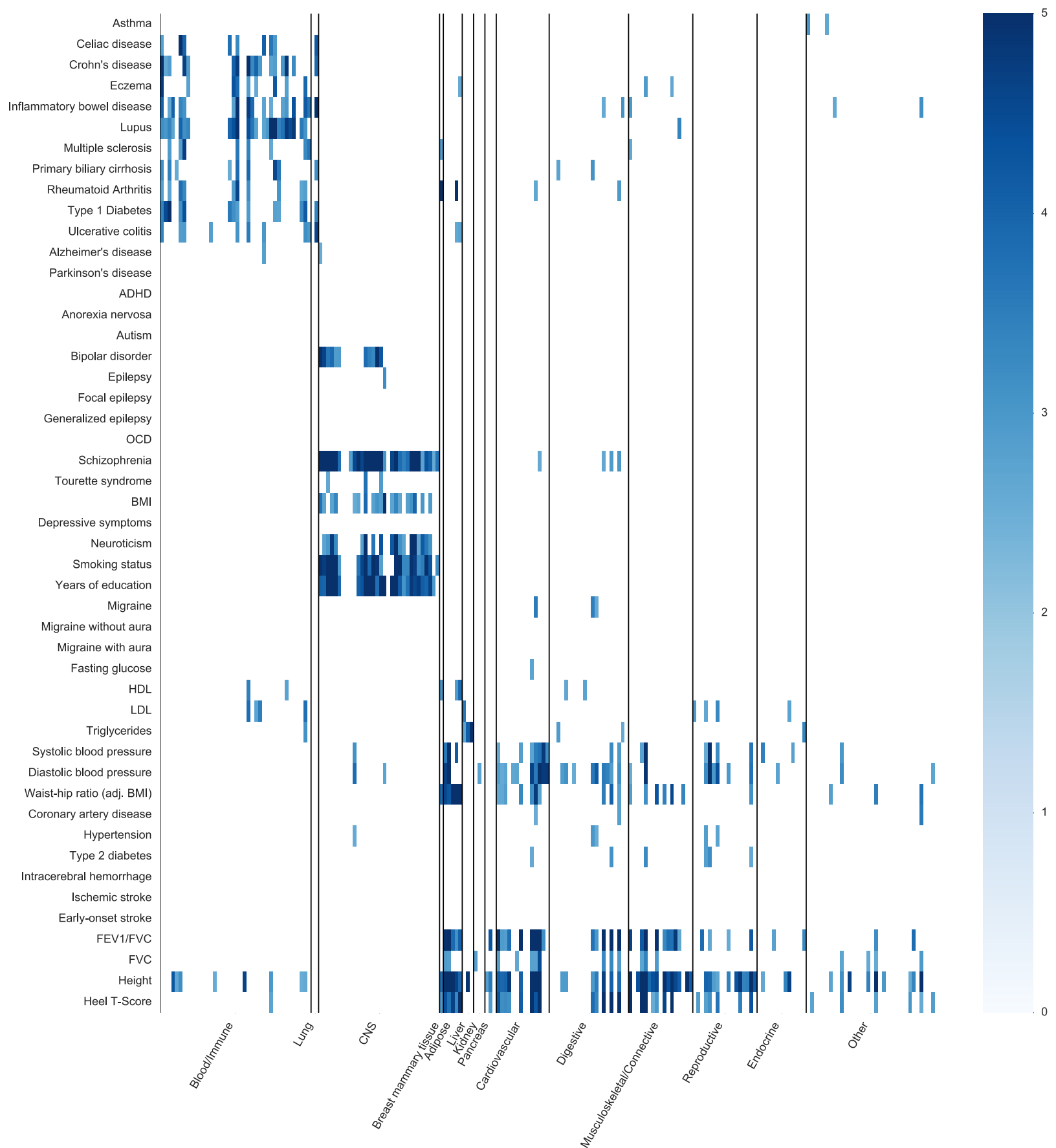
Supplementary Fig. 12. A heatmap of results from applying the SNPsea method to the gene expression data from the multiple-tissue analysis. $-\log_{10}(P)$ is displayed, truncated at 5, for results that pass the FDR<5% cutoff of $-\log_{10}(P)=2.74$. Grey boxes denote analyses that did not complete successfully at 8GB of RAM. GWAS data is described in **Supp. Table 4** and gene expression data is described in the Online Methods and **Supp. Tables 2-3**. Numerical results are reported in **Supp. Table 12**. SNPsea did not detect many of the CNS enrichments for brain-related traits identified by LDSC-SEG (see **Supplementary Fig. 2a** for comparison).



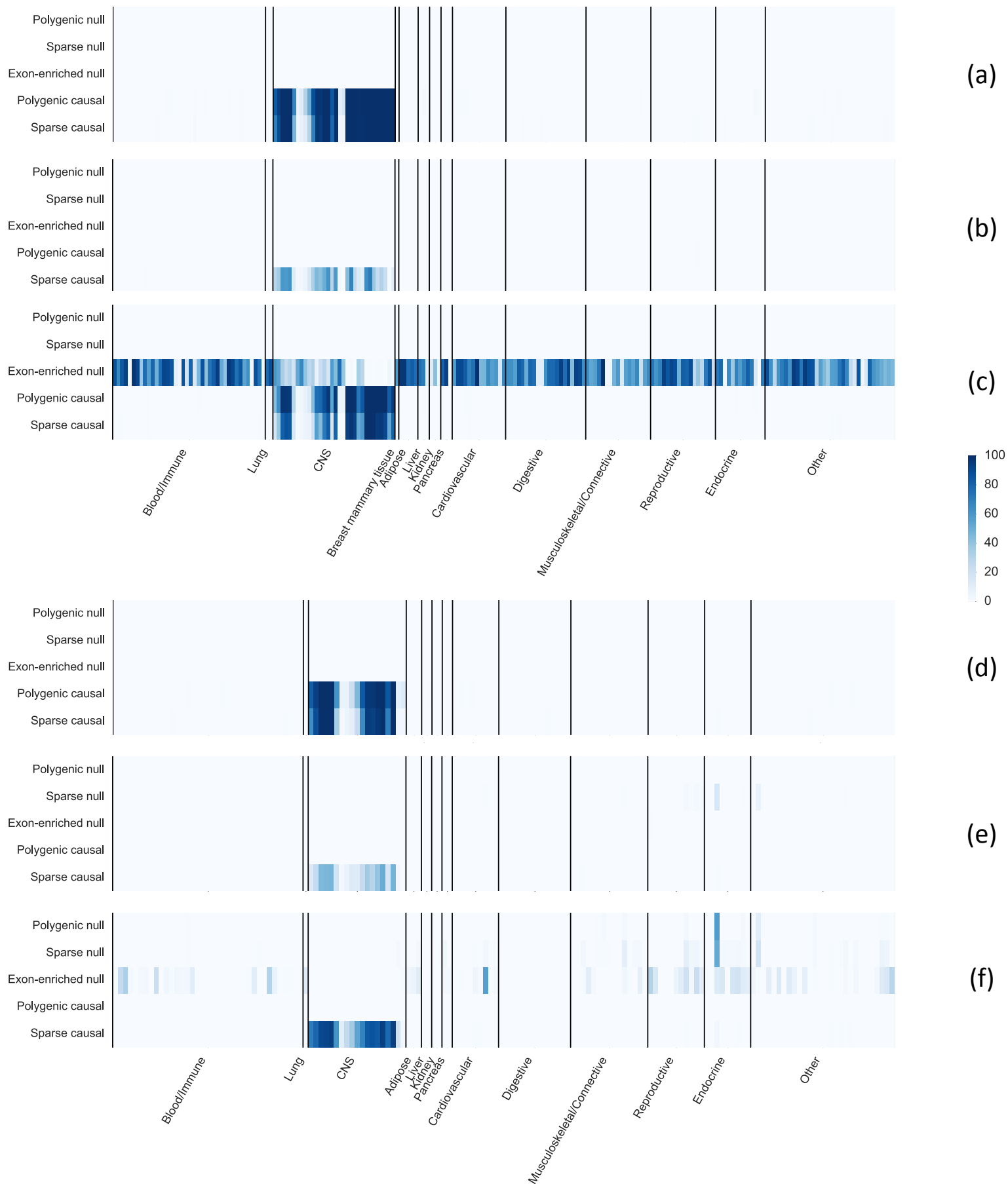
Supplementary Fig. 13. A heatmap of results from applying the DEPICT method with a P-value threshold of $5e-8$ to the gene expression data from the multiple-tissue analysis. $-\log_{10}(P)$ is displayed, truncated at 5, for results that pass the FDR<5% cutoff of $-\log_{10}(P)=2.60$. Grey boxes denote analyses that did not complete successfully. GWAS data is described in **Supplementary Table 4** and gene expression data is described in the Online Methods and **Supplementary Tables 3**. Numerical results are reported in **Supplementary Table 13**. DEPICT with a threshold of $5e-8$ did not detect many of the CNS enrichments for brain-related traits identified by LDSC-SEG (see **Supplementary Fig. 2a** for comparison).



Supplementary Fig. 14. A heatmap of results from applying the DEPICT method with a P-value threshold of $1e-5$ to the gene expression data from the multiple-tissue analysis. $-\log_{10}(P)$ is displayed, truncated at 5, for results that pass the FDR<5% cutoff of $-\log_{10}(P)=2.48$. Grey boxes denote analyses that did not complete successfully. GWAS data is described in **Supplementary Table 4** and gene expression data is described in the Online Methods and **Supplementary Tables 3**. Numerical results are reported in **Supplementary Table 14**. DEPICT with a threshold of $1e-5$ identified many enrichments, but in simulations did not have well-calibrated type I error (see **Supplementary Fig. 2a**).



Supplementary Fig. 15. A heatmap of results from applying MAGMA to the specifically expressed gene sets from the multiple-tissue analysis. $-\log_{10}(P)$ is displayed, truncated at 5, for results that pass the FDR<5% cutoff of $-\log_{10}(P)=2.54$. GWAS data is described in **Supplementary Table 4** and gene expression data is described in the Online Methods and **Supplementary Tables 2-3**. Numerical results are reported in **Supplementary Table 15**. MAGMA-SEG identified many enrichments, but in simulations did not have well-calibrated type I error (see **Supplementary Fig. 2a**).



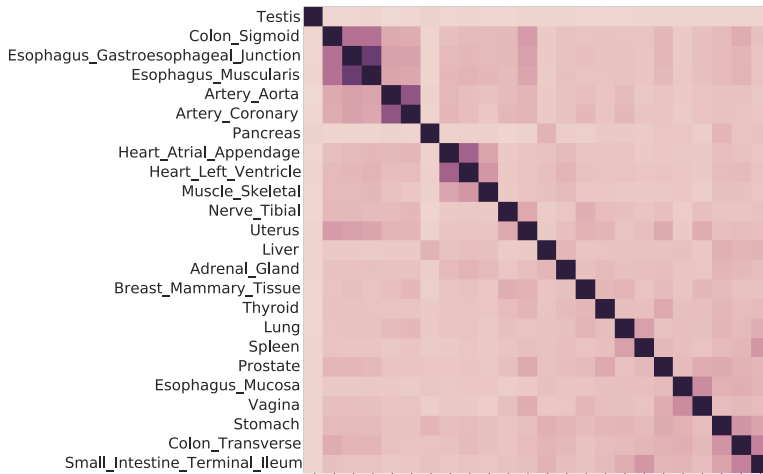
Supplementary Fig. 16. Number of the 100 simulated phenotypes that passed FDR < 5% for each method. Simulations are described in the Supplementary note, and have a sample size of n=47,360 individuals. (a) LDSC-SEG, (b) SNPsea, (c) MAGMA-SEG, (d)LDSC-SEG (Franke lab dataset only, included so that the comparison to DEPICT can be on the same set tissues/cell types), (e) DEPICT with 5e-8 cutoff, (f) DEPICT with 1e-5 cutoff. Numerical results are reported in **Supplementary Table 16**.



(a) H3K27ac



(b) Gene expression -
top 10% of genes by
total expression



(c) Gene expression -
top 10% of genes by
specific expression



Supplementary Fig. 17. The Jaccard index between pairs of annotations. **(a)** Annotations are H3K27ac peaks from EN-TEG. **(b)** Annotations are 100kb windows around the top 10% of genes by total average expression in GTEx. **(c)** Annotations are 100kb windows around the top 10% of genes by specific expression in GTEx.

SUPPLEMENTARY NOTE

Choice of parameters. Our approach includes two parameters: the proportion of genes selected, which we set to 10%, and the window size around each gene, which we set to 100kb. To choose these two parameters, we ran the approach with six different parameter settings ({2%, 5%, 10% of genes} x {20kb, 100kb windows}) on two diseases—schizophrenia and rheumatoid arthritis—and two corresponding GTEx tissues—brain (all brain regions) and blood (LCLs and whole blood)—which are widely known to be disease-relevant tissues. We determined that of the parameter settings we tested, 10% of genes and 100kb produced the most significant P-values for identifying brain enrichment for schizophrenia and blood enrichment for rheumatoid arthritis, so we used these parameters for the remaining analyses. Our results were robust to these choices (Supplementary Fig. 2).

Number of gene expression samples needed. Because the GTEx consortium data set included tens of samples for many of the tissues, we were able to assess how sensitive our results were to the sample size of the gene expression data set used to construct the gene sets. To do this, we repeatedly sub-sampled our data set to a variety of sample sizes, each time re-creating gene sets using the smaller sub-sampled data set. We chose two results to re-analyze in this way. First, we re-analyzed cortex enrichment for schizophrenia, in which cortex was compared to all non-brain samples and was highly significant ($P < 10^{-13}$; **Figure 2**). This result was very robust: the enrichment was highly significant in all of our downsampled data sets, even with only a single cortex sample (median $P < 10^{-9}$ for a single sample; **Supplementary Fig. 11a**). We then assessed enrichment for schizophrenia in the within-brain analysis, in which cortex was compared to all other brain regions and was moderately significant ($P < 10^{-5}$; **Figure 4a**). In this analysis, sample size was more important, and while there was high variance in z-score among random samples at a given sample size, there was a clear trend that increasing the sample size increases the significance of the enrichment on average (**Supplementary Fig. 11b**). In conclusion, these analyses provide evidence that sample size can be important when the enrichment being identified is near the border of significance, but that our method is well-powered to detect strong signals even with a single sample in the tissue of interest.

Comparison to existing methods: real phenotypes. To our knowledge, SNPsea^{1,2} is the only existing method that takes as input GWAS summary statistics, together with a matrix of gene expression values, and identifies enriched tissues and cell types. SNPsea leverages only genome-wide significant SNPs, rather than all SNPs, a notable difference from our approach. We ran SNPsea on the summary statistics and gene expression data analyzed in our multiple-tissue analysis; results are displayed in **Supplementary Fig. 12 and Supplementary Table 11**. We found that SNPsea identified biologically plausible enrichments at high levels of significance for traits such as LDL for which a large proportion of SNP-heritability lies in genome-wide significant loci, but that it was not well-powered for more polygenic traits; for example, it found zero tissues with FDR < 5% for bipolar disorder, while our approach found many brain regions to be enriched at P-values as low as $2e-12$ (**Supplementary Fig. 1**). The lack of power of SNPsea on more polygenic traits is unsurprising, as SNPsea leverages only genome-wide significant loci.

The DEPICT software³ includes a method for identifying disease-relevant tissues and cell types from GWAS summary statistics and gene expression data. However, this method takes as input only the GWAS summary statistics and not gene expression data; the method is designed to be run only with the Franke lab data set^{3,4}, which is built into the software. Thus, DEPICT could not be used to obtain the results in our brain-specific and immune-specific analyses, for which we analyzed data sets that allowed us to differentiate among tissues and cell types within each of these systems. However, DEPICT does perform a multiple-tissue analysis analogous to the Franke lab data set component of our multiple-tissue analysis, and so we ran DEPICT on the set of summary statistics that we analyzed. Like SNPsea, DEPICT is run on a subset of SNPs, but unlike SNPsea, DEPICT documentation recommends that it be run twice, once on SNPs that pass genome-wide significance at $5e-8$, and once on SNPs that pass a less stringent threshold of $1e-5$; we followed this recommendation, and our results are displayed in **Figures S13 and S14** and **Supplementary Tables 12 and S13**. We determined that DEPICT failed to identify some enrichments identified by our analysis of the Franke lab data set, such as brain enrichment for several brain-related traits (epilepsy, Tourette syndrome, neuroticism, and smoking status), but that it identified a large number of enrichments for other traits and tissues that our approach did not find. In simulations described below, we found that DEPICT sometimes reported significant results in the absence of true enrichment.

Our approach, described in Figure 1, has two main steps: constructing a genome annotation from gene expression data, and testing this annotation for enrichment with GWAS summary statistics using stratified LD score regression. We tested whether the success of our approach depended on using stratified LD score regression in the second step by instead analyzing the specifically expressed gene annotations from the first step using MAGMA⁵, a gene set enrichment method that allows inclusion of a window around each gene and leverages all SNPs in the gene set (**Supplementary Fig. 15, Supplementary Table 14**). MAGMA and LDSC-SEG identified many of the same enrichments, but MAGMA identified several enrichments that LDSC-SEG did not. We hypothesized that this may occur because in this analysis, we did not use the option in MAGMA to incorporate gene-level covariates. In simulations described below, we determined that MAGMA can report significant results in the absence of true enrichment due to uncorrected genomic confounding if no covariates are included to ameliorate potential confounding. We leave an exploration of how best to use covariates in MAGMA to account for potential confounding while preserving power for future work.

For comparison purposes, we report LDSC-SEG results for the multiple tissue analysis as a heatmap in **Supplementary Fig. 2a**, in addition to the scatter plots in **Figure 2** and **Supplementary Fig. 1**.

Comparison to existing methods: simulated phenotypes. We performed simulations using genotypes from Genetic Epidemiology Research on Aging (GERA) data set⁶⁻⁸ with 47,360 individuals and 6,507,309 SNPs with imputation $R^2 > 0.5$. We simulated five genetic architectures, where “null” refers to a heritable trait with no tissue-specific enrichment and “causal” refers to a heritable trait with cortex enrichment:

1. (Polygenic null) All SNPs causal, causal SNP effects are drawn independently from a normal distribution with mean zero and constant variance across the genome, with a total heritability of 0.9.
2. (Sparse null) Same as (1), but each SNP has probability 0.001 of being causal.
3. (Exon-enriched null) A SNP is causal if and only if it is in an exon, causal SNP effects are drawn independently from a normal distribution with mean zero and constant variance for all exonic SNPs, with a total heritability of 0.9.
4. (Polygenic causal) We use the annotation corresponding to cortex genes from the multiple-tissue analysis to simulate a true effect. All SNPs are causal, causal SNP effects are drawn independently from a normal distribution with a constant variance within the cortex annotation and constant variance outside of the cortex annotation so that 50% of the total heritability is assigned to the cortex annotation, 50% of the total heritability is distributed uniformly across the genome, and the total heritability is 0.2. We chose a smaller value of heritability in the causal simulations because we wanted to test power to identify true enrichment rather than control of type I error.
5. (Sparse causal) Same as (4), but each SNP has a probability of 0.001 to be causal.

For each genetic architecture, we simulated phenotypes and summary statistics using PLINK⁹ (see URLs) with 100 replicates for each genetic architecture. We then ran the multiple-tissue analysis as described above for every method on each of the simulated data sets, and for each method and each simulated genetic architecture we performed FDR correction within the set of 100 simulated phenotypes. Results are displayed in **Supplementary Fig. 16** and **Supplementary Table 15**.

Of the five methods tested (LDSC-SEG, SNPsea, DEPICT (1e-5), DEPICT (5e-8), and MAGMA), only LDSC-SEG and SNPsea correctly reported no significant enrichments passing $FDR < 5\%$ for all 3 null simulations (scenarios 1-3). In particular, DEPICT with a threshold of 1e-5 reported significant enrichments at $FDR < 5\%$ for all three null simulations (scenarios 1-3), while DEPICT with a threshold of 5e-8 reported significant enrichments at $FDR < 5\%$ for the sparse null simulation (scenario 2). MAGMA correctly reported no significant enrichment for the null simulations with no enrichment (scenarios 1-2) but reported a large number of significant enrichments at $FDR < 5\%$ for the null simulation with enrichment in exons (scenario 3); we note that we ran MAGMA without taking advantage of the option to incorporate gene-level covariates which would likely ameliorate the false positives.

All five methods reported significant cortex enrichments at $FDR < 5\%$ for the sparse causal simulation (scenario 5), but only MAGMA and LDSC-SEG reported significant cortex enrichments for the polygenic causal simulation (scenario 4). These simulations, together with the analysis of real phenotypes described above, indicate that when MAGMA is run without covariates, only LDSC-SEG and SNPsea control type I error, and that of these two methods, LDSC-SEG is better powered for polygenic traits.

Relationship of power and sample size at very large sample sizes. Power increases only modestly with sample size at very large sample sizes, as the finite size of the genome is a

stricter constraint for highly heritable traits at these sample sizes: for example, LD score regression coefficients of baseline model annotations had s.e. that were only 1.29x lower on average in analyses of the full UK Biobank data set (average $N=438,682$) vs. the interim UK Biobank data set (average $N=140,026$.)

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