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Genome-wide association studies in Africans and African Americans: Expanding the Framework of the Genomics of Human Traits and Disease

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Abstract

Genomic research is one of the tools for elucidating the pathogenesis of diseases of global health relevance, and paving the research dimension to clinical and public health translation. Recent advances in genomic research and technologies have increased our understanding of human diseases, genes associated with these disorders, and the relevant mechanisms. Genome-wide association studies (GWAS) have proliferated since the first studies were published several years ago, and have become an important tool in helping researchers comprehend human variation and the role genetic variants play in disease. However, the need to expand the diversity of populations in GWAS has become increasingly apparent as new knowledge is gained about genetic variation. Inclusion of diverse populations in genomic studies is critical to a more complete understanding of human variation and elucidation of the underpinnings of complex diseases. In this review, we summarize the available data on GWAS in recent-African ancestry populations within the western hemisphere (i.e. African Americans and peoples of the Caribbean) and continental African

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Conflict of Interest Notification

None

Internet Resources

1. http://projectreporter.nih.gov/reporter.cfm
2. http://www.genome.gov/gwastudies/
3. http://www.genome.gov/27529028
4. http://1000genomes.org
5. http://news.sciencemag.org/scienceinsider/2010/06/uk-to-sequence-10000-genomes.html

populations. Furthermore, we highlight ways in which genomic studies in populations of recent African ancestry have led to advances in the areas of malaria, HIV, prostate cancer, and other diseases. Finally, we discuss the advantages of conducting GWAS in recent African ancestry populations in the context of addressing existing and emerging global health conditions.

Keywords

Genomics; African American; Genetic Conditions; African Populations; African Ancestry; health; Genome-wide association studies; global health

Introduction

Since the first GWAS publication a few years ago, there has been a significant increase in studies that use GWAS as a tool to identify genetic variants associated with communicable and non-communicable diseases. GWAS have also been used to identify variants that influence human traits including eye color, hair color, and anthropometric characteristics[1–3]. Genomic variations have been associated with drug resistance and treatment outcome [4]. The number of GWAS and pharmacogenomics studies that have identified single nucleotide changes associated with treatment outcomes is rising[5–7]. In other areas of research, genomic studies have led to a greater comprehension of disease progression and pathogenesis in Crohn's disease and several neurological disorders[8,9]. Increased identification of variants associated with monogenic and polygenic disorders could contribute to more accurate diagnosis, effective clinical management, and specialized treatment improving the health of individuals and populations affected by these disorders[10,11].

An Overview of diversity in GWAS data

Despite the expansion of GWAS tools to identify disease- or trait-related variants in human populations, adequate studies inclusive of diverse populations are lacking. Previous assessments of the representation of non-European populations in GWAS utilizing publically available databases have revealed significant underrepresentation of these populations in published GWAS [12–14]. We queried the Research Portfolio Online Reporting Tools (RePORT) (Internet resource 1) to determine the numbers of NIH funded GWAS focused on or utilizing non-European populations. Our search yielded 2,267 current NIH funded studies matching the search term "genome-wide association studies" as of mid-2014. For a more accurate comparison we used search terms such as African American, Hispanic, or Jewish ancestry also utilized by aforementioned publications. For ongoing studies (e.g. 2011) in RePORT, GWAS accounted for only ~14%, ~3%, and < 1% for African American, Hispanic, or Jewish ancestry populations, respectively. Subsequent analysis of published GWAS from PubMed using the same search terms produced 4,942 publications, of which African Americans accounted for ~3% with Hispanics and Jewish accounting for < 1%, which are essentially in agreement with the previous reports. From the 2011 data, African Americans represented the largest non-European population included in GWAS.

Recently, several GWAS have included African ancestry populations in their discovery (initial stage) or replication datasets. From 2009 to May 2010, twenty-one such studies have been included in the National Human Genome Research Institute (NHGRI) GWAS catalogue[13]. We chose to use the NHGRI-GWAS catalogue for our review on African Americans and African ancestry populations because the catalogue includes literature that meets stringent inclusion criteria (Internet resource 2). Moreover, analysis using the NHGRI GWAS catalogue produced results that reflect paucity of data for the African American population. In this review, we examine and briefly summarize several GWAS in diasporic African populations and continental African populations from publication in the NHGRI GWAS catalogue until mid-2014.

Advantages of conducting GWAS in African Americans and African ancestry populations

Arguments have been made for broader inclusion of populations of African ancestry in GWAS[12–16]. With underrepresentation of African ancestry populations in GWAS one might ask: what is the utility in genetically characterizing populations of African ancestry? The occurrence of some genetic variants shows considerable frequency variation across populations which also includes the frequency of the risk allele, frequency of causal and correlated variants, and prevalence of diseases. Genetic determinants of disease and their effect sizes have also been shown to vary significantly between European and non-European populations such as populations of African ancestry[12]. It has been demonstrated that variants associated with diseases found in European ancestry populations do not always replicate in non-European populations [9,17,18] . GWAS conducted in European populations have frequently failed replication in non-European populations for several reasons including differences in allelic architecture, linkage disequilibrium, and confounding of environmental factors across populations[14]. As the continent where the human species originated, Africa harbors populations with longer histories compared to European populations[19,20]. GWAS provide opportunities for characterization of longer population histories and greater genetic heterogeneity found in African populations, allowing more accurate construction of ancestral haplotypes which cannot occur in non-African populations[21]. If one cannot determine the original haplotype, African populations offer opportunities to determine the evolutionary histories of these variants[22]. For example, the genetic origins of Fragile X syndrome (FXS) via haplotype analysis of the X chromosome have been well characterized in European populations[23]. However, the haplotypic origins of this mutation in African populations are yet unknown even though FXS has been found in an African population[24]. FXS and other Mendelian disorders offer a model to understand the evolutionary history of monogenetic disorders as humans migrated out of Africa. The information could also contribute to greater understanding of recombination and evolution of genes on the X chromosome. Thus, inclusion of populations of African ancestry and other diverse populations in GWAS is critical to understanding human variation in both monogenetic and more complex disorders.

Notable discoveries from GWAS in African American and African Ancestry populations

Non-communicable diseases

GWAS have had considerable influence on the identification of genetic variants associated with non-communicable diseases. We have identified several GWAS on non-communicable diseases and also traits that have been conducted with African ancestry populations. Publications from these studies are listed in Table 1. Asthma is a complex non-communicable disease that significantly affects both the young and old. Approximately 15 million Americans are affected, with ~5,500 deaths attributed to complications [25]. Hospitalizations for asthma are 2–3 times higher for African Americans compared to other ethnic groups [25,26]. GWAS exploring the genetic basis of this multifactorial disease in African ancestry populations have identified several associated genes (Table 1). Susceptibility loci for asthma were first identified in children of European ancestry (from Europe and the US) and then replicated in African American children[27]. Variants in the genes *CRB1* and *PDE4D* were associated with asthma in children of European ancestry[27,28]. For African American populations, association with asthma was found for variation in the gene *DENND1B* but not in *CRB1* or *PDE4D*[27,28]. SNP variants found in intergenic regions near *ADRA1B*, *PRNP*, *GNA13* and *DPP10* have been implicated in asthma and allergic diseases in African American and African Caribbean populations, but have not been replicated in European populations[29]. PDE4D, a regulator of airway smooth muscle contractility has been replicated in several European and Hispanic populations but not in populations of recent African origin[28]. Over 43 genes associated with asthma have been identified [30]. However, few of them have been replicated via subsequent GWAS in other populations [30].

Asthma is a serious chronic disorder characterized by airway inflammation[31]. The inflammatory process in asthma is characterized by significant elevation of white blood cell count (e.g. eosinophils, neutrophils and other white blood cells) [32]. GWAS has provided evidence that variation in white blood cell count (WBC) in African Americans has a genetic component. GWAS has replicated genes on 17q21.1 in two cohorts of African Americans[33,34]. Interestingly, 17q21.1 is also associated with inflammation and with childhood asthma[35]. This provides evidence suggesting that in some disorders the genetics of traits and diseases could be similar, as observed in WBC, asthma and 17.q21.1[33].

Unlike asthma, the primary genetic variant underlying sickle cell disease (SCD) has been identified, but the tools of GWAS are being used to determine the nature of the genetic modifiers associated with phenotypic diversity in SCD. Genes implicated in SCD severity include *BCL11A*, which has been shown to modulate fetal hemoglobin (HbF) levels and has been confirmed in GWAS in African Americans[36]. Sex stratified analysis also indicated *GLP2R* is an important modifier of HbF in males[36]. There has not been an established connection between SCD and asthma. Evidence supports asthma and SCD as distinct co-morbid conditions [37]. However, some argue that the high prevalence of asthma in individuals with SCD suggests that the underlying mechanisms of the two diseases might be similar[38,39]. GWAS of sickle cell anemia in African Americans have produced

associations with *OTUB3* and *KCNK6* [40]. *KCNK6*, a member of the K^+ channel protein family, is expressed in cardiomyocytes and in airway epithelial cells [41],[42]. *KCNK6* also showed differential expression in pulmonary artery endothelial cells when exposed to sickle cell plasma [40]. This suggests an uncharacterized role of *KCNK6* in SCD. For both asthma and SCD, the complexity of the phenotype would suggest that genetic heterogeneity is a major contributor to both diseases, so careful classifications of individuals based on clinical subphenotype or other classification schemes and the use of appropriate genetically matched controls might be worthwhile.

GWAS have identified several loci that are associated with prostate cancer (Table 3). Eeles et al found nine SNPs in seven genomic regions dispersed among five chromosomes in patients with prostate cancer[43]. Some of these variants were replicated in GWAS of African American males. However, the majority of associations were not replicated, which may have been due to the small sample sizes of the two studies[44]. Several of these genes including *TET2, NKX3.1,* and *ITGA6* have been found to have oncogenic properties. *ITGA6* is necessary for tumor formation in breast cancer cells but its expression is down-regulated in cervical cancer [45,46]. Some groups have reported TET2 associated with hematological cancers including myeloid leukemia and thrombocytosis[47,48],[49]. *NKX3.1* encodes an androgen-regulated transcription factor expressed in luminal epithelial cells in the prostate[50]. The function of NKX3.1 is to prevent other genetic insults from initiating tumor growth because over-expression of NKX3.1 *in vitro* inhibits cell proliferation and formation of anchorage-independent cell groups, which has been associated with early stages of prostate tumorigenesis[51]. Additional evidence suggests that the loss of NKX3.1 leads to aberrant regulation of gene clusters, which is a major initiating factor for prostate tumorigenesis[50]. NKX3.1 has an indispensable role in prostate cancer and is regarded as the “gatekeeper” to prevent tumorigenesis[50,52]. Subsequent GWAS using Tobagonian men as the replication sample have not found an association between prostate tumor development and TGFBR3, a tumor suppressor with a significant role in prostate tumor development [53,54]. These data suggest that the mechanism which produces tumorigenesis in prostate cells or other cell types could have different associated genetic variants in some non-European populations.

Recently, a GWAS and a family-based association study were conducted on podoconiosis (geochemical non-filarial elephantiasis of the lower legs) . So far, this study is the only published GWAS on non-communicable diseases among continental African population groups. The findings have shown that variants in *HLA-DRB1*, *HLA-DQB1*, and *HLA-DQA1* genes are associated with risk of susceptibility to podoconiosis [55]. Further evidence for the HLA class II association was found with HLA typing that showed *HLA-DRB1*0701*, HLA-*DQA1*0201*, and *HLA-DQB1*0202* are risk variants. These alleles may have a functional role in presenting antigens (currently unknown) to T cells, and imply that podoconiosis may be a T-cell mediated inflammatory disease[55].

In the past decades, considerable progress towards understanding the neurogenetics of social behavior has used twin studies to establish the heritability of several behavioral phenotypes [56]. These studies have produced substantial amounts of data including the association of oxytocin and vasopressin with several aspects of social behavior and also suggest that

structural variants might predispose families or individuals to such behaviors and neuropsychiatric disorders [56,57],[58]. Many of these studies need replication in non-European populations.

Numerous reports have explored the genetic underpinnings of schizophrenia (Table 1). This psychiatric disorder is a complex disease with heredity often playing a substantial role in predisposition to the disorder [59]. Several genes have been implicated in schizophrenia; however, previous findings have not been replicated, causing some to argue that new approaches and fundamental rethinking of schizophrenia are required [60],[61]. For example *HIST1H2AG*, *HIST1H2AB*, and other genes are implicated in schizophrenia in African Americans and populations of European ancestry without achieving genome-wide significance[62]. Bipolar disorder (BD) is a neuropsychiatric disorder characterized by episodic mania and depression. Similar to schizophrenia, BD has a significant genetic component with heritability ~80% [63]. GWAS of BD in African Americans and European ancestry populations yielded an association with *DPY19L3* which was found to be not significant after correcting for genome-wide multiple testing[64].

Several groups have used GWAS to understand the genetic components of dependent behaviors ranging from alcohol dependence to smoking behavior[65]. In European ancestry populations a variant located in a potential transcription factor binding site upstream of *IL15* is correlated to smoking frequency [65]. Cigarette smoke has been found to have decreased *IL15* expression and diminished activation of downstream signaling molecules [66]. It would be interesting to look at the mRNA/protein levels of these individuals to determine the expression of IL15. This would suggest a mechanism of smoking behavior that could also be associated with interleukins characterized in immunity [67]. If IL15 is truly associated to smoking behavior, therapeutic interventions could be developed based on the characterized function of IL15 in immunity [68]. For other behaviors, including alcohol dependency, GWAS in which African American patients were included have not yielded SNPs with genome-wide significance [69,70]. These studies have found areas in the genome that are correlated with dependence behaviors. For example, a region on Chr 11 is described as a candidate locus for alcohol dependence [69]. For dependency behaviors, replication of previous associations found in African Americans has been difficult.

GWAS exploring cardiovascular diseases have revealed several association signals. GWAS of African American hypertensive patients found associations with genes involved in systolic blood pressure including a $Na/K^+/Ca$ exchanger (*SLC24A4*), one class of calcium channel blockers (*CACNA1H*), *PMS1*, *YWHAZ*, and *IPO7* [71]. With the largest sample size using multiple cohorts of American Americans, Fox et al were not able to replicate initial genetic associations for systolic or diastolic blood pressure[72]. Fox et al suggest that within this large multiple cohort study, several issues (e.g. heterogeneity in blood pressure measurement across centers, amount of individuals on blood pressure lowering medication, antihypertensive medication, median age of cohorts) may have biased the results toward the null hypothesis[72].

GWAS on cardiac left ventricular hypertrophy (LVH) and stroke have showed associations with variants in *RAI14*, and *CD36* for LVH and *NINJ2* and *CD36* for stroke, showing that

CD36 is implicated in both conditions [73,74]. CD36 is a receptor with diverse functions including negative regulation of angiogenesis, internalizing pathogens in immune response, and facilitating lipid transport and muscle lipid utilization[75]. The lipid utilization function of CD36 is also implicated in signaling for systolic blood pressure for hypertension and adipose energy storage in obesity and diabetes [71,75]. CD36 mediated signaling could provide an example of common signaling paradigms in which other effectors could interact between pathways of hypertension, diabetes, stroke and cardiovascular disease. Further characterization in non-European populations of CD36 function in these different conditions is warranted.

In addition to identifying genes associated with non-communicable disorders, GWAS can also be used to identify genotypes associated with various treatment outcomes. In hypertension, variants in lysozyme (*LYZ*), *YEATS4*, and fibroblast growth factor (*FRS2*) are associated with differential responses to antihypertensive drugs (*e.g.*, thiazide diuretics) commonly used to regulate blood pressure[17]. In African Americans, the variant located in YEATS4 was significantly associated with good response to thiazide diuretics [17]. Thiazide diuretics can be used to distinguish good responders (patients that show improvement on diuretics) from non-responders or bad responders (patients with a negative response to diuretic mediations for the treatment of hypertension).

Communicable diseases

One of the major infectious diseases affecting sub-Saharan African populations is malaria. Studies have been conducted to characterize the regions of the *Plasmodium falciparum* genome under positive selection in order to monitor the development of drug resistance in the parasite [18]. Additionally, GWAS have utilized cases in endemic areas to determine loci in the human host that influence disease outcomes [76]. The rationale is that host genetics accounts for ~25% of the risk for life-threatening malaria, or more specifically, the anticipated effects of haemoglobinopathies (*e.g.*, α-thalassaemia) would only explain ~2.5% of the total variation. Thus it is hypothesized that protective genes of haemoglobinopathies result in small population effects suggesting that malaria resistance is under multigenic control with each individual gene having a relatively small impact[77]. Jallow et al identified genetic variants close to *SOC1*, *HBB* and *DDC* as protective against severe malaria in children (Table 2)[76]. SOC1 is a scaffolding protein with multiple functional motifs mediating interactions with other signaling molecules[78]. Similar to other Gab proteins, SOC1 is involved in signaling pathways mediated by receptor and non-receptor protein tyrosine kinases and is important in immunity[79]. Dihydroxyphenylalanine decarboxylase (DDC) converts specific chemical precursors to dopamine and serotonin via decarboxylation which also functions in cellular immunity and resistance to parasitic infections via melanization[80]. The hemoglobin β locus (*HBB*) has been replicated in several studies as a major locus for malaria resistance and is reviewed in other papers[81,82]. The locus has been under positive selection in humans because of its role in malarial resistance[83]. These data suggest that resistance to malaria infection also includes immune response mechanisms, which need further characterization.

GWAS have also been performed to identify genetic variants associated with pulmonary tuberculosis (TB) in West Africans [84]. The nearest genes to the variants identified were *GATA6, CTAGE1, RBBP8* and *CABLES1* along with several unannotated open reading frames [84]. GATA6 is a transcription factor identified as regulating the local epithelial innate immune response, with an essential function maintaining the lung epithelium [85,86]. In addition, other reports indicated that *GATA6* regulates the temporal appearance and number of bronchioalveolar stem cells, making *GATA6* essential for proper lung epithelial regeneration[87]. Human *GATA6* expression has a protective function in lung epithelial cells exposed to *Pseudomonas aeruginosa*[85]. Other genes involved in immunity have also been identified in diseases caused by viruses. For example, *HLA-B* located at chromosome 6p21 has been found to influence HIV viral load in both African Americans and Europeans [88–90]. Pelak et al. found that HLA-B*5703 influences viral load variation in African Americans[89]. HLA-B*5703 has not been found in European populations studied and has an allele frequency of ~5.8% in the Yoruba, indicating that its presence in African Americans is likely due to African ancestry [91]. The closely related allele HLA-B*5701 is also important in HIV-1 control; it has an allele frequency ~6.1% in Europeans but has not been found in the Yoruba [91,92]. Other determinants of HIV infection and viral load could lie within the HLA locus which has also been linked to HIV viral load [88]. In general, these data suggest that the mechanistic control of HIV in different populations (*i.e.*, African Americans and Europeans) is similar [90].

One major influence on treatment outcomes for Hepatitis C viral infections is a variant upstream of interleukin 28 β (*IL28B*), encoding interferon-λ-3[6]. This variant is associated with sustained absence of detectable virus or a sustained virological response (SVR). Using GWAS, Ge et al. observed that almost half of the difference in SVR between populations could be accounted for by the difference in the frequency of the C allele between African Americans and Europeans[6]. In viral infections, the mechanism of clearance seems to suggest that the variants are similar across populations, but it is the frequency of the variants that lead to differences in responses in diverse populations[6]. Additional research is needed to determine common variants that influence viral response.

Lessons from previous genome-wide association studies

Some lessons have emerged from GWAS that can inform other genomics-related studies. The unique lessons acquired from studies of non-European populations such as African Americans, Caribbeans, Hispanic Americans, and Africans are largely due to their increased genetic diversity. First, GWAS in one African population or diasporic African population may not always be replicated in another African or diasporic African population because of population diversity and allele frequency differences. Thorough understanding of population structure between and within these populations is needed when performing GWAS analysis. Currently, reference sequences for the majority of African or diverse populations are not available (with the exception of the limited number of African populations in the HapMap and 1000Genome Project databases). To circumvent this major problem, DNA sequencing is required to characterize population genetic diversity which can be used to generate very robust results[76]. This method overcomes issues of incorrect imputation due to the lack of inappropriate reference populations. Second, the use of genetically matched controls from

reference populations is also critical in GWAS. The introduction of non-genetically matched controls can decrease the statistical power to detect associations in GWAS or may result in spurious association because of population structure. Third, careful ascertainment of phenotype is crucial to prevent residual confounding effects of unmeasured phenotypes[93]. Fourth, generally weaker linkage disequilibrium (LD) pattern in African populations is both an advantage and a disadvantage. Weaker LD allows for improved localization of associations. On the other hand, coverage is lower and tag SNPs are less efficient in African or ancestry populations, making the initial discovery of association signals using the same commercial platforms used in European population GWAS less efficient in these populations. Moreover, improved localization and refinement of association signals have been demonstrated in African Americans and African populations leading to successful discoveries in infectious disease susceptibility[76],[94]. Some initial studies using European populations have failed to replicate findings in African ancestry populations suggesting some phenotypes may show genetic heterogeneity between populations[14]. Finally, many GWAS that involved African ancestry populations do not have adequate sample sizes. It is recommended that investigators should use appropriate sample sizes when performing GWAS in non-European populations; essentially, the samples sizes should be larger when compared to European populations to account for additional genetic diversity within the African ancestry populations.

Limitations of current GWAS are related to both the tools and methods. Currently, many GWAS in African populations are performed using arrays designed for European populations, directly or indirectly capturing ~60% of the genomic variation in any African population, leaving 40% of these variants unassayed [95,96]. These limitations also result in the lack of discovery of variants that could significantly contribute to the phenotype. Several non-profit entities have developed partnerships with for profit corporations to enhance variant coverage and power of genotyping arrays for African ancestry populations. Contemporary efforts to develop an Africa Diaspora Power SNP Chip that aims to contribute to a deeper understanding of genetic variation particularly in admixed African ancestry populations in the Americas is underway. As part of this effort, whole genome sequencing of approximately 700 African ancestry samples via the Consortium on Asthma among African-ancestry Populations in the Americas (CAAPA), has identified about 22 million novel variants, and the design of the array that includes common tag SNPs is anticipated to be valuable particularly for admixed African ancestry populations in the Americas (http://www.cidr.jhmi.edu/supported/20140519_AfricanDiasporaPowerChip2.pdf). However, given the vast genetic diversity of continental African populations that are not adequately represented by admixed Africans in the diaspora [19], sequencing of more divergent and diverse African population groups will uncover novel genetic variation, and will be valuable for developing widely representative sequence reference panels and genotyping arrays.

Finally, methods that capture gene-environment interactions are not well developed, despite the acknowledged complexity of disease. Statistical genetics methods only capture genetic variation but gene by environment interaction in the African and African ancestry context may be more important due to the different environments in which African populations have evolved and live. As GWAS move forward, methods will be needed to detect gene and

environment interactions in disease associations that could be significantly different within and among different African and African ancestry populations.

The future of genomic studies in African and African ancestry populations

Recently, initiatives such as the Human Heredity and Health in Africa Initiative jointly funded by the US National Institutes of Health and the Wellcome Trust in the UK has awarded genomic research funding to Africa-based researchers with an aim to build genomic research capacity locally. H3Africa along with other ongoing projects, such as the African Genome Variation Project (http://www.sanger.ac.uk/research/initiatives/globalhealth/research/africangenome.html), will help to elucidate the genetic landscape of population groups across sub-Saharan Africa and advance future genomic research endeavors in Africa.

Inclusion of African ancestry populations offers substantial advantages to investigators, but many challenges also exist in study design, implementation and data interpretation [97]. While problems in study design can often be localized and efficiently addressed, data interpretation in these populations could be difficult because of several challenges which include: 1) ascertainment of markers, 2) decreased levels of tag-SNP portability and 3) increased genotype imputation error[12]. Available software can be utilized to address many issues that arise from analyzing GWAS data in diverse populations[98]. Several methods have been designed to address unique issues of assessing population stratification of populations with admixed ancestries [99–101]. These new methods improve the ability to correctly account for several confounding factors which, if not properly addressed, could lead to serious errors in modeling data.

The art of conducting genomic studies in populations identified by ancestry is as important and daunting as the science itself. The unique and shared historical, social, cultural, and economic contexts within and between populations must be taken into account throughout the conceptualization and implementation of these studies. A growing body of research is exposing and exploring the range of ethical and policy issues pertaining to informed consent, data and sample sharing, management of results and secondary findings, and other aspects of genomic research in African and African ancestry populations [98,102–109] . In addition, ongoing community and public engagement in these and other populations involved in or affected by genomic research is increasingly highlighted as a means of building relations, facilitating understanding through exchange of information, and enhancing collaboration between researchers and communities [110–114]. As cutting edge genomic research gradually proliferates throughout Africa and the African diaspora, opportunities and challenges related to the identification and resolution of emerging issues will multiply. It is essential that our current training efforts adequately foster development of researchers in these locations who can rigorously examine these issues.

Conclusions

GWAS have uncovered genetic variants associated with susceptibility for several different traits and disease conditions including asthma, cancer, obesity, hypertension, blood pressure,

and malaria in recent African-ancestry populations. GWAS involving non-Europeans such as African American and African ancestry populations have greatly lagged behind the increasing number of GWAS that have been published. Some existing GWAS which use non-European populations at replication omit these populations in the initial discovery phase, resulting in subsequent failure to replicate the associated variant(s). Failure to replicate genetic variants associated with the phenotype of interest in these populations could be erroneously attributed to differences in population structure, allele frequencies and environmental factors suggesting the need to include larger cohorts of non-European populations in both discovery and replication.

Whereas non-communicable diseases impose huge burdens on US populations, infectious diseases have traditionally been more relevant and problematic on the African continent. However, within Africa the increase in a more sedentary lifestyle, in conjunction with high caloric intake is contributing to increases in the prevalence of several categories of non-communicable diseases. Both the relevance of infectious diseases and increasing prevalence of disease due to lifestyle offer unparalleled advantages of African populations in understanding the genetic and environmental underpinnings of diseases in human populations. Another unique advantage of African populations in discerning the evolutionary history of disease variants and haplotypes has not been well exploited and may provide directions in understanding pathways and mechanisms of human diseases[12–14]. Finally, the potential role of genomics research with more diverse non-European populations in understanding health disparities should be emphasized. Several projects are underway to characterize human genetic and phenotypic variation (Internet resources 4, 5). However, without the inclusion of multiple populations of African ancestry, the data generated by these multinational collaborative efforts might have limited benefit to humanity as a whole. Advances in genomics should help ameliorate rather than contribute to health disparities among diverse populations. With the collaborative efforts of global scientists and local communities, and the development of new data analysis capacity, state-of-the-art genomics research is poised to take advantage of humanity's most diverse populations and return the greatest benefit in the improvement of human health.

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Table 1

GWAS on non-communicable diseases and traits in recent African and African ancestry populations

Disease/Trait	Sample size	Replication sample size	Genes	Ref
Addiction	1,393 European ancestry women, 1,131 European ancestry men, 568 African ancestry women, 535 African ancestry men	NR	*NCK2*	[115]
Adiponectin levels	29,347 European ancestry individuals, 4,232 African American ancestry individuals, 1,776 Filipino individuals	NR	*LYPLAL1, IRS1, GNL3, ADIPOQ, TRIB1, GPR109A, CMIP, CDH13, PEPD, Intergenic*	[116]
Alcohol and nictotine co-dependence	818 European ancestry cases, 1,396 European ancestry controls, 449 African American cases, 480 African American controls	NR	*SIX3, RGPD2, SH3BP5, NR2C2, ZFYVE20, HIVEP1, PLEKHG1, PKNOX2, LOC339568, KCND2*	[117]
Alcohol and nictotine co-dependence	818 European ancestry cases, 1,396 European ancestry controls	Up to 907 European ancestry cases, up to 2,830 European ancestry controls, up to 449 African American cases, up to 480 African American controls	*HTR1A, IPO11*	[118]
Alcohol dependence	1,897 cases, 1,932 controls	219 European American families, 35 African American families, 4 other families, 487 German cases, 1,358 German controls	NS	[70]
Alcohol dependence	847 European descent cases, 552 European descent controls, 345 African American cases, 140 African American controls	262 families	NS	[119]
Alcohol dependence	2,357 European American individuals, 812 African American individuals	NR	*C3orf31, ZNF124, USP12*	[120]
Alcohol dependence	1,409 European ancestry cases, 1,518 European ancestry controls, 681 African American cases, 508 African American controls	NR	*SH3BP5, NXPH2, PKNOX2*	[121]
Alzheimer's disease	1,299 European ancestry, African American ancestry and Native American ancestry cases with psychosis, 735 European ancestry, African American ancestry and Native American ancestry cases without psychosis, 5,659 European ancestry, African American ancestry and Native American ancestry controls	NR	*SLC2A9, VSNL1, BIN1, RP11-291J9.2, AC015804.1, RP11-572M11.4, SLC2A9, AP003097.1, RP11-242G20.2, RIMBP2, MPP7*	[122]
Alzheimer's disease	**513 African American ancestry cases, 496 African American ancestry controls**		***PVRL2 ,SLC4A1AP, STK24, POLN, CNTNAP2, Intergenic 1, 2, 3 ,8, 12, 13***	[123]
Alzheimer's disease (late onset)	**1,968 African American cases, 3,928 African American controls**		***ABCA7, HMHA1, GRIN3B, Intergenic***	[124]
Amygdala reactivity	224 individuals	50 European ancestry individuals, 13 African	NS	[125]

Disease/Trait	Sample size	Replication sample size	Genes	Ref
		American individuals, 29 Asian ancestry individuals, 7 other ancestry individuals		
Anthropometric traits	**743 African Americans, 1,188 Nigerians**	**756 African American family members, 982 African Americans, 2,437 Jamaicans**	**NS**	[3]
Antipsychotic drug-induced weight gain	77 European ancestry individuals, 32 African American individuals, 30 individuals	183 European ancestry individuals, 22 African American individuals	*MC4R*	[126]
Aortic root size	**1,086 African American family members**	**NR**	***SIRPA, PDYNKCTD7, RABGEF1, GOT2, LOC401365, LOC493754, CRCP, FHIT, Intergenic 8q23.3***	[127]
Aortic-valve calcification	6,942 European ancestry individuals	745 European ancestry individuals, 2,497 African American individuals, 2,027 Hispanic individuals, 774 Chinese ancestry individuals	*LPA*	[128]
Asthma	422 cases, 1,533 controls	3,750 white cases, 13,365 white controls, 592 white trios, 1,903 black cases, 2,432 black controls, 929 black family members	*PDE4D*	[28]
Asthma	464 African American cases, 471 African American controls, 1,028 African Caribbean family members	994 European descent cases, 1,243 European descent controls; 2,331 African descent cases, 2,874 African descent controls (includes family members)	NS	[29]
Asthma	793 European ancestry child cases, 1,988 European ancestry child controls	917 European ancestry child cases, 1,546 European ancestry child controls, 1,667 African American child cases, 2,045 African American child controls	*DENND1B, CRB1*	[27]
Asthma	2,088 European American cases, 1,612 African American and African Caribbean cases, 1,688 Latino cases	2,727 European American cases, 2,147 African American and African Caribbean cases, 2,299 Latino cases	*GSDMB, IL1RL1, TSLP, IL33, PYHIN1, C11orf71, CRCT1*	[129]
Asthma (childhood onset)	429 European ancestry affected offspring trios	52 African American affected offspring trios, 46 Hispanic affected offspring trios	*IGSF3, HPSE2, PSAP, ATG3, MKLN1, XPR1, ABI3BP, KLHL5, Intergenic*	[130]
Autism	1,385 affected children from 1,369 families	1,086 affected children from 595 families, 1,965 European, African American and other controls	*MACROD2, PPP2R5C*	[131]
Beta-trace protein levels	6,720 European ancestry individuals	1,734 African American individuals	*PTGDS*	[132]
Bilirubin levels	**619 African American individuals**	**NR**	***UGT1A1, AC073072.5, AC068954.1, RP11-58O3.2, ERCC4, RP11-648C16.1, RP5-837I24.4, AC013262.1, KLHL1, RNU7-62P***	[133]
Bipolar disorder	1,001 Caucasian cases, 345 African American cases, 1,033 Caucasian controls, 670 African American controls	1,749 Caucasian family members, 1,263 Caucasian cases, 431 Caucasian controls	*DPY19L3*	[64]

Disease/Trait	Sample size	Replication sample size	Genes	Ref
Blood lipid traits	Up to 100,184 European descent individuals	9,705 South Asians, 15,046 East Asians, 8,061 African Americans, 7,063 Europeans	*CETP*, *SORT1*	[134]
Blood pressure	**7,473 African American individuals**	**11,882 African American individuals**	**NS**	[135]
Blood pressure	28,190 African American individuals, 1,188 Nigerian individuals	69,395 European ancestry individuals, 5,266 African American individuals, 6,497 African ancestry individuals, 19,601 East Asian ancestry individuals	*RSPO3, PLEKHG1, FAM46A, C6orf37, EVX1, HOXA, ULK4, SOX6, CYB5R2, SEC16B, ADCY3, GNPDA2, FTO, GALNT10, KLHL32, MIR148A, NFE2L3, MC4R, TMEM18*	[136]
Body mass index	**1,715 African American individuals**	**3,274 African American individuals**	***PP13439, TMEM212, MFAP3, GALNT10***	[137]
Body mass index (interaction)	8,203 African American women, 3,484 Hispanic ancestry women	NR	*LOC645687, PELI2K, LOC347097, PIP5K1B, CNTNAP2, LOC100128373, DIO3OS, LOC645687, PELI2,RPL15P2, DICER1, SLC39A11, LRP8, SGK1,LOC442261, PA2G4P2, SPTLC3, DCC, LOC100130692, CNTNAP, LOC100130240, KCNE2*	[138]
Bone mineral density	1,524 European descent sisters	669 related African American women	NS	[53]
Bone mineral density	1,000 white individuals	4,925 white individuals, 350 Chinese hip fracture cases, 350 Chinese controls, 2,955 Chinese individuals, 908 West African men	*ADAMTS18, TGFBR3*	[139]
Brain structure	2,020 European ancestry neuropsychiatric disorder cases, 5,775 European ancestry controls	599 European ancestry neuropsychiatric disorder cases, 11,915 European ancestry control, 143 European ancestry and African American neuropsychiatric disorder cases, 94 European ancestry and African American controls, 605 Hispanic ancestry controls	*HRK, FBXW8, HMGA2*	[140]
Bronchopulmonary dysplasia	21 Caucasian neonate cases, 75 Caucasian neonate controls, 21 African neonate cases, 86 African neonate controls	30 Caucasian neonate cases, 112 Caucasian neonate controls, 15 African neonate cases, 32 African neonate controls, 4 infant cases with one Caucasian parent and one black African parent, 19 infant controls with one Caucasian parent and one black African parent, 55 Finnish neonate cases, 158 Finnish neonate controls	NS	[141]
Bronchopulmonary dysplasia	117 African American newborn cases, 108 African American newborn controls, 448 Hispanic newborn cases, 460 Hispanic newborn controls, 74 Asian or Pacific Islander newborn cases, 93 Asian or Pacific Islander newborn control, 174 European ancestry newborn control	371 newborn cases, 424 newborn controls	*CARD17,CASP1P1, CHST9, COX19, CYP2W1, CTNNA3, FNIT, GRHL2, HIVEP3, ISCA1L, HTR1A, KLF12, LOC100129825, LOC100289139, LOC729992, LOC100288243, PAMR1, PLXDC2, PRR16, FTMT, STXBP5, YAP1P1, TNK2, CEP170, NDST4, TRAM1L1, SPOCK1, KLHL3, MAGI2, CSMD3, TRPS1, ZNF770, LOC441722, RASGRG1,*	[142]

Disease/Trait	Sample size	Replication sample size	Genes	Ref
			LOC729911, DSC3, DSC2, LOC646864, ZNF728	
Capecitabine sensitivity	Up to 84 East Asian ancestry lymphoblastoid cell lines, up to 164 European ancestry lymphoblastoid cell lines, up to 173 African ancestry lymphoblastoid cell lines, up to 82 African American lymphoblastoid cell lines	NR	*PDE4DIP, SLC44A5, SMARCAD1, ADCY2, MTRR, LOC643281, SH2D4B, SOX, Intergenic*	[143]
Cardiac structure and function	6,765 African American individuals	2,468 African American individuals, 12,612 European ancestry individuals	NS	[144]
Cardiac Tropo[145]nin-T levels	9,491 European ancestry individuals, up to 2,053 African American individuals	NR	*NCOA2, TRAM1, TNT2, LRRIQ3, NRG1, OR2B7P, LOC129656, CDH7, BCL2, STARD7, HNT, ATP6V1C2, FBLIM1, CASR, CXCL13, TNFAIP3, DLGAP1, GPR26, C8orf80*	
Chemotherapeutic susceptibility	**83 African American lymphoblastoid cell lines, 176 African lymphoblastoid cell lines**	**NR**	**NS**	[146]
Cholelithiasis-related traits in sickle cell anemia	**905 African American cases**	**2,152 African American cases**	**UGT1A1, UGT1A10**	[147]
Cocaine dependence	1,809 European ancestry cases, 570 European ancestry controls, 2,482 African American cases, 836 African American controls	4,498 European ancestry individuals, 2,114 African American individuals	*STEAP3, RANP6, RIMS2, OR3A2, OR3A1, FAM53B, NCOR2, CDK1, RANP6, OR3A2, OR3A1, FAM53B, CDK1, Intergenic*	[148]
Coronary artery calcification	5,823 African American individuals	9,992 European ancestry individuals	*AGBL1, ALDH8A1, ATXN3, CACNA1E, CACNA2D3, C10orf76, C2orf85, C6orf10, CAPS2, CCDC157, CDH9, EEF1E1, EMP1, ERBB4, FBXO15, FBXO3, FLJ43860, GRIN3A, IFT88, IPMK, KCNK13, KCNQ3, KLF6, LARGE, LOC100652953, LOC646730, LRP6, LYSMD4, MCART2, MSI2, MUTED, NRG1, PLD5, PRICKLE2, PRKCA, RGS2, RIT2, SEMA6D, SLC1A1, SORCS2, SOX9, SPATA7, STEAP1, SUCLG1, WDR33, ZFPM2, ZNF383*	[149]
Coronary heart disease	**8,090 African American individuals**	**8,849 African American or African-Caribbean individuals**	***CELSR2, LCAT, SMARCA4, PPP1R3B, SLC12A9, KLHL29, APOA5, ABCA1, CETP, RNF130, DNM2, TCF7L2, GCOM1, SLC30A1, PDGFD, LAMC2, TNIK, ZFHX3, DOCK6, OPRM1, DTNB, CSMD1, EDC4, PLEKHO2, IGSF5 and several Intergenic regions***	[150]
Coronary heart disease	**362 African American cases, 2,543 African American controls**	**862 African American cases, 7,293 African American controls**	**NS**	[151]
C-reactive protein	**837 African American individuals**	**486 West African ancestry individuals**	***CRPP1, CRP***	[152]

Disease/Trait	Sample size	Replication sample size	Genes	Ref
C-reactive protein	8,280 African American women, 3,548 Hispanic/Latin American ancestry women	3,787 African American women, 3,548 Hispanic/ Latin American ancestry women, 5,656 European ancestry individuals	*TREM2, CRP, APCS, DARC, FCER1A, DUSP23, OR10J1, OR10J5, OR10J3, OLFML2B, IFI16, FCRL6, IL1F10, IL1RN, HNF1A, TOMM40, LEPR, CRP, HNF1A, OASL, C12orf43, CRP, APCS, DARC, FCER1A, DUSP23, OR10J1, OR10J5, OR10J3, OLFML2B, IFI16, FCRL6, HNF4A*	[153]
Diabetic nephropathy	**965 African American cases, 1,029 African American controls**	**709 African American cases, 690 African American controls**	***SASH1, RPS12, MSRB3, HMGA2, AUH, LIMK2***	[154]
Dialysis-related mortality	**610 African American type 2 diabetics**	**NR**	***KLHL29, LOC339568, DHX35, PDZRN3, CALM2, COX18, ADAMTS3, EPHA7, GAS2, SLC24A4, CPSF2, NCRNA00113, ADAMTS5, TET3, DGUOK, PTPRM, GPATCH2, ESRRG, NCRNA00113, ADAMTS5, LOC729980, IL6, RAPGEF5, ABCA4, PCSK2, SVIP, HAS2, NRG1, GCNT1, RPSAP9, RIN3, SLC24A4, PTPRM, IRX5, IRX3, Intergenic chr 2, SH3BP4***	[155]
End-stage renal disease	**952 African American cases, 988 African American controls**	**640 African American cases, 683 African American controls**	**NS**	[156]
End-stage renal disease (non-diabetic)	**464 African American cases, 478 African American controls**	**336 African American cases, 363 African American controls**	***MYH9***	[157]
Erectile dysfunction and prostate cancer treatment	**27 African American cases, 52 African American controls**	**NR**	***FSHR, TTC7A, PTGFRN, KIAA1166, CMKLR1, TSN, CHMP5, IGSF21, TMEM178, LRP1B, DDX53, FAM82A1, ZNF608, C9orf3, ELA2A, GLI2, CNNM3, HEPH, APOB, MAGEB18, GGTLC1, WDR42B, SYTL5***	[158]
Estradiol plasma levels (breast cancer)	700 European ancestry cases, 50 African ancestry cases, 17 Asian ancestry cases, 5 American Indian cases	NR	*TSPYL5*	[159]
Event-related brain oscillations	431 European American cases, 340 European American controls, 209 African American cases, 84 African American controls	683 individuals from affected multiplex families, 412 affected individuals	*ARID5A, GNAS1, ANXA13*	[160]
Fasting plasma glucose	2,349 European ancestry individuals, 664 Chinese ancestry individuals, 1,366 African American individuals, 1,171 Hispanic ancestry individuals	NR	*MTNR1B, GCKR, GAPC2*	[161]
Fasting plasma glucose	2,029 African American individuals, 7,428 European ancestry individuals	1,571 African American individuals, 3,825 European ancestry individuals	*FOXA2*	[162]
Fat body mass	6,433 European ancestry individuals, 709 African American individuals, 408 Hispanic individuals, 1,622 Han Chinese ancestry individuals	4,967 European ancestry individuals, 2,740 Han Chinese ancestry individuals	*MC4R, CTSS*	[163]

Disease/Trait	Sample size	Replication sample size	Genes	Ref
F-cell distribution	440 African ancestry individuals	NR	*BCL11A, B3GAT2, TSSK1, MOSC1, PHEX, PRDM5, ATP6V0A4, MAD2L1, UBXD4, YTHDC2*	[36]
Fetal hemoglobin levels	848 Black cases	305 Black cases, 406 Chinese ancestry cases, 113 Thai cases,	*BCL11A, OR51B5,OR51B6*	[164]
Fibrinogen	91,323 European ancestry individuals	8,423 African American individuals, 1,447 Hispanic individuals	*ACTN1, C5orf56, IRF1, CD300LF, CHD9, CPS1, DIP2B, FARP2, FGB, HGFAC, LRPAP1, IL1F10, IL1RN, IL1R1, IL1R2, IL6R, JMJD1C, LEPR, MS4A6A, MSL2, PCCB, NLRP3, PLEC1, PSMG1, SHANK3, ARSA, CPT1B, SNx13, PRPS1L1, SPPL2A, TOMM7, IL6, C5orf56, IRF1, CD36, PPP1R3B, LPL, CETP, LOC55908, APOA, APOC, CTEP, Intergenic*	[165]
Glomerulosclerosis	56 African American cases, 61 European descent cases	1,759 African American controls, 1,531 European-American controls	*APOL1, MYH9*	[166]
Heart failure	20,926 European ancestry participants, 2,895 African ancestry participants	NR	*USP3, LRIG3, TBC1D4, SH3GL2, PRICKLE1, BTG1, RPUSD4, TMTC1, LOC339760,SNX16, MOBKL2B, GNA15, BCHE, LOC100129376, EVX1, CH25H*	[167]
Heart rate	455 African American individuals	NR	SERPINI1, TMEM132D, DAB2IP, DAB2IP	[168]
Height	**20,427 African ancestry individuals**	**Up to 16,436 African American individuals**	***LCORL, ARSE, PPARD, DYM, ZBTB38, MAP3K3, HMGA2, ACAN, ANTXR1, HMGA1, CCDC88A, TTLL5, SYN3, DCLK1, ADAMTSL3, SULF1, ZFAT1, TNS1, LYRM4, FBN2, ATF7, ENPP2, C19orf35, Intergenic chr 2, 4, 6, 15, 17***	[169]
Height	**8,149 African American ancestry women**	**Up to 20,809 African American ancestry and African ancestry individuals**	***LCORL, ARSE, HMGA2, MAP3K3, DYM, SERPINH1, TMEM100, PCTP, PRKCA***	[170]
Hematology traits	7,943 African American children, 6,234 European ancestry children	NR	*HBE1, HBB, HBD, HBBP1, HBG1, Alpha-globin cluster, MPP1, DARC, ZBTB12, CFB, STK19, TMPRSS6, HFE, HBS1L, MYB, MUC21, HCG22, C6orf15, CDSN, PSORS1C1, PSORS1C2, CCHCR1, Intergenic*	[171]
Heroin addiction	200 Caucasian and 125 African American severe former addicts, 150 Caucasians and 100 African American controls	NR	NS	[172]
Hippocampal atrophy	1149 European ancestry Alzheimer disease cases, 336 European ancestry individuals with mild cognitive impairment, 188 European ancestry controls	419 African American Alzheimer disease cases	*APOE, TTC27, METTL8, CHD6, SLC1A7, F5, SELP, GCFC2, TLE1, LHFP, COL18A1, APOE, Intergenic*	[173]

Disease/Trait	Sample size	Replication sample size	Genes	Ref
Hypertension	**509 African American cases, 508 African American controls**	**366 West African cases, 614 West African controls**	***ALDH1A2, ADH7***	[71]
IgE levels	2,469 African American/ Afro-Caribbean individuals, 259 Latino individuals, 1,564 European ancestry individuals	2,961 African American/ Afro-Caribbean individuals, 1,477 Latino individuals, 649 European ancestry individuals, 680 Hutterites	*SUCLG2, HLA-DQB1, WWP2, HLA-DQA2*	[174]
Insulin-related traits	927 non-diabetic African Americans	570 non-diabetic West Africans	*SLC10A6, SC4MOL, PTTG1, TCERG1L*	[175]
LDL cholesterol	**1,249 African American individuals**	**NR**	***APOE***	[176]
LDL cholesterol	7,861 African American individuals, 3,425 Hispanic individuals	7,138 African American individuals	*PCSK9, APOB, ABCG8, LDLR, APOE*	[177]
LDL cholesterol	94,595 European ancestry individuals	up to 4,420 African ancestry individuals	*LDLR*	[178]
Left ventricular mass	101 Caucasian cases, 101 Caucasian controls	704 Caucasian siblings, 1,467 African American siblings	*RAI14, CD36*	[73]
Left ventricular mass	1,264 African Americans	989 African Americans, 1,316 Whites	*NCAM1*	[179]
Lipid levels in hepatitis C treatment	1,017 European ancestry cases, 207 African American ancestry cases, 95 Hispanic cases	NR	*IL28B*	[180]
Lipid traits	282 European ancestry children, 66 African American children, 63 Hispanic children	1,627 European ancestry children, 1,478 Caucasian children, 1,443 Mexican American children	NS	[181]
Lipoprotein diameter	817 European ancestry individuals	2,430 European ancestry individuals, 1,594 African American individuals, 1,422 Hispanic individuals, 758 Chinese ancestry individuals	NS	[182]
Lung function (forced expiratory flow between 25% and 75% of forced vital capacity)	1,015 European ancestry individuals, 541 African American individuals	NR	*INTS12, GSTCD, MYBPC1, CDH2, CTNNA3,*	[183]
Major depressive disorder	353 European descent cases, 366 European descent controls	1,512 German cases, 2,415 German controls, 1,160 Dutch individuals, 991 African Americans, 1,636 European ancestry cases, 7,246 European ancestry controls	*SLC6A15*	[184]
Male fertility	269 Hutterite men	72 Hispanic ancestry men, 32 African American men, 11 Middle Eastern ancestry men, 5 European ancestry men, 3 Asian ancestry men	NS	[185]
Maximal oxygen uptake response	473 European ancestry individuals from 99 families	295 individuals, 247 black individuals from 105 families or sibships	NS	[186]
Mean corpuscular hemoglobin	7,943 African American children, 6,234 European ancestry children	NR	*Alpha-globin cluster, TMPRSS6, HBS1L, MYB, TMPRSS6, HFE, CITED2, RCL1, HBE1, HBB, HBD, HBBP1, HBG1, ATP2B4, MPP1, USP49, MED20, BYSL, CCND3*	[171]

Disease/Trait	Sample size	Replication sample size	Genes	Ref
Mean platelet volume	16,388 African American individuals	NR	*LRRC16A, BAK1, HBS1L, MYB, CD36, PIK3CGM, JMJD1C, BAD, ACAD10, TPM4, SLMO2, TUBB1, PIK3CG, TAOK1*	[187]
Melanoma	1,804 European ancestry cases, 1,026 European ancestry controls	6,483 European and Middle East/North African ancestry cases, 23,324 European and Middle East/North African ancestry controls	*ANXA9*	[188]
Metabolite levels	1,260 African American individuals	NA	*SLCO5A1, LOC100131022, LOC138412, KC6, GTFE2, DAB2IP, CCL28, CADPS, PRKCE, CAT8, C20orf82, NRG1, MS4A13, CDKN3, LOC399774, LRRIQ3, MGMT, CNTN1, ZNF213, LOC149844, C18orf34, ALMS1, LPHN2, LOC729635, COMMD10,KIF13B, CDH4, LOC100129158, DGKH*	[189]
Mitral annular calcification	3,795 European ancestry individuals	745 European ancestry individuals, 2,497 African American individuals, 2,027 Hispanic individuals, 774 Chinese ancestry individuals	NS	[128]
Monocyte count	9,849 European ancestry individuals, 894 African ancestry individuals, 271 other ancestry individuals	NR	*ITGA4, RPN1, CCBP2, PTGR1, IRF8*	[190]
Mortality among heart failure patients	2,526 European ancestry individuals, 466 African ancestry individuals	NR	*CMTM7, OTUD7A, LPHN1, LOC338797, ADAMTS12, LOC400804, GPM6A, KCNMA1, PARVA, KCNK13, IFRD1*	[191]
Naphthyl-keratin adduct levels	100 European ancestry, Hispanic, Asian and African American individuals	NR	*NS*	[192]
Narcolepsy	807 Caucasian cases, 1,074 Caucasian controls	363 Caucasian cases, 355 Caucasian controls, 561 Asian cases, 605 Asian controls, 133 African American cases, 144 African American controls	*TRA-alpha, TRAJ10*	[193]
Nicotine dependence	2,267 European ancestry individuals, 99 Hispanic ancestry individuals, 999 African American individuals	835 individuals	*CHRNB3*	[194]
Obsessive-compulsive disorder	1,279 European ancestry cases, 5,139 European ancestry controls, 93 South African Afrikaner cases, 158 South African Afrikaner controls, 93 Ashkenazi Jewish cases, 260 Ashkenazi Jewish controls, 299 European ancestry trios, 101 trios	NR	*FAIM2, AQP2, GRIK2, HACE1, DACH1, MZT1*	[195]
Opioid sensitivity	1,383 European ancestry cases, 996 European ancestry controls, 683 African American cases, 2,635 African American controls	2,116 European ancestry individuals, 4,496 African American individuals	*APBB2, KCNC1, KCNG2*	[196]

Disease/Trait	Sample size	Replication sample size	Genes	Ref
Orofacial clefts (interaction)	272 European ancestry case-parent trios, 259 Asian ancestry case-parent trios, 19 African ancestry or other ancestry case-parent trios	NR	*C6orf105, SMC2*	[197]
Ovarian reserve	232 European ancestry women, 200 African American ancestry women	NR	*MYADML, JARID2, GRIN2B, NPR3, ITIH2, TPRXL, TMEM86A*	[198]
Pemphigus vulgaris	100 Jewish ancestry cases, 397 Jewish ancestry controls	59 Jewish ancestry cases, 285 Jewish ancestry controls, 124 European ancestry cases, 275 European anestry controls, 126 North African ancestry controls, 246 North African ancestry controls	NS	[199]
Pericardial fat	5,487 European ancestry individuals	1,442 African ancestry individuals, 1,399 Hispanic ancestry individuals, 761 Chinese ancestry individuals	*TRIB2*	[200]
Periodontitis	4,504 European ancestry individuals	656 European ancestry and African American individuals	*NPY, NCR2, EMR1, VAV1*	[201]
Platelet aggregation	Up to 3,991 European ancestry individuals	Up to 840 African American individuals	*PEAR1, GP6, ADRA2A, JMJD1C, SHH, PTPRD, NEURL, MST151, MRVI1, HSD17B6, PRNP, TRIM27, SGCZ, KCNQ1*	[202]
Platelet counts	**115 black HIV-negative individuals**	**NR**	***AC130454.2, AC130454.1, ABCB9AC008620.2, PITPNM2, CHRM3, NFYC, EEPD1, AC105105.1, AC007425.1, DPYD***	[203]
Platelet counts	7,943 African American children, 6,234 European ancestry children	NR	*ARHGEF3, BAK1, ARHGEF3, COPZ1, JMJD1C, RCL1*	[171]
Podoconiosis	**194 cases and 203 controls from Africa**	**202 family trios (two parents and one affected child) for family-based association testing; 94 cases and 94 controls for HLA-typing**	***HLA-DQA1***	[55]
Post-traumatic stress disorder	295 European ancestry cases, 196 European ancestry controls	143 African American cases, 462 African American controls	NS	[204]
Post-traumatic stress disorder	300 European ancestry cases, up to 1,538 European ancestry controls, 444 African American cases, up to 2,936 African American controls	207 European ancestry cases, up to 1,692 European ancestry controls, 89 African American cases, up to 655 African American controls	*TLL1*	[205]
Post-traumatic stress disorder	81 African American female cases, 261 African American female controls, 10 European ancestry female cases, 35 European ancestry female controls, 3 female cases, 22 female controls	578 European ancestry female cases, 1,963 European ancestry female controls	NS	[206]
PR interval	**6,247 African American individuals**	**2,022 African American individuals**	***SCN5A***	[207]
PR interval	**13,415 African American individuals**	**NR**	***MEIS1, ITGA9, SCN5A, ARHGAP24, CAV1, TBX5, SCN5A, SCN10A, SICAL2,***	[208]

Disease/Trait	Sample size	Replication sample size	Genes	Ref
			MYO3A, VWC2L, BCL6, MAGI1, MFSD2, Intergenic	
QT interval	**13,105 African American individuals**	**NR**	***NOS1AP, PLN, KCNH2, ATP1B1, LITAF, KCNQ1, DPP6, FGFBP2, LDB2, Intergenic***	[209]
Radiation response	Human lymphoblastoid cell lines from 93 African Americans, 89 Caucasian-Americans, and 95 Han Chinese Americans	NR	*TINAG, PLEKHF2, WWOX, WDR64, KIAA0319, FSHR, KDM4C, ADARB2, ULBP1, PLEKHF2, LOC100132612, DLX6AS*	[210]
Red blood cell traits	Up to 16,485 African American individuals	9,692 African American individuals, 21,020 European ancestry individuals, 14,088 Japanese ancestry individuals	*G6PD, TKTL1, MECP2, MPP1, PRKCE, ITFG3, LUCL7, NPRL3, POLR3K, RPL2B, MPG, CD164, FAM3A, F8, MPP1, CTAG2, HFE, NME4, DECR, RHOT2, LMF1,WDR90*	[211]
Response to acetaminophen (hepatotoxicity)	60 Caucasian American lymphoblastoid cell lines, 56 African- American lymphoblastoid cell lines, 60 Han Chinese-American lymphoblastoid cell lines	NR	*C3orf38, LMX1A, LOC100129661,KIAA1712, ETNK2*	[212]
Response to amphetamines	1 American Indian ancestry individual, 18 African American/Afro-Caribbean ancestry individuals, 10 East Asian and South Asian ancestry individuals, 325 European ancestry individuals, 17 Latin American ancestry individuals, 6 other ancestry individuals, 4	NR	*ABL1, ADRA1A, ANKRD31, CA8, CCDC146, CDH13, CNTLN, CNTNAP4, CSMD2, FAM190A, FARP1, FBX17, FHIT, IGSF11, KCTD8, KLHL1, MAP2K4, MFSD9, NEDD4L, NELL1, ODZ3, PAX7, PLBD1, PTPRE, PRPRN2, SMGS1, SRD5A1, THADA, TMEM106B, TRAPPC9, WWOX, Integenic*	[213]
Response to angiotensin II receptor blocker therapy	198 European ancestry hypertensive individuals, 193 African American hypertensive individuals	NR	*IQSEC3, C10orf110, SYNRG, FUT4, EYA4, SLC9A9, PRRX1, JAKMIP1, TMC7, APBB1IP, CTB-212O16.1, DNAJC21, WBSCR17, MIR1261, EMCN, EIF4BP8, AC112482.3, TMEM212, AC010148.1, C6orf214, GPR83, AC007246.3, RGMA, EIF4BP8*	[214]
Response to antiplatelet therapy	565 Amish individuals	710 European ancestry individuals, 237 African American/Afro-Caribbean individuals, 276 Hispanic individuals, 4 individuals	NS	[215]
Response to antipsychotic treatment	738 European American, African American, and other schizophrenia cases	NR	*MEIS2, GPR98, PRKAR2B, SOX5, FHOD3, CLMN, RNF144A, ASTN2, PPARD, ATF7IP2, CDH13, LOC729993,KIRREL3 and several intergenic regions*	[216]
Response to antipsychotic treatment	Up to 421 European ancestry Schizophrenia cases, up to 214 African American individuals, up to 103 individuals	NR	*ATP1A2, TNFRSF11A, PPA2, SPOPL, PDE4D, TJP1, Intergenic*	[217]
Response to citalopram treatment	1,392 European ancestry depression cases, 264 African American depression cases, 106 depression cases	NR	*EMID2. LAMA1, EGFLAM, AOX2P, FNIT, RPT2, Intergenic*	[218]

Disease/Trait	Sample size	Replication sample size	Genes	Ref
Response to clopidogrel therapy	429 Amish individuals	140 white, 83 African American, and 4 unspecified individuals	*CYP2C18, CYP2C19, CYP2C9, CYP2C8*	[219]
Response to dabigatran etexilate treatment	1,490 European ancestry atrial fibrillation patients at risk of stroke	204 European ancestry atrial fibrillation patients at risk of stroke, 66 Latin American ancestry atrial fibrillation patients at risk of stroke, 1 Arab ancestry atrial fibrillation patient at risk of stroke, 5 Black African atrial fibrillation patients at	*CES1*	[220]
Response to diuretic therapy	194 blacks, 195 whites	NR	*LYZ, YEATS4, FRS2*	[17]
Response to hepatitis C treatment	871 Caucasian, 191 African American, and 75 Hispanic participants	NR	*IL28B, AKD2, Intergenic 4q34.3*	[6]
Response to platinum-based chemotherapy in small cell and non-small cell lung cancers	283 African American, Caucasian American and Han Chinese lymphoblastoid cell lines	222 European ancestry small cell lung cancer cases, 961 European ancestry non-small cell lung cancer cases	NS	[221]
Response to statin therapy	667 European ancestry individuals with an event, 2,246 European ancestry individuals without an event, 18 African American individuals with an event, 60 African American individuals without an event, 20 Hispanic ancestry individuals with an event, 65 His	590 individuals with an event, 4,654 individuals without an event	*DNAJC5B, TRIM55, CRH*	[222]
Resting heart rate	**13,372 African American individuals**	**NR**	***GJA1, HMGB3P18, MYH6***	[223]
Schizophrenia	2,681 European ancestry cases, 2,653 European ancestry controls, 1,286 African American cases, 973 African American controls	5,327 European ancestry cases, 16,424 European ancestry controls	*SLC17A1, SLC17A3, BTN3A2, BTN2A2, BTN3A1, HIST1H2AG, HIST1H2BJ, PRSS16, POM121L2, ZNF184,HLA-DQA1*	[62]
Schizophrenia	1,658 European ancestry cases, 1,655 European ancestry controls	5,203 European ancestry cases, 5,277 European ancestry controls, 1,875 Irish individuals, 1,142 African American cases, 985 African American controls	NS	[224]
Schizophrenia	11,185 European ancestry cases, 10,768 European ancestry controls	1,262 African American ancestry individuals, 2,740 European ancestry individuals, 2,296 Asian ancestry individuals	*GRIK3, NOTCH4, AS3MT, CNNM2, NT5C2, BRD1, SEC16B, FBXO11, ARHGAP31, POM121L2, NOTCH4, NKAIN2, TCF4, CLC, LGALS17A, FEZ1, PRRC2A, BAG6*	[225]
Serologic markers in systemic lupus erythematosus	20 African American cases, 36 European American cases, 32 Hispanic American cases, 16 Asian American cases, selected for extremes of serum IFN-alpha activity	280 African American cases, 173 European American cases, 85 Hispanic American cases	NS	[226]
Serum urate	**8,651 African American individuals**	**1,996 African American individuals**	***MAP4K2, SLC22A12, MEN1, SF1 ,PYGM, RASGRP2, CDC42BPG, NRXN2 Intergenic chr 6 and 11***	[227]

Disease/Trait	Sample size	Replication sample size	Genes	Ref
Serum uric acid	**1,017 African American individuals**	**NR**	***SLC2A9, AL162718.1, ARID1B, MYO18B, AC007953.1, AC106810.1, RP11, 523018.1, WDR1***	[94]
Sickle cell anemia (haemolysis)	**1,117 individuals**	**958 African, West African, Afro-Caribbean, NR individuals**	***NPRL3, OR51L1, BCL11A, OR51I2***	[228]
Sickle cell anemia (severity)	**177 African American severe patients, 1,088 African American mild patients**	**68 severe patients, 95 mild patients**	**NS**	[40]
Smoking behavior	417 Caucasian males, 423 Caucasian females	412 African American males, 839 African American females, 3,491 Caucasian males, 4,132 Caucasian females	NS	[65]
Smoking behavior	8,842 Korean smokers	1,366 African American smokers and family members, 671 European ancestry smokers and family members	*C7orf66, LOC154907, PNPLA8, THAP5, DNAJB9, intergenic*	[229]
Smoking behavior	**Up to 32,389 African American individuals**	**NR**	***CHRNA5, C1orf100, LOC503519, CHRNA5, SPOCK2***	[230]
Stroke	19,602 Caucasian individuals	3,004 African American individuals, 652 Caucasian cases, 3,613 Caucasian controls	*NINJ 2*	[74]
Stroke	466 European ancestry cases, 377 African American cases, 46 Chinese, Japanese, Asian and other unspecified cases, 523 European ancestry controls, 357 African American controls, 47 Chinese, Japanese, Asian and other unspecified controls	1,586 European ancestry cases, 2,690 European ancestry controls	NS	[231]
Subclinical brain infarct	9,401 white individuals	1,822 white individuals, 644 black individuals	NS	[232]
Substance dependence	2,524 individuals of European ancestry, 1,103 individuals of African ancestry	NR	*PKNOX2*	[233]
Systolic blood pressure in sickle cell anemia	**1617 African American cases**	**NR**	***NCK2, C2orf40, ACTR3, DPP10, ABCB11, THRB, ODZ3, PLEKHG1, CSMD1, KIAA0020, RFX3, DRD2, MIR4301, CLEC12B***	
Tardive dyskinesia	88 white ancestry cases, 40 African ancestry cases, 3 other ancestry cases, 129 white ancestry controls, 62 African ancestry controls, 5 other ancestry controls	52 Ashkenazi ancestry TD individuals, 44 non-Ashkenazi ancestry individuals, 41 Ashkenazi ancestry non-TD individuals, 33 non-Ashkenazi ancestry non-TD individuals	NS	[234]
Telomere length	3,417 European ancestry individuals	1,893 African American and white individuals, 2,876 British women	*OBFC1, ZNF676, CXCR4, SLC44A4*	[235]
Thiazide-induced adverse metabolic effects in hypertensive patients	425 European ancestry cases, 342 African American cases	NR	*SLC39A11, MYO10, PHF17, NMUR1, HTR2B, PPARGC1A, GRIN3A, IDDM8, LOX, MGAT1, ADAM12, MEF2C, GCLM, PHF17, PHLDB1,*	[236]

Disease/Trait	Sample size	Replication sample size	Genes	Ref
			CYP7B1, COX4I1, BCKDHB, JAZF1, CD44, PCDH15, CDC14C, IGF1, FBXO8, NIPAL2, PPP1R12A, WDR37, MFSD9, SCL9A2, BCAT1, CA10, ZNF626, PMFBMP1, CYP19A1, NELL-1, GOLIM4, FAM38B, GDF3, AGBL1, ASAH2, ZNF238, ERLIN1, DAB2IP, TNRC6C, ANGPTL6, UBL5, CHRM3, GRIN2A, EYA, SLC35F1, ZDHHC20, IQGAP2, c14ORF143, ARRB1, CT62, STOX2, NUDT12, OLIG3, Intergenic	
Triglycerides	7,601 African American individuals, 3,335 Hispanic individuals	7,138 African American individuals	*GCKR, LPL, APOA, APOC, APOC1,*	[177]
Type 2 diabetes	2,413 European ancestry cases, 810 African American cases, 2,392 European ancestry controls, 873 African American controls	NR	*TCF7L2*	[237]
Type 2 diabetes	**965 African American ancestry cases, 1,029 African American ancestry controls**	**2,167 African American ancestry cases, 2,288 African American ancestry controls**	***RBM43, RND3, TMEM45B, BARX2, GALNTL4, LOC729013SLC44A3, F3***	[238]
Waist circumference	**Up to 23,564 African American individuals**	**Up to 10,027 African American individuals**	***LHX2, DENND1A, MAP3K1, BRE, PCSK1, ASZ1, IL1RL2, IL1RL1, SATB2***	[239]
Waist-to-hip circumference ratio (interaction)	8,203 African American women, 3,484 Hispanic ancestry women	NR	*ITGBL1, MGMT, ZNF385D, LOC728516, LOC642340, MOSPD2, LOC100128621, LOC152225, ZPLD1, BCAM, PVRL2, LOC359819, EEF1B3, DNAJC10, FRZB, SLC28A3, NTRK2, MAML2, CDK4PS*	[138]
Warfarin maintenance dose	**533 African American individuals**	**432 African American individuals**	***CYP2C, CYP2C18, CYP2C9, CYP2C8, CYP2C19***	[240]
White blood cell count	62 American Indian or Alaska Native ancestry individuals, 158 Asian ancestry individuals, 3,272 African American ancestry individuals, 114 other ancestry individuals, 23,244 European ancestry individuals, 996 unknown ancestry individuals	NR	*DARC, GSDMA*	[33]
White blood cell count	16,388 African American individuals	3,551 Hispanic American individuals, 14,767 Japanese individuals, 19,509 European American individuals	*CXCL2, CDK6*	[34]

NR not replicated, NS not significant, Bold GWAS publication with only African ancestry populations, Population names are as used in the related publications

Table 2

GWAS on communicable diseases in recent African and African ancestry populations

Disease	Sample size	Replication sample size	Genes	Ref
Chronic Hepatitis C infection	988 European-American cases, 198 African-American cases, 100 Hispanic cases	NR	*ITPA*	[241]
HIV (mother-to-child transmission)	**100 Malawian infant cases, 126 Malawian infant controls**	**NR**	**NS**	[242]
HIV-1	515 African American cases	NR	*MCMB, HLA-B, AOAH, EVI5L, GPC5, ACO23798.16, RP11-100A16.1, PPP3CC, SORBS3,* Intergenic 11q14.1	[92]
HIV-1 control	516 European cases, 1,196 European controls, 341 African American cases, 892 African American controls, 117 Hispanic controls, 560 Hispanic controls	NR	*HLA-C, MICA, HLA-B, PSORS1C3* Intergenic 6p21.33	[243]
HIV-1 susceptibility	**848 Malawian cases, 531 Malawian controls**	**NR**	***AL591509.5, GLRX3, TXNL3, FAM174B, AC009271.7, ZDHHC19, BUD13***	[244]
HIV-1 viral setpoint	496 HIV-1 infected individuals of African ancestry, 302 HIV-1 exposed and uninfected individuals of African ancestry	NR	*VEGFC, EPHA5, HIST1H4A, AL391500.13, KB-67B5.12, CMTM8, AC095058.3, AC087190.5-2, DNAJC5B, ZFP90, MAD2L1, HSP90AB3P, Intergenic chr 2, GALNT14*	[245]
IFN-related cytopenia	984 European Americans with genotype 1 HCV, 201 African Americans with genotype 1 HCV, 99 Hispanics with genotype 1 HCV	NR	*IPTA*	[246]
Immune response to smallpox (secreted IFN-alpha; IL-10, IL-12p40, IL-1beta, IL-2, TNF-alpha)	Up to 512 European ancestry individuals, up to 199 African American individuals	NR	*WDR92, ECSM2, TMEM173, LOC100128265, ZNF827, MNAT1, MAMLD1, TIMELESS, KCND3, LOC152118, COL4A4, RAB14, ATP10A, PHEX, LOC728241, OR2H1, LOC344332, CEP110, BMP4, LTBP1,UBE2D2, LPP, PTCHD1, ODZ1, DIP2C, LOC100129027, CYMP, ELAC1, ATP8A1, hCG_1820717, SGK1, DAPK1, NLRP13, NLRP8*	[247]
Immune response to smallpox vaccine (IL-6)	217 African American ancestry individuals, 580	NR	*MKX, LOC388460, GPR158, ZHX2, SPIRE1, GREM2, CSMD1, RUNX1, RBM24, LOC100132612, SPIRE1, RASAL2, LOC388460, VENTXP5, IL5RA,*	[248]

Disease	Sample size	Replication sample size	Genes	Ref
	European ancestry individuals, 217 Hispanic ancestry individuals		*PRKCQ, KIF6, LOC1001311899, CYP2C9, ANKLE2, GOLGA3, CYP2C8, PDYN, UNC13C, IRX1, SNX18, CRBN, FAM108C1, LOC387761, TMTC2, FEV, LOC151300, FLJ45139, TMTC2, LOC654254, CACNA2D3, RAB10, BCR, LOC647132, MEX3C, PDE4D, LTBP1, LOC100129725, NDUFB6, TOPORS, CDC42, BLK, ODZ2, C6orf190*	
Malaria	**958 Gambian cases, 1,382 Gambian controls, all children**	**1,087 Gambian cases, 2,376 Gambian controls, all children**	***HBB, SCO1, DDC***	[76]
Malaria	**1,325 African ancestry, 828 African ancestry controls**	**2,229 African ancestry cases, 3,526 African ancestry controls**	***ATP2B4, ABO, HBB, MARVELD3***	[249]
Malaria	**5,425 African cases, 6,891 African controls**	**NR**	***ABO, HBB***	[250]
Tuberculosis	**921 Ghanaian cases 1,740 Ghanaian controls, 1,316 Gambian cases, 1,382 Gambian controls**	**1,226 Ghanaian cases, 3,825 Ghanaian controls, 236 Malawian cases, 779 Malawian controls, 332 Ghana parent/child trios and duos**	***GATA6,CTAGE1,RBBP8,CABLES1***	[84]
Tuberculosis	1,329 African ancestry cases, 1,847 African ancestry controls	2,024 African ancestry cases, 5,154 African ancestry controls, 1,025 Indonesian ancestry cases, 983 Indonesian ancestry controls, 4,441 European ancestry cases, 5,874 European ancestry controls	*WT1*	[251]
Tuberculosis	**642 South African coloured cases, 91 South African coloured controls**	**NR**	***C2CD2, CNOT6L, CYP2C8, DCUN1D5, DSCAM, DYNC2H1, E2F7, IL2RB, LOC100508120, NAA60, PLD5, RNF187, SMOC1, SOX11, VWA8, WT1, ZFPM2, DMRTA1, SPON1, SNORD114-31, WT1,* Intergenic regions**	[252]

NR not replicated, NS not significant, Bold GWAS publication with only African ancestry populations, Population names are as used in the related publications

Table 3

GWAS on cancer related diseases in recent African and African ancestry populations

Disease/Trait	Sample Size	Replication Sample Size	Genes	Ref
Acute lymphoblastic leukemia (childhood)	972 European ancestry cases, 1,386 European ancestry controls, 89 African American cases, 1,363 African American controls, 305 Hispanic cases, 1,008 Hispanic controls	574 European ancestry cases, 2,601 European ancestry controls, 128 African American cases, 1,075 African American controls, 143 Hispanic cases, 640 Hispanic controls	*IKZF1, DDC, GRB10, ARID5B, CEBPE*	[253]
Asparaginase hypersensitivity in acute lymphoblastic leukemia	211 European ancestry child cases, 40 Black child cases, 46 Hispanic child cases, 4 Asian child cases, 21 child cases	99 European ancestry child cases, 33 Black child cases, 24 Hispanic child cases, 2 Asian child cases, 5 child cases	*GRIA1*	[254]
Breast cancer	**3,016 African American cases, 2,745 African American controls**	**3,533 African ancestry cases, 11,046 African ancestry controls**	***GALC***	[255]
Breast cancer	3,666 European ancestry cases, 28,864 European ancestry controls, 1,004 African American cases, 2,744 African American controls	562 European ancestry cases, 6,410 European ancestry controls, 84 Japanese ancestry cases, 830 Japanese ancestry controls, 300 Hispanic/ Latin American cases, 1,164 Hispanic/Latin American controls	*RALY, EIF2S2, ASIP, FAM46A, C6orf37*	[256]
Breast cancer	**3,016 African American cases; 2,745 African American controls**	**NR**	***SLC45A1, TNIP3***	[257]
Breast cancer	1,004 African ancestry cases, 2,745 African ancestry controls,1,718 European ancestry cases, 3,670 European ancestry controls	2,222 European ancestry cases, 16,363 European ancestry controls	*TERT*	[258]
Erectile dysfunction and prostate cancer treatment	132 African American, European ancestry, Hispanic/Latin	128 African American, European ancestry, Hispanic/Latin American ancestry, East Asian ancestry, South Asian	NS	[259]

Disease/Trait	Sample Size	Replication Sample Size	Genes	Ref
	American ancestry, East Asian ancestry, South Asian ancestry cases, 103 African American, European ancestry, Hispanic/Latin American ancestry, East Asian ancestry, South Asian ancestry controls	ancestry cases, 102 African American, European ancestry, Hispanic/Latin American ancestry, East Asian ancestry, South Asian ancestry controls		
Methotrexate clearance (acute lymphoblastic leukemia)	22 East Asian ancestry cases, 58 African ancestry or African American/ Afro-Caribbean cases, 266 Hispanic/Latin American ancestry cases, 806 European ancestry cases, 127 other ancestry cases	699 European ancestry cases	*SLCO1B1*	[260]
Methotrexate phramacokinetics (acute lymphoblastic leukemia)	5 Asian, unspecified child cases; 73 African American child cases; 315 European ancestry child cases; 41 Other ancestry child cases; 206 child cases	NR	*C10orf11*,*GLIS3*,*KIAA0774*,*SLCO1A2*,*SLCO1B*, Intergenic regions	[261]
Neuroblastoma	2,101 European ancestry cases, 4,202 European ancestry controls	351 Italian cases, 780 Italian controls, 365 African American cases, 2,491 African American controls	*HACE1*, *LIN28B*, *BARD1*, *LINC00340*, *FLJ44180*, *LMO1*, *HSD17B12*	[262]
Paclitaxel-induced neuropathy	855 European ancestry breast cancer cases	154 European ancestry breast cancer cases, 117 African American breast cancer cases	NS	[263]
Paclitaxel-induced neuropathy	77 European ancestry lymphoblastoid cell lines, 87 Yoruban lymphoblastoid cell lines, 83 African American lymphoblastoid cell lines	NR	NS	[264]
Pancreatic cancer	252 European ancestry cases	798 European ancestry cases, 21 African American cases, 10 East	NS	[265]

Disease/Trait	Sample Size	Replication Sample Size	Genes	Ref
		Asian cases, 4 Asian Indian cases		
Prostate cancer	**474 West African ancestry cases, 458 West African ancestry controls**	**5,096 African American cases, 4,972 African American controls**	**NS**	[266]
Prostate cancer	1,854 European ancestry cases, 1,894 European ancestry controls	19,879 cases, 18,761 controls (European, Chinese, Japanese, African American, Latino, and Hawaiian ancestry)	*IGF2, IGF2AS, INS, TH, NKX3.1, ITGA6, PDLIM5,TET2, THADA, JAZF1, EHBP1* and several intergenic regions	[43]
Prostate cancer	6,621 European ancestry cases, 6,939 European ancestry controls	22,957 European ancestry cases, 23,234 European ancestry controls, 285 Japanese cases, 298 Japanese controls, 135 Chinese cases, 135 Chinese controls, 112 African American cases, 298 African American controls, 7,140 cases, 5,455 controls	*TERT, CLDN11, SKIL, GGCX, VAMP8, VAMP5, RNF181, PRPH, Intergenic chr 3, AR, ZBTB38, CCHCR1, FGF10*	[267]
Prostate cancer	3,425 African American cases, 3,290 African American controls	1,275 African American cases, 1,695 African American controls, 86 Senegalese cases, 414 Senegalese controls, 271 Ghanaian cases, 968 Ghanaian controls, 246 Barbadian cases, 253 Barbadian controls	*ZNF652*	[268]
Prostate cancer	316 cases, 229 controls	55 Asian ancestry cases, 1,382 European ancestry cases, 184 African American ancestry cases, 42 Other ancestry cases, 134 Asian ancestry controls, 1,428 European ancestry controls, 127 African American ancestry controls, 87 Other ancestry controls	*Intergenic chr 10, 15*	[269]
Response to mTOR inhibitor (everolimus, and rapamycin)	87 European ancestry individuals, 91 African American individuals, 94 Han Chinese ancestry individuals	NR	*NKX2-6 – STC1, MGC46496, PBX3, USP10, AGA, RNA5SP173 – LINC00290, RGS4, RGS5, MCTP2, APBA2, PCAF, RIMS1*	[270]
Response to taxane treatment (docetaxel, and placlitaxel)	96 African American lymphoblastoid cell lines, 96 European ancestry lymphoblastoid cell lines, 96 Han Chinese lymphoblastoid cell lines	NR	*TTLL7, RYR2, ZNF670, POU3F3, SLC616, GHR, CANA2D1, DKK3, TRIM49, COL1A1, HRH4, KIAA0427, ZNF254, OSCAR, C20orf23, NPHP4, IL12B, TMEM106B, TMEM26, C10orf107, TSPAN15, SC5DL, ASB7, SEZ6L2, ZNF254, PRDM15, FGF13*	[271]

Disease/Trait	Sample Size	Replication Sample Size	Genes	Ref
Urinary symptoms in response to radiotherapy in prostate cancer	346 European, African, Hispanic and Asian individuals	377 European, African, Hispanic and Asian individuals	*IFNK*, *MOB3B*	[272]

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