

Social and Genetic Pathways in Multigenerational Transmission of Educational Attainment

American Sociological Review
1–27
© American Sociological
Association 2018
DOI: 10.1177/0003122418759651
journals.sagepub.com/home/asr



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Abstract

This study investigates the complex roles of the social environment and genes in the multigenerational transmission of educational attainment. Drawing on genome-wide data and educational attainment measures from the Framingham Heart Study (FHS) and the Health and Retirement Study (HRS), I conduct polygenic score analyses to examine genetic confounding in the estimation of parents' and grandparents' influences on their children's and grandchildren's educational attainment. I also examine social genetic effects (i.e., genetic effects that operate through the social environment) in the transmission of educational attainment across three generations. Two-generation analyses produce three important findings. First, about one-fifth of the parent-child association in education reflects genetic inheritance. Second, up to half of the association between parents' polygenic scores and children's education is mediated by parents' education. Third, about one-third of the association between children's polygenic scores and their educational attainment is attributable to parents' genotypes and education. Three-generation analyses suggest that genetic confounding on the estimate of the direct effect of grandparents' education on grandchildren's education (net of parents' education) may be inconsequential, and I find no evidence that grandparents' genotypes significantly influence grandchildren's education through non-biological pathways. The three-generation results are suggestive, and the results may change when different samples are used.

Keywords

educational attainment, multigenerational influence, socio-genomics

Intergenerational transmission of socioeconomic status (SES) is a central theme in social stratification and mobility research. Sociologists have made seminal contributions to understanding how SES is transmitted across generations. In particular, research shows education to be the most important mechanism of social reproduction and mobility (Blau and Duncan 1967; Bourdieu and Passeron 1977; Coleman 1988; Featherman and Hauser 1976; Hauser 1971; Hout 1988; Mare 1993; Sewell, Haller, and Portes 1969; Teachman 1987).

The highest level of education that individuals achieve is largely due to the availability of

financial, social, and cultural resources in their family of origin (Shavit and Blossfeld 1993). In addition to socioeconomic factors, genetic inheritance also plays a crucial role in educational attainment (Conley et al. 2015; Eckland 1967, 1979; Nielsen 2008; Nielsen

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and Roos 2015; Scarr and Weinberg 1978). According to family-based heritability studies, genetic factors account for 40 percent of the variation in educational attainment (Branigan, McCallum, and Freese 2013). Importantly, genes do not determine one's educational attainment, but their effects depend on the social context in which individuals' lives unfold. Genetic influences on education-related traits vary by gender, family background, and birth cohort (Guo and Stearns 2002; Heath et al. 1985; Turkheimer et al. 2003).

Considering genetics in social stratification and mobility research is important for many reasons. The present study highlights two of them. First, the influence of family origin on educational attainment has traditionally been assessed using the zero-order association between parents' SES (measured by parental education or occupation) and children's educational attainment. However, because parents and children share both their living environment and half of their DNA, the parent-child association in education is ambiguously social and genetic. Without separating the two components, the variation in children's educational attainment is assumed to be driven merely by the social environment. As a result, the estimate of socio-environmental effects on educational attainment is likely to be biased. To better model socio-environmental effects, it is crucial to take genetic factors into account (Conley et al. 2015; Liu and Guo 2016).

Second, genetics can provide novel insights into understanding specific mechanisms in the intergenerational transmission of education. Genes may influence one's educational attainment through direct or indirect pathways. On the one hand, genotypic differences contribute to variation in individual characteristics that are associated with educational attainment, such as cognitive ability and personality-related traits (i.e., direct genetic effects) (Belsky et al. 2016; Okbay, Beauchamp, et al. 2016). On the other hand, individuals' own or proximate others' (e.g., parents, spouses, friends) genotypes may affect selection of educational environment

(i.e., social genetic effects) (Domingue and Belsky 2017; Fletcher and Conley 2013; Jaffee and Price 2007; Plomin, DeFries, and Loehlin 1977; Scarr and McCartney 1983; Wagner et al. 2013). Unlike direct genetic effects that operate through one's own traits, social genetic effects often rely on social interactions with other individuals; they are therefore more susceptible to socio-environmental changes. For example, social policies made to increase educational opportunities for individuals of one generation may consequently help their offspring realize their genetic potential for educational attainment. Understanding social genetic effects enables us to better predict the long-term effects of such policies.

Genetic influences are typically investigated using twins, adoptees, or other family data (e.g., Boardman, Blalock, and Pampel 2010; Guo and Stearns 2002; Nielsen 2006; Nielsen and Roos 2015; Turkheimer et al. 2003). Yet in these family studies, genetic factors are not directly observed but usually modeled as latent variables based on critical assumptions, such as equal environments for identical and fraternal twins and an absence of assortative mating (Barnes et al. 2014; Burt and Simons 2014; Goldberger 1979). Recent developments in genome-sequencing technology have produced tremendous molecular genetic data and opened up a new field of scientific inquiry—socio-genomics (Robinson, Grozinger, and Whitfield 2005). Socio-genomic studies have identified dozens of specific genetic variants that are significantly associated with various human traits of interest to social scientists, including educational attainment (Okbay, Beauchamp, et al. 2016; Rietveld et al. 2013), reproductive behavior (Barban et al. 2016; Day et al. 2016), and subjective well-being (Okbay, Baselmans, et al. 2016). Based on the results of these studies, polygenic scores (i.e., PGSs) can be constructed as compound measures that aggregate estimates of multiple genetic effects on a trait. PGSs are especially useful in investigations of complex human traits that are influenced by a large number of genetic variants

with moderate or small effects. In particular, PGS analysis of educational attainment has been successfully performed using different samples (Belsky et al. 2016; Conley et al. 2015; Domingue et al. 2015). The PGS for educational attainment offers sociologists opportunities to examine genetic confounding and social genetic effects in the multigenerational transmission of educational attainment.

Using genome-wide data and educational attainment measures from the Framingham Heart Study (FHS), I conduct a PGS analysis to investigate (1) genetic confounding in the estimation of parents' influence on children's educational attainment and (2) social genetic effects in the transmission of educational attainment from parents to children. I extend the investigation to consider (3) genetic confounding in the estimation of grandparents' influence on grandchildren's educational attainment and (4) social genetic effects in the transmission of educational attainment across three generations. Analyses are replicated using data from the Health and Retirement Study (HRS).

BACKGROUND AND AIMS OF THE STUDY

Intergenerational Transmission of Education

In their landmark book *The American Occupational Structure*, Blau and Duncan (1967) conducted the first systematic analysis of stratification in U.S. society by examining processes of social mobility from one generation to the next. They found that much of the influence of family origin on social mobility operates through education. Since this seminal work, intergenerational transmission of education has become a centerpiece in social stratification and mobility research. Social scientists have traditionally focused on economic, cultural, and social explanations of intergenerational transmission of education. These explanations emphasize various pathways through which parents influence children's educational success, including investment of financial resources (Bailey and

Dynarski 2011; Blossfeld and Shavit 1993; Boudon 1974; Downey 1995; Reardon 2011; Schneider and Coleman 1993), development of social capital (e.g., relationships and networks) (Coleman 1988; Gaddis 2012; Lin 2001), and reproduction of cultural capital (e.g., norms, values, attitudes, expectations) (Bourdieu and Passeron 1977; De Graaf and Ganzeboom 1993; DiMaggio 1982; Gaddis 2013; Jæger and Breen 2016; Sakamoto, Goyette, and Kim 2009).

In addition to the economic, social, and cultural pathways, there is an increasing awareness of the role of genetic inheritance in intergenerational transmission of education (Conley et al. 2015; Heath et al. 1985; Mare 2011; Nielsen 2006, 2008; Nielsen and Roos 2015). Without considering genetic inheritance, traditional sociological research implicitly assumes that education-related ability is randomly distributed at birth. If this assumption is violated—for example, if pro-education genetic compositions are correlated with pro-education environments—then estimates of socio-environmental effects on intergenerational transmission of education would be upwardly biased.

Recent advances in genomic sciences and technology have enabled researchers to collect genome-wide genetic markers from large and representative samples. Rietveld and colleagues (2013) conducted the first genome-wide association study (GWAS) on educational attainment. Using a discovery sample of 101,069 individuals, they identified three single nucleotide polymorphisms (SNPs) associated with educational attainment at the genome-wide significance level (i.e., $p < 5 \times 10^{-8}$). Based on results of this GWAS, Conley and colleagues (2015) performed the first polygenic score analysis to assess genetic and social effects in the intergenerational transmission of education. They reported that genetic factors account for approximately one-sixth, and social inheritance accounts for five-sixths, of the parent-child association in educational attainment.

Socio-genomic investigation of intergenerational transmission of education is still in the early stages, and many critical questions remain unanswered. For example, what are

the roles of parents' genotypes in the transmission of education to their children? What roles do children's own genotypes play? Are parents' or children's genes important omitted variables in the estimation of socio-environmental effects? Moreover, current PGS analysis of educational attainment suffers from underpowered scores, due to insufficient samples used to estimate genetic effects in the original GWAS. Educational attainment is a complex trait that may be influenced by a large number of genetic variants with moderate to small effects. To detect these genetic effects, large sample size is crucial. If the GWAS sample size is insufficient, the resulting polygenic scores would be underpowered in predicting genetic variation. Conley and colleagues (2015) thus call for the use of better powered polygenic scores in the investigation of intergenerational transmission of educational attainment.

As a result of advances in genomic science and technology and increases in sample size, socio-genomic research has improved the estimates of genetic associations with educational attainment. Okbay, Beauchamp, and colleagues' (2016) study extended the discovery sample size to 293,723 and identified 74 SNPs significantly associated with educational attainment. This enables a more powerful analysis of the intergenerational transmission of education. *Aim 1 of this study is to provide a comprehensive assessment of genetic confounding in the estimation of parental influence on offspring's educational attainment based on findings from the most recent GWAS on educational attainment.*

Mechanisms of genetic influence on educational attainment are complicated. There is evidence that genes may influence an individual's educational attainment by affecting intermediate traits such as intelligence and self-control (i.e., direct genetic effects) (Belsky et al. 2016). Other than that, genetic influences can be indirect. These indirect genetic influences are referred to as gene-environment correlation (rGE) (Jencks 1980; Plomin et al. 1977; Scarr and McCartney 1983) or social genetic effects (SGE) (Domingue and Belsky 2017). One's genotypes may partially

determine the selection of the social environment in which one lives (i.e., active rGE) (Dickens and Flynn 2001; Tucker-Drob, Briley, and Harden 2013). Moreover, some decisions parents make for their children (e.g., selecting children's schools and where they live) may reflect parents' genetic characteristics. Because biological parents and children share about 50 percent of their DNA, parental genetic effects may operate as if children's own genotypes influence their selection of the social environment (i.e., passive rGE) (Conley and Fletcher 2017).

Being aware of social genetic effects is also important in understanding specific mechanisms of social environment effects. In contrast to direct genetic effects that operate directly through one's own traits, social genetic effects are often contingent on interactions with other individuals, and are therefore more susceptible to socio-environmental changes. For example, the influence of parents' genes on children may be weakened when interactions between parents and children become less frequent (e.g., when children leave home for college). An accurate estimate of social genetic effects can be very useful for predicting the long-term effects of public policies that aim to create new environments (e.g., initiating new training programs) or reduce environmental variation (e.g., equalizing educational opportunities).

Social genetic effects have rarely been investigated in sociological research. *Aim 2 of this study is to examine social genetic effects in the transmission of education from parents to children.*

Multigenerational Transmission of Education

A growing number of studies have extended the investigation of intergenerational transmission of SES beyond two generations (Aldous 1995; Chan and Boliver 2013; Cherlin and Furstenberg 1992; Deleire and Kalil 2002; Erola and Moisio 2007; Jæger 2012; Mare 2011, 2014; Mare and Song 2012; Pfeffer 2014; Sharkey and Elwert 2011; Song 2016; Song and Mare 2017; Warren and

Hauser 1997; Zeng and Xie 2014; Ziefle 2016). Two models of grandparents' influence on grandchildren have been developed: the Markovian Model and the non-Markovian Model. The former assumes that grandparents' influence on grandchildren is completely mediated by parental characteristics. For example, using data from the Wisconsin Longitudinal Study, two studies show grandparents' influence on grandchildren's educational success disappears after controlling for parental characteristics (Jæger 2012; Warren and Hauser 1997). Yet, these findings might be limited by the time, geographic location, and sample population (Mare 2011, 2014; Pfeffer 2014). As a consequence of recent demographic changes, grandparents now live longer and are healthier, and as a result, they may have longer and more active relationships with their grandchildren. This means grandparents may have more influence on grandchildren independent of parents. Consistent with the non-Markovian Model, research shows that grandparents can directly affect their grandchildren's education by providing financial assistance (Aldous 1995), monitoring grandchildren's school activities (Deleire and Kalil 2002), serving as role models, and promoting traditional values (Bengetson 1975; King and Elder 1997).

Additionally, genes may play an important part in the multigenerational processes of educational transmission. Grandchildren inherit a quarter of their grandparent's DNA. These inherited genes may contribute to grandchildren's traits during their developmental process, including education-related traits. Limited research has examined the role of genetics in the multigenerational transmission of education. It is unclear, for example, to what extent the association between grandparents and grandchildren's education reflects genetic inheritance versus social inheritance. *Aim 3 of this study is to disentangle genetic and social components in the grandparent-grandchild association in educational attainment.*

Other than the biological pathways, grandparents' genes may also indirectly influence grandchildren's education through various social pathways (i.e., grandparents' social

genetic effects). For example, grandparents' genes may directly or indirectly affect parental SES, which, in turn, influences grandchildren's education. Moreover, grandparents' influence that does not operate through parents (e.g., providing financial resources and serving as role models) may reflect grandparents' own genetic characteristics. *Aim 4 of this study is to examine social genetic effects in the transmission of educational attainment across three generations.*

MULTIGENERATIONAL TRANSMISSION OF EDUCATION MODEL

Figure 1 demonstrates transmission of educational attainment from parent to child. Suppose $EDUCATION_{Parent}$ and $GENE_{Parent}$ denote educational attainment and genotypes of the parent, and $EDUCATION_{Child}$ and $GENE_{Child}$ denote educational attainment and genotypes of the parent's child. As Figure 1 shows, $EDUCATION_{Parent}$ and $EDUCATION_{Child}$ are linked through multiple pathways. Three of these pathways are of particular interest: (a) $EDUCATION_{Parent}$ and $EDUCATION_{Child}$ can be associated through $GENE_{Parent}$ and $GENE_{Child}$ (i.e., the parent's genotypes associated with his/her educational attainment are biologically inherited by the child); (b) $GENE_{Parent}$ is associated with both $EDUCATION_{Parent}$ and unobserved factors that contribute to $EDUCATION_{Child}$ (i.e., parents' influence on children's education reflects the parent's genetic characteristics, such as selecting the child's schools); (c) $EDUCATION_{Parent}$ and $GENE_{Child}$ are both associated with unobserved factors that may affect $EDUCATION_{Child}$ (i.e., unobserved factors that influence children's education may be influenced by the parent's education and the child's genetic characteristics, such as selecting the child's peers). These paths may lead to omitted variable biases in the estimation of socio-environmental effects in intergenerational transmission of education when genetic measures are ignored. Controlling only for parents' genetic measures would account for

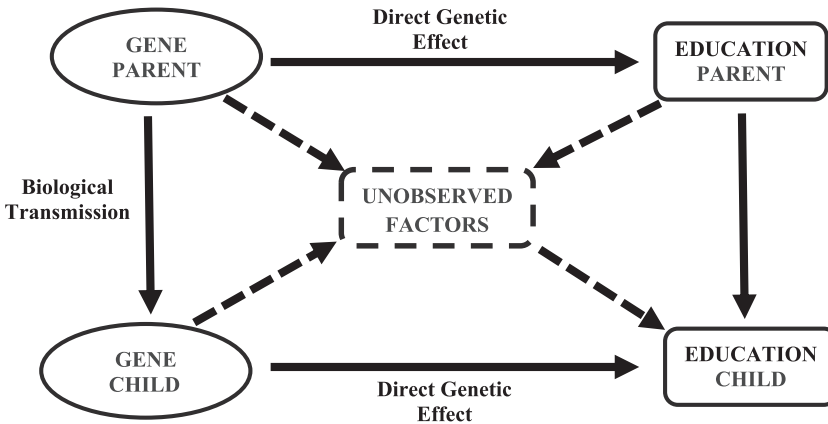


Figure 1. Intergenerational Transmission of Education

confounding effects due to (a) and (b); controlling only for child's genetic measures would account for confounding effects due to (a) and (c); and controlling for both would account for confounding effects due to (a), (b), and (c).

Intergenerational transmission of educational attainment can be modeled as follows:

$$\text{EDUCATION}_{\text{Child}} = \beta \text{EDUCATION}_{\text{Parent}} + \gamma_1 \text{GENE}_{\text{Parent}} + \gamma_2 \text{GENE}_{\text{Child}} + \varepsilon$$

This model can be used to estimate (2G.1) the effect of parents' education on children's education (β , when γ_1 and γ_2 are set to 0) (i.e., an estimate of parents' influence ignoring genetic confounding); (2G.2) the effect of parents' genotypes on children's education (γ_1 , when β and γ_2 are set to 0); (2G.3) the effect of children's genotypes on their own education (γ_2 , when β and γ_1 are set to 0); (2G.4) the effect of parents' education on children's education net of parents' genotypes (β , when γ_2 is set to 0) (i.e., an estimate of socio-environmental effects after taking into account genetic confounding due to parents' genotypes); (2G.5) the effect of parents' education on children's education net of children's genotypes (β , when γ_1 is set to 0) (i.e., an estimate of socio-environmental effects after taking into account genetic confounding due to children's genotypes); (2G.6) the effect of parents' genotypes on children's education net of children's

genotypes (γ_1 , when β is set to 0), and the effect of children's genotypes on their own education net of parents' genotypes (γ_2 , when β is set to 0); and (2G.7) the effect of parents' education on children's education net of parents' and children's genotypes (β , when there are no restrictions on the parameters) (i.e., a purer estimate of socio-environmental effects after taking into account genetic confounding due to both parental and children's genotypes).

Figure 2 demonstrates transmission of education across three consecutive generations (G1: generation 1; G2: generation 2; G3: generation 3). Suppose EDUCATION_{G1} , EDUCATION_{G2} , and EDUCATION_{G3} denote educational attainment of the three generations, and GENE_{G1} , GENE_{G2} , and GENE_{G3} denote genotypes of the three generations. Similar to the two-generation model, estimation of the socio-environmental effects of G1's education on G3's education can be confounded due to correlations between genotypes of three generations and unobserved factors that link to both G1's and G3's education. The full model of transmission of education across three generations can be written as follows:

$$\begin{aligned} \text{EDUCATION}_{G3} = & \beta_1 \text{EDUCATION}_{G1} \\ & + \beta_2 \text{EDUCATION}_{G2} \\ & + \gamma_1 \text{GENE}_{G1} + \gamma_2 \text{GENE}_{G2} \\ & + \gamma_3 \text{GENE}_{G3} + \varepsilon \end{aligned}$$

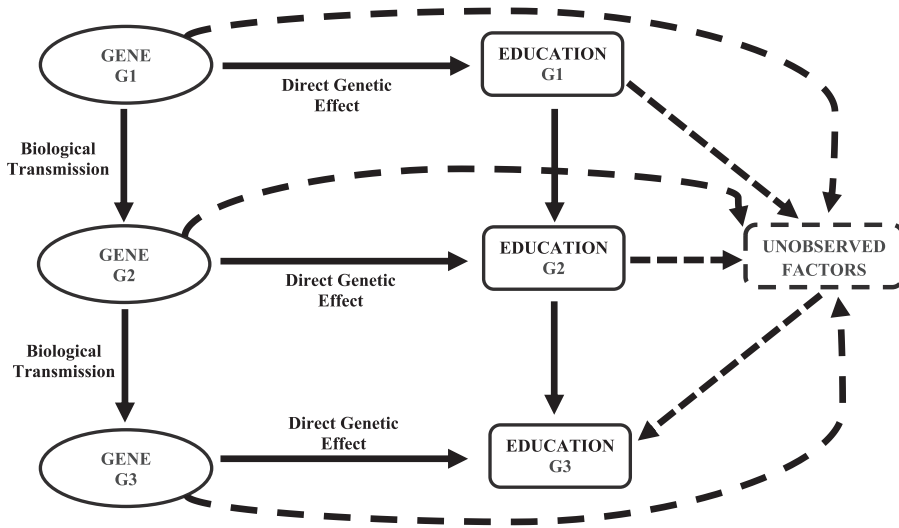


Figure 2. Multigenerational Transmission of Education

This model can be used to estimate (3G.1) the effect of grandparents' education on grandchildren's education (β_1 , when β_2 , γ_1 , γ_2 , and γ_3 are set to 0) (i.e., an estimate of grandparents' influence ignoring genetic confounding); (3G.2) the effect of grandparents' genotypes on grandchildren's education (γ_1 , when β_1 , β_2 , γ_2 , and γ_3 are set to 0); (3G.3) the effect of parents' genotypes on grandchildren's education (γ_2 , when β_1 , β_2 , γ_1 , and γ_3 are set to 0) (this is similar to 2G.2); (3G.4) the effect of grandchildren's genotypes on their own education (γ_3 , when β_1 , β_2 , γ_1 , and γ_2 are set to 0) (this is similar to 2G.3); (3G.5) the effect of grandparents' education on grandchildren's education net of grandparents' genotypes (β_1 , when β_2 , γ_2 , and γ_3 are set to 0) (i.e., an estimate of socio-environmental effects after taking into account genetic confounding due to grandparents' genotypes); (3G.6) the effect of grandparents' education on grandchildren's education net of parents' genotypes (β_1 , when β_2 , γ_1 , and γ_3 are set to 0) (i.e., an estimate of socio-environmental effects after taking into account genetic confounding due to parents' genotypes); (3G.7) the effect of grandparents' education on grandchildren's education net of grandchildren's genotypes (β_1 , when β_2 , γ_1 , and γ_2 are set to 0) (i.e., an estimate of socio-environmental effects after taking into account

genetic confounding due to grandchildren's genotypes); (3G.8) the effect of grandparents' genotypes on grandchildren's education net of parents' genotypes and grandchildren's genotypes (γ_1 , when β_1 and β_2 are set to 0); (3G.9) the effect of grandparents' education on grandchildren's education net of three generations' genotypes (β_1 , when β_2 is set to 0) (i.e., an estimate of socio-environmental effects after taking into account genetic confounding due to all three generations' genotypes); (3G.10) the effect of grandparents' education on grandchildren's education net of parents' education (β_1 , when γ_1 , γ_2 , and γ_3 are set to 0); (3G.11) the effect of grandparents' education on grandchildren's education net of parents' education and grandparents' genotypes (β_1 , when γ_2 and γ_3 are set to 0) (i.e., an estimate of grandparents' direct effect after taking into account genetic confounding due to grandparents' genotypes); (3G.12) the effect of grandparents' education on grandchildren's education net of parents' education and parents' genotypes (β_1 , when γ_1 and γ_3 are set to 0) (i.e., an estimate of grandparents' direct effect after taking into account genetic confounding due to parents' genotypes); (3G.13) the effect of grandparents' education on grandchildren's education net of parents' education and grandchildren's genotypes (β_1 , when γ_1 and γ_2 are set to 0) (i.e., an estimate

of grandparents' direct effect after taking into account genetic confounding due to grandchildren's genotypes); and (3G.14) the effect of grandparents' education on grandchildren's education net of parents' education and three generations' genotypes (β_1 , when there are no restrictions on the parameters) (i.e., an estimate of grandparents' direct effect after taking into account genetic confounding due to three generations' genotypes).

Because GWAS data are relatively new in social science studies, data limitations make it difficult to examine the role of genetics beyond the parental generation. However, the unique three-generation design of FHS provides an opportunity to conduct a preliminary analysis and produce results that can inform future research. Analyses in the present study are based on GWAS findings using samples of European descent. It is uncertain whether these findings are replicable in other racial/ethnic populations. To minimize confounding effects of population stratification, this study focuses on non-Hispanic whites.

DATA

The Framingham Heart Study (FHS) is a community-based longitudinal study following three generations of participants in Framingham, Massachusetts. The original cohort enrolled in 1948 ($N = 5,209$); the offspring cohort (children of the original cohort) enrolled in 1971 ($N = 5,124$); and the generation three cohort (grandchildren of the original cohort) enrolled in 2002 ($N = 4,095$). Of the 14,428 participants, a total of 9,237 were genotyped. Genotyping for FHS participants was performed using the Affymetrix 500K GeneChip array; 8,639 individuals with 287,525 single nucleotide polymorphisms (SNPs) passed standardized quality control processes.

To confirm the results based on FHS data, I replicated analyses using data from the Health and Retirement Study (HRS), a nationally representative sample of approximately 20,000 participants over age 50. HRS collected information on economic, health, social, and other factors relevant to aging and retirement every two years from 1992 to

2014. DNA samples were collected in 2006 and 2008. Of the collected samples, 13,129 were put into genotyping production using the Illumina Human Omni-2.5 Quad beadchip, with coverage of approximately 2.5 million SNPs. Of these samples, 9,342 non-Hispanic whites passed quality control.

I measured educational attainment using "the number of years of education completed." In FHS, "years of education completed" was self-reported by participants in each of the three cohorts. In HRS, participants (G2) reported their own educational attainment and provided information about their parents' (G1) and children's (G3) education. Some participants had multiple children, and some of these children (G3) might not have completed their highest grade when their parents were interviewed. To address these issues, I selected the oldest child in each household who was most likely to have completed their highest grade of school, and I excluded those who had not reached 30 years of age when the last wave of data was collected. Self-reported parent-child relationships in the data might be biological or non-biological (e.g., adopted children). Analyses in this study are restricted to biological relationships.

METHOD

Analyses in this study are based on polygenic scores (PGSs). This section introduces how PGSs in the present study are calculated, followed by the strategies I used to analyze transmission of educational attainment across three generations, using data from FHS and HRS.

Polygenic Score Calculation

I calculated PGSs using the following equation:

$$PGS_i = \sum_{j=1}^J b_j G_{ij},$$

where PGS_i is the PGS of individual i , b_j is the coefficient for SNP j estimated in GWAS, and G_{ij} is the number of effect alleles (i.e., the

Table 1. Summary Statistics of Key Variables in Framingham Heart Study (FHS) and Health and Retirement Study (HRS) Genetic Samples

Variable	Mean/%	SD
FHS		
G1 Educational Attainment (Years of School)	12.01	3.28
G2 Educational Attainment	14.15	2.43
G3 Educational Attainment	15.08	1.95
G1 Polygenic Score	7.63e-05	1.95e-05
G2 Polygenic Score	7.57e-05	2.01e-05
G3 Polygenic Score	7.56e-05	2.01e-05
G1 Female	.61	
G2 Female	.53	
G3 Female	.53	
G1 Birth Year	1,909.90	5.96
G2 Birth Year	1,935.16	9.86
G3 Birth Year	1,960.47	8.97
<i>N</i> of Persons	8,639	
HRS		
G1 Educational Attainment	10.19	3.46
G2 Educational Attainment	13.16	2.57
G3 Educational Attainment	14.06	2.19
G2 Polygenic Score	3.35e-05	7.07e-06
G1 Female	.50	
G2 Female	.58	
G3 Female	.49	
G1 Birth Year	1,913.04	11.78
G2 Birth Year	1,937.88	10.57
G3 Birth Year	1,960.26	9.74
<i>N</i> of Persons	9,342	

Note: Summary statistics are based on raw values in the variables before standardization. *N* is number of individuals whose genotypes are available. In FHS, genotypes are available for all three generations. In HRS, genotypes are only available for G2.

allele positively associated with the outcome) on SNP j that individual i possesses. I constructed PGSs using b -weights from the recent GWAS on years of education (Okbay, Beauchamp, et al. 2016).¹ Before calculating the polygenic score, I matched SNPs in FHS and HRS with the GWAS results. Based on all matched SNPs, I conducted polygenic scoring according to the methods described by Dudbridge (2013) using the PRSice software (Euesden, Lewis, and O'Reilly 2015).² PGSs were normally distributed in FHS and HRS. Table 1 shows the means and standard deviations of raw PGSs in FHS and HRS. Greater PGSs are associated with higher levels of educational attainment. PGSs were standardized

to have a mean of 0 and a standard deviation of 1 for regression analyses.

Two-Generation Analyses

Based on educational PGSs, I conducted a series of regression analyses to examine inter-generational transmission of educational attainment. Using all parent-child pairs with measures of educational attainment and genotypes in FHS,³ I regressed children's educational attainment on parents' education controlling for parents' PGS and children's PGS. These analyses were conducted to (1) examine genetic confounding and provide a purer estimate of the socio-environmental

effects on educational attainment, and (2) assess the extent to which genes influence educational attainment through social pathways (i.e., social genetic effects). The Sobel (1982) test was used to determine the significance of the mediating effects. Because intergenerational pathways from a parent to a child might differ between mother and father, I also stratified these analyses for mother-child and father-child pairs.

Three-Generation Analyses

I performed similar regression analyses for grandparent-grandchild pairs. G3's educational attainment was regressed on G1's educational attainment to estimate the effect of grandparents' education on grandchildren's education. G2's education was added to the model as a covariate in the estimation of the direct effect of grandparents' education. PGSs from three generations were then added to examine genetic confounding and social genetic effects in the transmission of education across three generations. According to evolutionary theory, grandparents' influence on grandchildren may differ between grandfather and grandmother and between patrilineal and matrilineal lines due to sex-specific reproductive strategies (Coall and Hertwig 2010). I thus also stratified the three-generation analyses for paternal grandfather-grandchild, paternal grandmother-grandchild, maternal grandfather-grandchild, and maternal grandmother-grandchild pairs.

Replication Analyses Using HRS

The two-generation and three-generation analyses were replicated using HRS. In replicating the two-generation analyses, because PGS is only available for G2 in HRS, I conducted two separate analyses to optimize the use of data: the first focused on G1–G2 parent-child pairs with PGSs from the child, and the second focused on G2–G3 parent-child pairs with PGSs from the parent. In replicating the three-generation analyses, I used educational measures from three generations and PGSs from G2.

To account for potential population stratification, I adjusted all analyses for the first seven principal components computed from the genome-wide SNP data using the EIGENSOFT software (Price et al. 2006).

RESULTS

Univariate Distributions

Table 1 displays distributions of the key variables for all three generations in FHS and HRS. The gender-ratio and birth-year distributions of each generation are similar between the two samples (except for the higher female ratio of G1 in FHS). The most important difference between the two samples is that genotypes are available for all three generations in FHS, but they are only available for G2 in HRS (i.e., genotypes are not available for HRS participants' parents and children). PGS can thus only be calculated for G2 in HRS. Also, the average level of educational attainment is higher in FHS than in HRS. This reflects the fact that Massachusetts has a higher educational level than the national average (U.S. Census Bureau 2017). "Years of schooling," the measure of educational attainment in this study, differs by birth cohort and gender. More years of schooling is more common in younger generations than in older ones, and it is more common among males than among females in older generations. In bivariate and multivariate analyses, "years of schooling" is standardized by birth cohort and gender.

Bivariate Correlations

Table 2 shows the Pearson's correlations in educational attainment and educational PGSs among three generations in FHS. All the correlations are statistically significant ($p < .01$). The parent-child correlations in educational attainment are between .30 and .40 (.32 between G1 and G2 in FHS, .33 between G2 and G3 in FHS, .37 between G1 and G2 in HRS, and .39 between G2 and G3 in HRS). The grandparent-grandchild correlations in education (.15 in FHS and .16 in HRS) are

Table 2. Bivariate Correlations between Key Variables in FHS and HRS

FHS	(1)	(2)	(3)	(4)	(5)	(6)
G1 Educational Attainment (1)	1					
G2 Educational Attainment (2)	.324***	1				
G3 Educational Attainment (3)	.147***	.330***	1			
G1 Polygenic Score (4)	.136***	.249***	.122***	1		
G2 Polygenic Score (5)	.050***	.170***	.156***	.546***	1	
G3 Polygenic Score (6)	.039**	.122***	.192***	.299***	.538***	1
HRS	(1)	(2)	(3)	(4)		
G1 Educational Attainment (1)	1					
G2 Educational Attainment (2)	.365***	1				
G3 Educational Attainment (3)	.164***	.390***	1			
G2 Polygenic Score (4)	.131***	.256***	.192***	1		

Note: Bivariate correlations are calculated using standardized variables.

** $p < .01$; *** $p < .001$ (two-tailed tests).

slightly lower than half of the parent-child correlations.

In FHS, the correlation between one's PGS and education is larger in younger generations than in older ones (.14 for G1, .17 for G2, and .19 for G3). This is consistent with family-based estimates of heritability (Braniigan et al. 2013). One possible explanation is that, compared to older generations, younger generations have more educational opportunities, and therefore their genetic potential to achieve high levels of education is more likely to be realized. The parent-child correlation in PGS is slightly more than .50 (.55 between G1 and G2, and .54 between G2 and G3 in FHS), and the grandparent-grandchild correlation in PGS is about .30, suggesting a moderate degree of assortative mating on genotypes related to educational attainment.

In HRS, G2's PGS is significantly associated with educational attainment of all three generations. Remarkably, the correlation between G2's PGS and G3's education (.19) is significantly greater than the correlation between G2's PGS and G1's education (.13). The same pattern is found in FHS. This is likely because parents' genes contribute to their children's educational attainment through both biological and social pathways, whereas children's genes and parents' education are linked merely through the biological pathway (i.e., due to shared genotypes).

Transmission of Educational Attainment from Parents to Children (Two-Generation Analyses)

Panel 1 in Table 3 displays results of two-generation models using 6,298 parent-child pairs in FHS. Consistent with the bivariate results in Table 2, the parent-child association in education is estimated to be .35, the association between parents' PGS and child's education is .16, and the association between child's PGS and child's education is .20 (see Models 1, 2, and 3). Models 4, 5, and 7 present results for assessing genetic confounding and disentangling the biological and social pathways of genetic effects on educational attainment. The parent-child association in education is reduced by 5.5 percent when parental PGS is controlled, and by 7.2 percent when child's PGS is controlled. This suggests that parents' and children's genotypes are both influential, and they may play different roles in the analysis of intergenerational transmission of education. Controlling for either parents' PGS or children's PGS would correct biases due to biological inheritance. Parents' genotypes are needed to address biases caused by correlations between parents' genotypes and unobserved factors that contribute to children's education, and children's genotypes are needed to address biases caused by correlations between a child's

Table 3. Coefficients (Standard Errors) of Two-Generation Models of Children's Educational Attainment

	Model 1	Model 2	Model 3	Model 4	Model 5	Model 6	Model 7
Panel 1: FHS							
Parent's Education	.345*** (.012)			.326*** (.012)	.320*** (.012)		.316*** (.012)
Parent's PGS		.162*** (.012)		.100*** (.012)		.076*** (.014)	.032* (.014)
Child's PGS			.203*** (.012)		.149*** (.012)	.163*** (.014)	.133*** (.014)
Adjusted <i>R</i> -square	.122	.028	.043	.132	.144	.048	.145
<i>N</i> of Observations	6,298	6,298	6,298	6,298	6,298	6,298	6,298
Panel 2: HRS (G1 and G2)							
Parent's Education	.314*** (.008)				.292*** (.008)		
Parent's PGS							
Child's PGS			.210*** (.007)		.175*** (.007)		
Adjusted <i>R</i> -square	.143		.072		.184		
<i>N</i> of Observations	12,579		12,579		12,579		
Panel 3: HRS (G2 and G3)							
Parent's Education	.432*** (.013)			.406*** (.014)			
Parent's PGS		.177*** (.011)		.088*** (.011)			
Child's PGS							
Adjusted <i>R</i> -square	.156	.039		.163			
<i>N</i> of Observations	6,900	6,900		6,900			

Note: Standard errors are robust to clustering on individual ID and family ID in the data. All models control for the largest seven principal components for adjusting population stratification.

* $p < .05$; ** $p < .01$; *** $p < .001$ (two-tailed tests).

genotypes and unobserved factors that link to both parental and children's education. When parents' PGS and children's PGS are both controlled, the parent-child association in education is reduced by 8.4 percent.

When parents' PGS and children's PGS are both included as predictors, the coefficient of parents' PGS drops by 53 percent (Sobel test $p < .001$) but remains significant (see Model 6). This suggests that about half of the effect of parents' genotypes on children's educational attainment operates through the biological pathway, and the other half operates through the social pathway. Model 7 shows that after controlling for parents' education and PGS, the coefficient for children's PGS drops by 34 percent, indicating that about one-third of the association between children's genotypes and their own education can be attributed to parents' genotypes and education.

The patterns are similar in HRS. Panel 2 in Table 3 shows results using 12,579 parent-child pairs with genotypes of the child in HRS (i.e., G1–G2 pairs). The parent-child association in education is .31. When parents' education and children's PGS are both included as predictors in the model (see Model 5 in Panel 2), the effect size of parents' education is reduced by 7.0 percent. Panel 3 in Table 3 shows results using 6,900 parent-child pairs with genotypes of the parent in HRS (i.e., G2–G3 pairs). The parent-child association in education is .43, and the association between parents' PGS and child's education is .18. When parents' education and parents' PGS are included as predictors in the model (see Model 4 in Panel 3), the coefficient for parents' education drops by 6.0 percent, and the coefficient for parents' PGS drops by 50 percent (Sobel test $p < .001$).

Most of the results are similar for father-child and mother-child pairs (see Appendix Table A1). To summarize, about 7.0 percent of the father-child association in education attainment is explained by PGSs, and 9.5 percent of the mother-child association in education attainment is explained by PGSs. There is significant evidence for social genetic

effects. Father's or mother's education mediates at least one-third of the association between father's or mother's PGS and children's education (Sobel test $p < .001$ for both father-child and mother-child pairs in FHS and HRS). More than one-quarter of the association between children's PGS and children's education can be attributed to father's or mother's PGS and education. Notably, although the association between father's PGS and child's education disappears when paternal education and child's PGS are added to the models, the association between mother's PGS and child's education is still significant after controlling for maternal education and children's PGS ($p < .05$ for interaction).

Transmission of Educational Attainment across Three Generations (Three-Generation Analyses)

Panel 1 in Table 4 displays results of the three-generation analyses using 1,411 grandparent-grandchild pairs with both educational attainment and genetic measures in FHS. Model 1 shows that the grandparent-grandchild association in education is .16. Models 2, 3, and 4 display associations between G1's, G2's, and G3's PGSs and G3's educational attainment. The association between G1's PGS and G3's education is smaller than the association between G2's PGS and G3's education and smaller than the association between G3's PGS and G3's education in magnitude. Models 5, 6, 7, and 9 show the results of assessing genetic confounding in the grandparent-grandchild association in education. The G1–G3 association in education drops by 6.2 percent when controlling for all three generations' PGSs. When all three generations' PGSs are included in the model to predict G3's education, the coefficient for G1's PGS is reduced by 85 percent (Sobel test $p < .001$) and becomes non-significant. This suggests that the effect of grandparents' genotypes on grandchildren's education is mediated by parents' genotypes and grandchildren's genotypes (see Model 8 in Panel 1). Model 10 shows that the effect size of G1's education

Table 4. Coefficients (Standard Errors) of Three-Generation Models of Grandchildren's Educational Attainment

	Model 1	Model 2	Model 3	Model 4	Model 5	Model 6	Model 7	Model 8	Model 9	Model 10	Model 11	Model 12	Model 13	Model 14
Panel 1: FHS														
G1 Education	.161*** (.027)	.126*** (.026)	.146*** (.027)	.156*** (.026)	.150*** (.026)	.151*** (.026)	.068** (.026)	.066* (.026)	.075** (.026)	.068** (.026)	.077** (.026)			
G2 Education										.332*** (.025)	.324*** (.026)	.297*** (.026)	.300*** (.025)	.294*** (.026)
G1 PGS					.104*** (.026)		.019 (.031)	-.010 (.035)		.035 (.026)				-.049 (.029)
G2 PGS			.204*** (.026)		.200*** (.026)		.112*** (.035)	.127*** (.035)				.137*** (.026)		.094** (.033)
G3 PGS				.219*** (.027)			.211*** (.025)	.156*** (.030)	.148*** (.030)				.163*** (.025)	.129*** (.029)
Adjusted <i>R</i> -square	.039	.029	.056	.064	.049	.079	.084	.073	.094	.130	.130	.147	.155	.159
<i>N</i> of Observations	1,411	1,411	1,411	1,411	1,411	1,411	1,411	1,411	1,411	1,411	1,411	1,411	1,411	1,411
Panel 2: HRS														
G1 Education	.162*** (.009)				.142*** (.008)					.028*** (.008)		.025** (.008)		
G2 Education										.425*** (.010)		.402*** (.010)		
G1 PGS														
G2 PGS			.169*** (.008)		.151*** (.008)							.081*** (.008)		
G3 PGS														
Adjusted <i>R</i> -square	.033		.036		.057					.152		.159		
<i>N</i> of Observations	12,579		12,579		12,579					12,579		12,579		

Note: Standard errors are robust to clustering on individual ID and family ID in the data. All models control for the largest seven principal components for adjusting population stratification.

* $p < .05$; ** $p < .01$; *** $p < .001$ (two-tailed tests).

drops by 58 percent after controlling for G2's education (Sobel test $p < .001$). However, adding PGSs to the model does not significantly reduce the estimate of the direct effect of grandparents' education on grandchildren's education net of parents' education (see Models 11 through 14 in Panel 1).

In HRS, the G1–G3 association in education is .16. This drops by 12 percent after controlling for G2's PGSs. The estimate of the effect of grandparents' education on grandchildren's education net of parents' education is .03. Similar to FHS, including G2's PGS as a covariate does not significantly reduce the effect size of grandparents' effect net of parents' education (see Model 12 in Panel 2).

Stratified analyses were conducted for paternal grandfather-grandchild, paternal grandmother-grandchild, maternal grandfather-grandchild, and maternal grandmother-grandchild pairs. Results from FHS and HRS consistently show four findings (see Appendix Table A2). First, the grandparent-grandchild association in educational attainment is greater in the matrilineal line than in the paternal line ($p < .05$ for interaction) (see Model 1 in Table A2). Second, whereas paternal grandparent-grandchild association in education is completely mediated by father's education (Sobel test $p < .001$), maternal grandparent-grandchild association in education drops but remains significant after including mother's education as a covariate in the models (Sobel test $p < .001$) (see Model 10 in Table A2). Third, the association between grandparents' PGS and grandchildren's education is completely mediated by parents' PGS and grandchildren's PGS (Sobel test $p < .001$). Fourth, including PGSs from three generations does not significantly change the estimate of the direct effect of grandparents' education on grandchildren's education net of parents' education (see Models 11 through 14 in Table A2).

Sensitivity Analyses

The three-generation results may suffer from sample attrition. In FHS, genotypes are only

available for 21 percent of the participants in the original cohort (G1) (versus 71 percent in G2 and 95 percent in G3). Compared to participants whose genotypes are missing, those who provided genotypes are younger and better educated. This may lead to biased model estimates (Domingue et al. 2016; Liu and Guo 2015).

The influence of missing genotypes in G1 can be assessed by taking advantage of the unique multigenerational design of FHS. Because parents and children share 50 percent of their genes, children's genotypes can be used as proxies of parents' genotypes (Marioni et al. 2016). As shown in Table 2, PGSs in FHS are highly correlated between parents and children. To conduct a sensitivity test, I imputed missing PGSs in G1 based on G2's PGSs and G1's educational attainment using the multiple imputation technique (Rubin 1987). As a result, I imputed PGSs of an additional 1,897 G1 participants.

I replicated the three-generation analyses using the imputed data. Table 5 shows the results. Consistent with the original results, including PGSs from three generations does not significantly change the estimate of the effect of grandparents' education on grandchildren's education net of parents' education. Notably, the estimate of the association between grandparents' PGS and grandchildren's education remains significant after controlling for parents' PGS and grandchildren's PGS using the imputed data (see Model 8). This is partially due to the fact that the model estimates based on the imputed data have smaller standard errors as a result of an increase in the sample size.

DISCUSSION AND CONCLUSIONS

This study makes several important contributions to stratification and education research. First, I directly address genetic confounding, a critical concern in stratification studies. Stratification scholars have long been interested in complex socio-environmental mechanisms that operate at multiple levels and

Table 5. Sensitivity Analyses: Coefficients (Standard Errors) of Three-Generation Models Using Imputed Data in FHS

	Model 1	Model 2	Model 3	Model 4	Model 5	Model 6	Model 7	Model 8	Model 9	Model 10	Model 11	Model 12	Model 13	Model 14
G1 Education	.160*** (.013)		.142*** (.014)	.143*** (.013)	.143*** (.013)	.135*** (.013)	.063*** (.013)	.058*** (.012)	.057*** (.013)	.058*** (.013)	.058*** (.013)	.058*** (.013)	.058*** (.013)	.058*** (.013)
G2 Education							.337*** (.014)	.329*** (.014)	.318*** (.014)	.310*** (.014)	.310*** (.014)	.310*** (.014)	.310*** (.014)	.308*** (.014)
G1 PGS		.126*** (.015)			.101*** (.016)			.044* (.017)	.022 (.018)		.043* (.019)			-.016 (.022)
G2 PGS			.166*** (.013)			.151*** (.013)		.063** (.018)	.062*** (.018)			.101*** (.013)		.048** (.018)
G3 PGS				.202*** (.013)			.190*** (.013)	.159*** (.015)	.154*** (.015)				.142*** (.012)	.122*** (.014)
Adjusted <i>R</i> -square	.028	.018	.031	.045	.037	.050	.064	.051	.064	.122	.123	.131	.141	.143
N of Observations	5,596	5,596	5,596	5,596	5,596	5,596	5,596	5,596	5,596	5,596	5,596	5,596	5,596	5,596

Note: Standard errors are robust to clustering on individual ID and family ID in the data. All models control for the largest seven principal components for adjusting population stratification.

* $p < .05$; ** $p < .01$; *** $p < .001$ (two-tailed tests).

various dimensions in the reproduction of SES across generations (Blau and Duncan 1967; Bourdieu and Passeron 1977; Coleman 1988; Featherman and Hauser 1976; Grusky and DiPrete 1990; Hauser 1971; Hout 1988; Mare 1993; Sewell et al. 1969; Teachman 1987). However, estimation of the socio-environmental effects might be confounded by unobserved genetic heterogeneity. Recent advances in molecular genetics have produced tremendous molecular genetic data, allowing us to directly address genetic confounding. This study shows that around 8 percent of the intergenerational association in educational attainment is accounted for by PGSs, based on a recent GWAS on educational attainment (Okbay, Beauchamp, et al. 2016). PGS, however, is known to underestimate genetic variation, so researchers have developed methods to correct for PGS results (Conley et al. 2015; DiPrete, Burki, and Koellinger 2017; Tucker-Drob 2017). Based on the method proposed by Tucker-Drob (2017), the estimate of genetic contribution to intergenerational transmission of educational attainment is about 20 percent,⁴ which is slightly higher than the one-sixth estimate in Conley and colleagues' (2015) study based on an earlier GWAS (Rietveld et al. 2013).

Second, this study is among the first to empirically investigate social genetic effects. Analyses using data from FHS show that the association between parents' PGS and children's educational attainment in FHS remains significant when children's PGS is controlled (see Table 3). This result offers strong evidence for social genetic effects that operate through non-biological pathways. As additional results show, as much as half of the association between parents' PGS and children's education is mediated by parents' education, and one-third of the association between children's PGS and their own educational attainment is attributable to parents' PGS and education. These findings significantly improve our understanding of the complex mechanisms through which genes and the social environment jointly influence education. These results imply that the genetic

association with children's educational attainment can be modified through changes in parents' education. Children's genetic potential to achieve high levels of education cannot be fully realized without parents providing a good educational environment.

Moreover, the social genetic effects remain statistically significant after controlling for parents' education, suggesting that parents' genotypes may generate social advantages beyond their own education. Yet this result only holds for mother-child pairs; the association between father's PGS and children's educational attainment is completely mediated by children's PGS and father's education.

Third, this study extends the intergenerational analyses to three generations. Despite increasing interest in the influence of grandparents on grandchildren (Aldous 1995; Chan and Boliver 2013; Cherlin and Furstenberg 1992; Deleire and Kalil 2002; Erola and Moisio 2007; Jæger 2012; Mare 2011; Sharkey and Elwert 2011; Song 2016; Song and Mare 2017; Warren and Hauser 1997; Zeng and Xie 2014), investigation of genetic factors in multigenerational processes has been limited. Using genetic and educational attainment measures from three generations in FHS, I examined to what extent the effect of grandparents' education on grandchildren's educational attainment reflects genetic and social inheritance, and to what extent the effect of grandparents' genotypes operates through social pathways. Results of three-generation analyses show that the estimate of the effect of grandparents' education on grandchildren's education net of parents' education does not change significantly after controlling for PGSs. Moreover, the association between grandparents' PGS and grandchildren's education is no longer significant when parents' PGS and grandchildren's PGS are controlled.

Due to data limitations, the three-generation results should be interpreted with caution. Analyses based on a larger imputed sample show that the association between grandparents' PGS and grandchildren's education is small in magnitude but remains significant after controlling for parents' PGS and

grandchildren's PGS. This suggests that the social genetic effects of grandparents on grandchildren may exist, but detecting such effects requires large samples. Moreover, as shown in Table 2, the genetic correlation with education is lower in older generations than in younger generations. This is likely because older generations had fewer educational opportunities, and thus there was less room for their genetic potential to be realized. Because G1's genetic effects on their own education are small, their social genetic effects on their offspring are expected to be small as well. However, genetic effects on education have increased over time, and grandparents' genes may become more influential in grandchildren's lives in future generations (e.g., G2's social genetic effects on G4 [i.e., generation 4] may exceed G1's social genetic effects on G3). In other countries or cultures (e.g., China) where grandparents are more involved in raising their grandchildren (Zeng and Xie 2014), social genetic effects may play a more important role. These hypotheses can be tested when data from future generations and other countries and cultures become available.

Finally, this study highlights the importance of integrating advances in socio-genomics with conventional sociological research. Genetic contributions to human traits of interest to social scientists have traditionally been assessed using heritability estimates based on twins, adoptees, or other family data (e.g., Boardman et al. 2010; Boardman et al. 2012; Guo and Stearns 2002; Nielsen 2006, 2008; Nielsen and Roos 2015; Turkheimer et al. 2003). However, as Jencks (1980) argued almost four decades ago, heritability estimates only set an upper limit on the outcome traceable to genetic variation, they cannot separate endogenous environmental variance (e.g., phenotypic variation due to social genetic effects) and exogenous environmental variance (e.g., phenotypic variation due to environmental factors independent of genotypes). Heritability estimates are thus of limited use for public policy, as they cannot be used to assess the effects of creating new

environments. As shown in this study, molecular genetic data enable us to disentangle endogenous environmental influences and exogenous environmental influences. Such data are increasingly available in large-scale social science datasets (e.g., the Fragile Families Study, the National Longitudinal Study of Adolescent to Adult Health, and the Wisconsin Longitudinal Study), providing social scientists unprecedented opportunities to study complex social outcomes.

Some limitations must be acknowledged. First, the PGS approach suffers from a lack of statistical power in predicting genetic variation. GREML results show that the genome-wide SNPs explain at least 20 percent of the variation in education (Rietveld et al. 2013), but the PGSs only produce an *R*-square of 3.9 percent in FHS and 6.6 percent in HRS. This discrepancy may be due to the fact that PGSs are constructed based on results of GWAS that typically assume homogeneous genetic effects. The true genetic effects, however, may vary across samples, probably due to heterogeneity in phenotypic measurement or gene-environment interactions (de Vlaming et al. 2017). Advances in gene-environment interaction studies and increases in the sample size of GWAS may produce better-powered polygenic scores that can improve the analysis. Second, different methods have been developed to adjust PGS results, yet current methods typically treat SNP heritability and the proportion of phenotypic variance explained by PGS as fixed terms. As a result, the standard error of adjusted PGS results might be downwardly biased (Tucker-Drob 2017). Third, the two-generation analysis in this study focuses on parent-child pairs. In addition to genotypes of the parent in the analysis, the other parent's genotypes could be an important omitted variable in the estimation of socio-environmental effects in intergenerational transmission of education. Ideally, genotypes of both biological parents should be considered. However, the sample size would be largely reduced if the analytic sample is limited to families in which both parents' genotypes are available. The three-generation

analysis suffers from the same issue. Fourth, whereas genotypes are available for all three generations in FHS, they are only available for G2 in HRS. Replication analyses in the present study are thus incomplete. More extensive analyses should be conducted in future studies when more data become available.

Despite these limitations, this study provides important insights and opens future avenues for both stratification studies and socio-genomic research. Integrating genetic

measures in stratification models not only improves the estimate of socio-environmental effects, but it also helps us obtain a better estimate of direct genetic effects. Additionally, the multigenerational model developed in this study can be expanded to include more generations, beyond grandparents, so that the influence of remote ancestors on offspring can be studied. This model can also be used for other outcomes produced by both genetic and environmental effects.

APPENDIX

Table A1. Coefficients (Standard Errors) of Two-Generation Models (Stratified by Father-Child and Mother-Child Pairs)

	Model 1	Model 2	Model 3	Model 4	Model 5	Model 6	Model 7
Panel 1: FHS Father							
Father's Education	.345*** (.018)			.330*** (.018)	.321*** (.018)		.321*** (.018)
Father's PGS		.145*** (.018)		.078*** (.018)		.055** (.021)	.005 (.020)
Child's PGS			.197*** (.017)		.144*** (.017)	.169*** (.020)	.141*** (.020)
Adjusted <i>R</i> -square	.127	.021	.040	.132	.148	.042	.147
<i>N</i> of Observations	2,806	2,806	2,806	2,806	2,806	2,806	2,806
Panel 2: FHS Mother							
Mother's Education	.346*** (.016)			.323*** (.016)	.319*** (.016)		.313*** (.016)
Mother's PGS		.179*** (.016)		.120*** (.016)		.095*** (.020)	.055** (.019)
Child's PGS			.209*** (.016)		.154*** (.016)	.157*** (.020)	.125*** (.019)
Adjusted <i>R</i> -square	.118	.034	.045	.132	.140	.051	.142
<i>N</i> of Observations	3,492	3,492	3,492	3,492	3,492	3,492	3,492
Panel 3: HRS (G1 and G2) Father							
Father's Education	.313*** (.011)				.290*** (.010)		
Father's PGS							
Child's PGS			.211*** (.011)		.172*** (.010)		
Adjusted <i>R</i> -square	.149		.072		.188		
<i>N</i> of Observations	6,178		6,178		6,178		
Panel 4: HRS (G1 and G2) Mother							
Mother's Education	.316*** (.011)				.295*** (.011)		
Mother's PGS							
Child's PGS			.209*** (.010)		.178*** (.010)		
Adjusted <i>R</i> -square	.136		.072		.179		
<i>N</i> of Observations	6,401		6,401		6,401		
Panel 5: HRS (G2 and G3) Father							
Father's Education	.421*** (.021)			.393*** (.021)			
Father's PGS		.190*** (.019)		.105*** (.018)			
Child's PGS							
Adjusted <i>R</i> -square	.150	.041		.160			
<i>N</i> of Observations	2,546	2,546		2,546			
Panel 6: HRS (G2 and G3) Mother							
Mother's Education	.438*** (.017)			.414*** (.017)			
Mother's PGS		.168*** (.014)		.078*** (.014)			
Child's PGS							
Adjusted <i>R</i> -square	.159	.038		.165			
<i>N</i> of Observations	4,354	4,354		4,354			

Note: Standard errors are robust to clustering on individual ID and family ID in the data. All models control for the largest seven principal components for adjusting population stratification.

* $p < .05$; ** $p < .01$; *** $p < .001$ (two-tailed tests).

Table A2. Coefficients (Standard Errors) of Three-Generation Models (Stratified by Parents' and Grandparents' Sexes)

	Model 1	Model 2	Model 3	Model 4	Model 5	Model 6	Model 7	Model 8	Model 9	Model 10	Model 11	Model 12	Model 13	Model 14
Panel 1: FHS Paternal Grandfather														
G1 Education	.099 (.075)				.113 (.075)	.054 (.072)	.087 (.071)		.082 (.071)	-.001 (.070)	.017 (.071)	-.015 (.069)	-.004 (.070)	.013 (.068)
G2 Education										.364*** (.059)	.370*** (.058)	.316*** (.064)	.343*** (.059)	.302*** (.064)
G1 PGS		-.057 (.084)			-.086 (.077)									
G2 PGS			.280*** (.074)			.270*** (.075)						.161* (.078)		.217* (.093)
G3 PGS				.165*** (.057)			.161** (.056)	.046 (.066)	.045 (.066)				.112* (.056)	.044 (.066)
Adjusted <i>R</i> -square	.005	-.002	.060	.030	.005	.059	.032	.083	.085	.122	.126	.137	.133	.156
N of Observations	235	235	235	235	235	235	235	235	235	235	235	235	235	235
Panel 2: FHS Paternal Grandmother														
G1 Education	.130** (.045)				.121** (.044)	.145** (.044)	.137** (.044)		.141** (.044)	.048 (.041)	.048 (.041)	.060 (.042)	.057 (.042)	.064 (.042)
G2 Education										.385*** (.041)	.375*** (.044)	.358*** (.044)	.361*** (.042)	.357*** (.045)
G1 PGS		.150*** (.042)			.142*** (.042)			.062 (.050)	.039 (.049)					-.032 (.047)
G2 PGS			.198*** (.046)			.211*** (.047)		.092 (.061)	.119 (.062)			.095* (.048)		.060 (.061)
G3 PGS				.198*** (.046)			.204*** (.046)	.128* (.054)	.130* (.054)				.126*** (.045)	.109 (.052)
Adjusted <i>R</i> -square	.008	.015	.025	.025	.029	.047	.045	.036	.056	.162	.161	.167	.174	.172
N of Observations	451	451	451	451	451	451	451	451	451	451	451	451	451	451
Panel 3: FHS Maternal Grandfather														
G1 Education	.221*** (.061)				.195** (.062)	.177** (.062)	.176** (.059)		.172** (.061)	.151* (.060)	.140* (.061)	.127* (.060)	.121* (.058)	.126* (.060)
G2 Education										.272*** (.064)	.262*** (.065)	.228*** (.062)	.240*** (.063)	.229*** (.063)
G1 PGS		.156* (.075)			.102 (.076)			-.004 (.081)	-.046 (.083)		.053 (.076)			-.071 (.083)
G2 PGS			.243*** (.059)			.214*** (.060)		.157* (.074)	.160* (.072)			.176** (.060)		.136 (.070)

(continued)

Table A2. (continued)

	Model 1	Model 2	Model 3	Model 4	Model 5	Model 6	Model 7	Model 8	Model 9	Model 10	Model 11	Model 12	Model 13	Model 14
G3 PGS				.253*** (.068)			.221** (.068)	.158 (.081)	.139 (.077)				.191** (.067)	.130 (.076)
Adjusted <i>R</i> -square	.059	.037	.081	.080	.063	.103	.101	.090	.109	.107	.106	.134	.137	.141
N of Observations	277	277	277	277	277	277	277	277	277	277	277	277	277	277
Panel 4: FHS Maternal Grandmother														
G1 Education	.184*** (.052)				.160** (.053)	.179*** (.052)	.159** (.051)		.154** (.050)	.083 (.056)	.074 (.056)	.090 (.055)	.078 (.054)	.078 (.053)
G2 Education										.297*** (.052)	.277*** (.053)	.265*** (.051)	.250*** (.051)	.244*** (.051)
G1 PGS		.151*** (.041)			.125** (.042)			.075 (.055)	.041 (.054)		.080 (.042)			.001 (.053)
G2 PGS			.169*** (.046)			.165*** (.046)		.013 (.069)	.036 (.067)			.128** (.045)		.026 (.065)
G3 PGS				.245*** (.044)			.232*** (.044)	.217*** (.056)	.203*** (.055)				.199*** (.042)	.183*** (.053)
Adjusted <i>R</i> -square	.047	.041	.050	.086	.060	.075	.105	.087	.104	.099	.103	.114	.140	.137
N of Observations	448	448	448	448	448	448	448	448	448	448	448	448	448	448
Panel 5: HRS Paternal Grandfather														
G1 Education	.135*** (.020)					.117*** (.020)				-.004 (.020)		-.005 (.020)		
G2 Education										.439*** (.023)		.412*** (.024)		
G1 PGS														
G2 PGS			.185*** (.020)			.173*** (.020)								
G3 PGS												.101*** (.019)		
Adjusted <i>R</i> -square	.022	.039	.039	.022	.052	.052	.052	.052	.052	.147	.147	.157	.157	.157
N of Observations	2,318	2,318	2,318	2,318	2,318	2,318	2,318	2,318	2,318	2,318	2,318	2,318	2,318	2,318
Panel 6: HRS Paternal Grandmother														
G1 Education	.138*** (.022)									.014 (.021)	.014 (.021)	.014 (.021)	.014 (.021)	.014 (.021)
G2 Education						.125*** (.022)				.425*** (.023)		.399*** (.023)		
G1 PGS														
G2 PGS			.179*** (.020)			.171*** (.020)								.097*** (.019)

(continued)

Table A2. (continued)

	Model 1	Model 2	Model 3	Model 4	Model 5	Model 6	Model 7	Model 8	Model 9	Model 10	Model 11	Model 12	Model 13	Model 14
G3 PGS														
Adjusted <i>R</i> -square	.022		.037		.051	.145						.154		
N of Observations	2,355		2,355		2,355	2,355						2,355		
Panel 7: HRS Maternal Grandfather														
G1 Education	.168*** (.014)				.149*** (.015)	.041** (.015)				.410*** (.018)		.037* (.015)		
G2 Education												.392*** (.019)		
G1 PGS														
G2 PGS			.156*** (.015)		.133*** (.015)							.067*** (.015)		
G3 PGS														
Adjusted <i>R</i> -square	.038		.032		.056	.149						.154		
N of Observations	3,860		3,860		3,860	3,860						3,860		
Panel 8: HRS Maternal Grandmother														
G1 Education	.184*** (.015)				.163*** (.015)	.043** (.015)				.428*** (.019)		.039** (.015)		
G2 Education												.407*** (.019)		
G1 PGS														
G2 PGS			.166*** (.015)		.144*** (.015)							.075*** (.015)		
G3 PGS														
Adjusted <i>R</i> -square	.040		.035		.062	.159						.164		
N of Observations	4,046		4,046		4,046	4,046						4,046		

Note: Standard errors are robust to clustering on individual ID and family ID in the data. All models control for the largest seven principal components for adjusting population stratification.
 * $p < .05$; ** $p < .01$; *** $p < .001$ (two-tailed tests).

Data and Funding

This article is based on data from the Framingham Heart Study (FHS) and the Health and Retirement Study (HRS). FHS is conducted and supported by the National Heart, Lung, and Blood Institute (NHLBI) in collaboration with Boston University (Contract No. N01-HC-25195). Funding for sharing genotyping was provided by NHLBI Contract N02-HL-64278. HRS is sponsored by National Institute on Aging Grants NIA U01AG009740, RC2AG036495, and RC4AG039029, and conducted by the University of Michigan. This manuscript was not prepared in collaboration with investigators of the two studies and does not necessarily reflect their opinions or views. This research benefitted from GWAS results made publicly available by Social Science Genetic Association Consortium.

Acknowledgments

Many thanks go to Guang Guo, Kathleen M. Harris, François Nielsen, Michael J. Shanahan, Yang C. Yang, J. C. Barnes, the *ASR* editors, and anonymous reviewers for their helpful comments on the manuscript. An earlier version of this manuscript was presented at the 2017 Integrating Genetics and Social Sciences annual meeting.

Notes

1. The original GWAS included HRS participants. To calculate PGSs for HRS participants, I requested, from the Social Science Genetic Association Consortium (<https://www.thessgac.org/>), revised b -weights estimated from data excluding the HRS.
2. I conducted sensitivity analyses based on PGSs produced using different pruning and clumping strategies. The main results are similar. The results reported here are based on the PGSs that best fit the data.
3. This included G1–G2 and G2–G3 pairs.
4. According to Tucker-Drob (2017),

$$\beta_{adj} = \beta \sqrt{\frac{h_{SNP}^2}{R_{PGS}^2}}, \text{ where } \beta_{adj} \text{ is the adjusted coefficient,}$$

β is the original coefficient, R_{PGS}^2 is the proportion of phenotypic variance explained by the polygenic score, and h_{SNP}^2 is the SNP heritability. In this analysis, R_{PGS}^2 and h_{SNP}^2 are calculated based on HRS data. h_{SNP}^2 is estimated using the Genomic-relatedness-matrix Restricted Maximum Likelihood Method (i.e., GREML) (Yang et al. 2011).

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