Supplementary Information

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Supplementary Results

Non-additive effects

Given that additive models can identify variants that exhibit stronger dominant or recessive effects[1], we tested all the identified signals for departure from an additive model. We identified three variants exhibiting non-additive effects (**Supplementary Table 3 and Supplementary Figure 1**). For a common variant in *PIWIL1* (rs28416520, MAF=46%, $P=2\times10^{-14}$) a recessive model was the best fit (**Supplementary Figure 1c**). Deletion of *Piwil1* in mice results in sterility in males, but not females, and its role in human oogenesis is uncertain. It is however expressed as a dense paranuclear granule in human primordial follicle oocytes[2]. A low-frequency missense variant in *HELB* (rs75770066, MAF=3%, $P=7\times10^{-16}$) appeared to exhibit a heterozygous advantage effect (**Supplementary Figure 1d**), with higher mean ANM in the heterozygous group (95% CI 51.37-51.58 years) than the common (50.24-50.30) and rare homozygote (48.58-50.16) groups. Further fine-mapping and experimental work will be required to understand the complex biological mechanism(s) at this locus.

Menopause associated genes act across the life-course

Previous large-scale genetic analyses highlighted a clear involvement of homologous recombination and the *BRCA1-A* complex in the regulation of ovarian ageing. Our current study supports much broader DDR involvement, providing increased resolution of these pathways and informing when in the life-course they might act.

Our identified genes and pathway analyses strongly implicate repair pathways associated with replication stress, in particular removal of interstrand crosslinks, which covalently join both strands of the DNA helix, as well as DNA-protein crosslinks and R loops (DNA:RNA hybrids). All of these lesions stall DNA replication and prevent transcription (**Extended Data Fig. 5)**. This observation is supported by recent work demonstrating the role of the interstrand crosslink pathway *in utero* for resolving DNA damage in pre-meiotic, primordial germ cells[3]. This process begins with replication fork remodelling at interstrand crosslinks by *FANCM*[4–6], where we identify two independent ANM-associated missense variants (**Supplementary Table 4**). This subsequently leads to recruitment of the core Fanconi Anaemia (FA) complex to signal DNA damage, where we map missense variants in two of the eight genes – *FANCA* and *FANCB*. Furthermore we identify variants mapping key genes in the downstream repair systems coordinated by the FA pathway, including homologous recombination (e.g *RAD51*, *BRCA1*, *BRCA2*) as well as translesion synthesis (e.g *REV1*, *REV3L* and *RAD18*)[7].

Several DDR genes highlighted by our study have critical meiotic functions in fetal oocytes where at least 500 programmed double-strand breaks (DSBs) initiate recombination[8]. We implicate key recombination and synaptonemal complex genes with functions in meiotic prophase (*STAG3*, *SMC1β, EXO1*, *RAD51, DMC1, HELQ, RAD52, MSH5*). Mouse models of these genes show defective repair of meiotic recombination and subsequent apoptosis of fetal oocytes resulting in decreased primordial follicles from birth and infertility[9–17]. We note that several of our ANM-associated variants overlap those recently reported for recombination rate[18], however, despite more nominally significant associations than expected by chance, there was no clear relationship between the direction of effect on menopause and recombination rate across the 290 ANM loci (**Supplementary Table 19**).

A range of factors likely contribute to the rate at which follicles are recruited and the follicular reserve depleted. Our data implicate key genes in the mTOR complex 1 (mTORC1) in ANM, including *STK11* and *DEPTOR.* The mTOR protein kinase that controls cell growth by regulating protein and

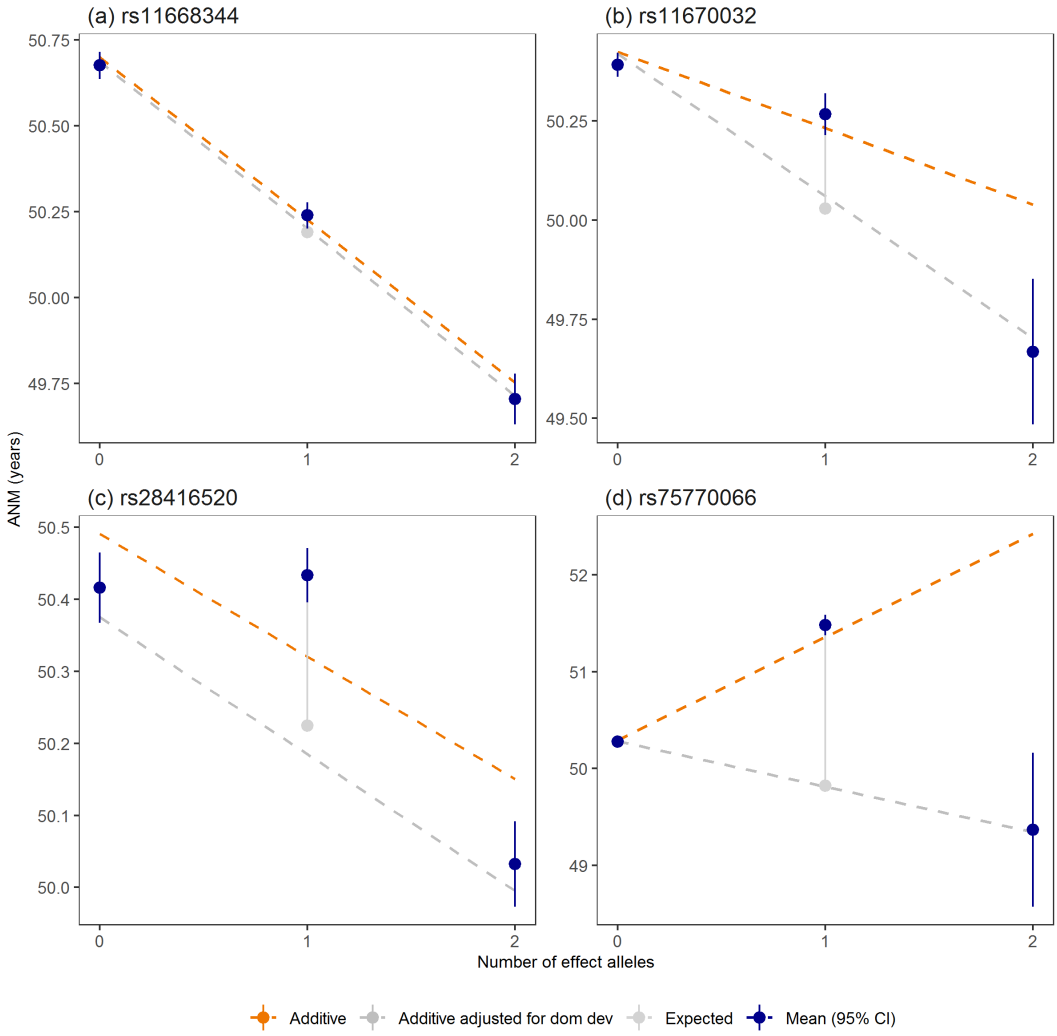
nucleotide synthesis and is activated by the PI3K pathway. Oocyte-specific deletion of *Pten* in mice removes the inhibiting effect of the PI3K pathway on primordial follicle activation, leading to premature recruitment and exhaustion of the entire primordial follicle pool[19]. Other ANM-implicated genes include *FSHB, NOBOX, INHBB, INHBC, LHCGR, IGF1, IGFBP1, PPARG* and *BMPR1B,* highlighting broader endocrine and metabolic mechanisms governing ANM. We also identified common variants in *FTO* associated with ANM (**Supplementary Table 2)** which are distinct from the well-established body weight association in this region (r^2 with lead BMI variant rs1558902 = 0.0002).

Finally, the majority of known genes causing POI implicate aberrant DNA damage or the inability to repair it, with limited evidence in humans that defects in the downstream cell-death signaling pathways impact variation in reproductive ageing. In contrast, our study identifies more than 58 genes implicated in regulation of apoptosis associated with ANM (**Supplementary Table 20**), providing evidence that variation in cell death following DDR is an important mechanism. This includes components and interactors of the central, conserved DDR checkpoint kinases ATR-CHEK1 (single stranded DNA) and ATM-CHEK2 (double strand breaks), that integrate and determine repair and cellular response from a broad variety of DNA repair pathways (**Extended Data Fig. 5**).

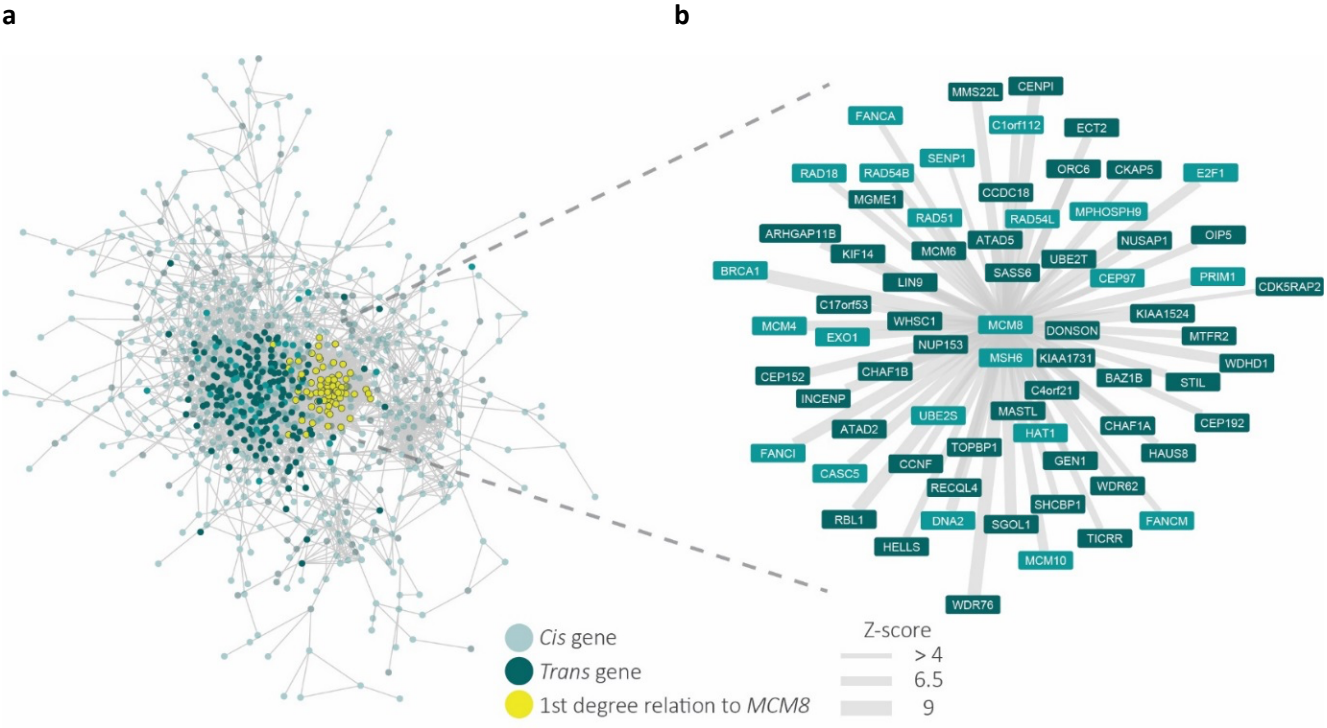
Whilst the breadth of DDR pathways identified suggests our identified loci may exert their effect at different stages across the life-course, we sought to evaluate this by assessing patterns of germ cell gene expression across different developmental stages. The individual expression profiles of our 283 consensus genes (**Supplementary Table 2**) were assessed in human fetal primordial germ cells from 5 to 26 weeks gestation, in addition to oocyte and granulosa expression in adult follicles at different stages of growth (**Extended Data Fig. 6 and Supplementary Table 21**). Collectively these data identified distinct clusters of genes that were active at different stages of life and follicle growth. The majority of our identified genes appeared most active in fetal primordial germ cells and fetal oocytes, however distinct expression profiles were evident across all developmental stages and between oocytes and granulosa cells (**Extended Data Fig. 6**). In many cases the pattern of expression was consistent with the known biological roles of those genes, for example Fanconi anemia genes were predominantly expressed in the fetal germ cells as well as the oocytes of the growing follicles, with less pronounced expression in granulosa cells (**Supplementary Table 21**). In contrast, genes such as *POLG* and *TP63* were predominantly expressed during follicular stages, consistent with apoptotic inducing activity in response to DNA damage observed in growing oocytes in mouse[20–23]. Further studies will be required to build on our observations and confirm the mechanism underlying the genetic associations.

Supplementary Figures

Supplementary Figure 1. Genome-wide significant signals showing departure from an additive model. We tested the identified signals for departure from an additive allelic model. **a,** rs11668344 shows no deviation from an additive allelic model; **b,** rs11670032 and **c,** rs28416520 show deviation from the additive allelic model and a recessive effect; and **d,** rs75770066 shows a heterozygote effect. The mean and 95% confidence interval around the mean estimate are shown for each genotype. The expected mean ANM for the heterozygotes is the average of the mean ANM in the homozygote groups. The dashed orange line shows the effect estimate by genotype from linear regression based on an additive allelic model. Estimated ANM for each genotype was calculated as constant from regression model + number alleles × effect estimate from regression model. The dashed grey line indicates the additive effect estimate by genotype from a model adjusting for the dominance deviation effect of the heterozygote group (solid grey line). All regression models were adjusted for centre, genotyping chip and genetic principal components. ANM, age at natural menopause; dom dev, dominance deviation.



Supplementary Figure 2. Gene co-regulation networks for age at menopause genes with those co-regulated with *MCM8* highlighted. a, Gene co-regulation network for genes relating to age at menopause. Nodes indicate genes that either in a *cis* region from the GWAS or have been prioritized by Downstreamer, edges indicate a co-regulation relationship with a Z-score >4. Co-regulation is defined as the Pearson correlation between genes in a scaled eigenvector matrix derived from a multi-tissue gene network [Deelen et al, Nat. Commun. 2019]. *Cis* genes are defined as genes that are within +/-300kb of a GWAS top hit for age at menopause. *Trans* genes are defined as having been prioritized by Downstreamer's co-regulation analysis and are not within +/-300kb of a GWAS top hit. Downstreamer prioritizes genes by associating the gene p-value profile of the GWAS (calculated using PASCAL [Lamparter et al, PLOS Comput. Biol. 2016]) to the co-regulation profile of each protein coding gene. Only genes where this association passes Bonferroni significance are shown as trans genes. Colours of nodes indicate the following: Teal indicates *Cis* genes, Dark Teal indicates *Trans* genes and Yellow indicates genes with a 1st degree relation to *MCM8*. **b,** Gene co-regulation network showing the genes that have a first degree relationship with *MCM8* with a Z-score >4. Width of the edge indicates the Z-score of the co-regulation relationship. Colours indicate the same as in **a**, with the exception of Yellow, as all genes indicated have a 1st degree relation to *MCM8.*



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Supplementary Notes

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Study acronym	Full study name	Acknowledgments and sources of funding
23andMe	23andMe	We would like to thank the research participants and employees of 23andMe for making this work possible. The following members of the 23andMe Research Team contributed to this study: Michelle Agee, Stella Aslibekyan, Adam Auton, Elizabeth Babalola, Robert K. Bell, Jessica Bielenberg, Katarzyna Bryc, Emily Bullis, Briana Cameron, Daniella Coker, Gabriel Cuellar Partida, Devika Dhamija, Sayantan Das, Sarah L. Elson, Teresa Filshtein, Kipper Fletez-Brant, Will Freyman, Pooja M. Gandhi, Karl Heilbron, Barry Hicks, David A. Hinds, Karen E. Huber, Ethan M. Jewett, Yunxuan Jiang, Aaron Kleinman, Katelyn Kukar, Vanessa Lane, Keng-Han Lin, Maya Lowe, Marie K. Luff, Jennifer C. McCreight, Matthew H. McIntyre, Kimberly F. McManus, Steven J. Micheletti, Meghan E. Moreno, Joanna L. Mountain, Sahar V. Mozaffari, Priyanka Nandakumar, Elizabeth S. Noblin, Jared O'Connell, Aaron A. Petrakovitz, G. David Poznik, Morgan Schumacher, Anjali J. Shastri, Janie F. Shelton, Jingchunzi Shi, Suyash Shringarpure, Chao Tian, Vinh Tran, Joyce Y. Tung, Xin Wang, Wei Wang, Catherine H. Weldon, Peter Wilton
AGES	Age, Gene/Environment Susceptibility-Reykjavik Study	This study has been funded by NIH contracts N01-AG-1-2100 and 271201200022C, the NIA Intramural Research Program, Hjartavernd (the Icelandic Heart Association), and the Althingi (the Icelandic Parliament). The study is approved by the Icelandic National Bioethics Committee, VSN: 00-063. The researchers are indebted to the participants for their willingness to participate in the study.
ALSPAC	Avon Longitudinal Study of Parents and Children	We are extremely grateful to all the families who took part in this study, the midwives for their help in recruiting them, and the whole ALSPAC team, which includes interviewers, computer and laboratory technicians, clerical workers, research scientists, volunteers, managers, receptionists and nurses. The UK Medical Research Council and the Wellcome Trust (Grant ref: 217065/Z/19/Z) and the University of Bristol provide core support for ALSPAC. GWAS data for ALSPAC mothers was funded by the Wellcome Trust (WT088806) and phenotype data by the British Heart Foundation (SP/07/008/24066), Wellcome Trust (WT092830M) and MRC (G1001357). GWAS data for ALSPAC offspring was generated by Sample Logistics and Genotyping Facilities at the Wellcome Trust Sanger Institute and LabCorp (Laboratory Corporation of America) using support from 23andMe. DAL, NJT, SMR and GDS work in a Unit that receives support from the University of Bristol and MRC (MC_UU_00011/1 and MC_UU_00011/6).
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BCAC/ iCOGs	Breast Cancer Association Consortium/ iCOGs	See separate section below for details of individual studies.
CARL	INGI-CARLANTINO	We would like to thank all the participants in the study for their contribution and support The study was supported through the Italian Ministry of Health
CHS	Cardiovascular Health Study	This CHS research was supported by NHLBI contracts HHSN268201200036C, HHSN268200800007C, HHSN268201800001C, N01HC55222, N01HC85079, N01HC85080, N01HC85081, N01HC85082, N01HC85083, N01HC85086; and NHLBI grants U01HL080295, R01HL087652, R01HL105756, R01HL103612, R01HL120393, U01HL130114 and 75N92021D00006 with additional contribution from the National Institute of Neurological Disorders and Stroke (NINDS). Additional support was provided through R01AG023629 from the National Institute on Aging (NIA). A full list of principal CHS investigators and institutions can be found at CHS-NHLBI.org. The provision of genotyping data was supported in part by the National Center for Advancing Translational Sciences, CTSI grant UL1TR001881, and the National Institute of Diabetes and Digestive and Kidney Disease Diabetes Research Center (DRC) grant DK063491 to the Southern California Diabetes Endocrinology Research Center. The content is solely the responsibility of the authors and does not necessarily represent the official views of the National Institutes of Health.
CILENTO	CILENTO	We thank the populations of Cilento for their participation in the study. This work was supported by grants from the Italian Ministry of Universities (FIRB-RBNE08NKH7, INTEROMICS Flagship Project), the Assessorato Ricerca Regione Campania, the Fondazione con il SUD (2011-PDR-13) and the Istituto Banco di Napoli - Fondazione to MC.
COLAUS	CoLaus (Etude Cohorte Lausannoise)	The CoLaus study was and is supported by research grants from GlaxoSmithKline, the Faculty of Biology and Medicine of Lausanne, and the Swiss National Science Foundation (grants 33CSCO-122661, 33CS30-139468, 33CS30-148401 and 33CS30_177535/1).
CROATIA Korcula	CROATIA Korcula	We would like to acknowledge the contributions of the recruitment team in Korcula, the administrative teams in Croatia and Edinburgh and the people of Korcula. The SNP genotyping for the KORCULA cohort was performed in Helmholtz Zentrum München, Neuherberg, Germany. Medical Research Council UK and the Ministry of Science, Education and Sport in the Republic of Croatia (number 108-1080315-0302).
CROATIA Vis	CROATIA Vis	We would like to acknowledge the staff of several institutions in Croatia that supported the field work, including but not limited to The University of Split and Zagreb Medical Schools, Institute for Anthropological Research in Zagreb and Croatian Institute for Public Health. Medical Research Council UK and the Ministry of Science, Education and Sport in the Republic of Croatia (number 108-1080315-0302).
EGCUT-370 and OmniX	Estonian Genome Center, University of Tartu	This study was supported by EU H2020 grants 692145, 676550, 654248, Estonian Research Council Grant IUT20-60, NIASC, and EU through the European Regional Development Fund (Project No. 2014-2020.4.01.15-0012 GENTRANSMED).
EPIC-Norfolk	The EPIC-Norfolk Study	The EPIC-Norfolk study (DOI 10.22025/2019.10.105.00004) has received funding from the Medical Research Council (MR/N003284/1 MC-UU_12015/1 and MC_UU_00006/1) and Cancer Research UK (C864/A14136). The genetics work in the EPIC-Norfolk study was funded by the Medical Research Council (MC_PC_13048). We are grateful to all the participants who have been part of the project and to the many members of the study teams at the University of

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FHS	Framingham Heart Study	The authors thank the Framingham Heart Study participants and staff. The Framingham Heart Study phenotype-genotype analyses were supported by NIA R01AG29451 JMM, KLL). The Framingham Heart Study of the National Heart Lung and Blood Institute of the National Institutes of Health and Boston University School of Medicine was supported by the National Heart, Lung and Blood Institute's Framingham Heart Study Contract No. N01-HC-25195 and its contract with Affymetrix, Inc for genotyping services (Contract No. N02-HL-6-4278). Analyses reflect intellectual input and resource development from the Framingham Heart Study investigators participating in the SNP Health Association Resource (SHARe) project. A portion of this research was conducted using the Linux Cluster for Genetic Analysis (LinGA-II) funded by the Robert Dawson Evans Endowment of the Department of Medicine at Boston University School of Medicine and Boston Medical Center. Framingham Heart Study Contract No. N01-HC-25195, HHSN268201500001 The authors are pleased to acknowledge that the computational work reported on in this paper was performed on the Shared Computing Cluster which is administered by Boston University's Research Computing Services. URL: www.bu.edu/tech/support/research/. The authors thank the participants for their dedication to the study.
FVG	INGI- FRIULI VENEZIA GIULIA	We would like to thank all the participants in the study for their contribution and support The study was supported by Regione FVG (L.26.2008) and Italian Ministry of Health
GS	Generation Scotland: Scottish Family Health Study	We are grateful to all the families who took part, the general practitioners and the Scottish School of Primary Care for their help in recruiting them, and the whole Generation Scotland team, which includes interviewers, computer and laboratory technicians, clerical workers, research scientists, volunteers, managers, receptionists, healthcare assistants and nurses. Generation Scotland received core support from the Chief Scientist Office of the Scottish Government Health Directorates [CZD/16/6] and the Scottish Funding Council [HR03006] and is currently supported by the Wellcome Trust [216767/Z/19/Z]. Genotyping of the GS:SFHS samples was carried out by the Genetics Core Laboratory at the Edinburgh Clinical Research Facility, University of Edinburgh, Scotland and was funded by the Medical Research Council UK and the Wellcome Trust (Wellcome Trust Strategic Award "STratifying Resilience and Depression Longitudinally" (STRADL) Reference 104036/Z/14/Z).
HANDLS		
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HRS	Health and Retirement Study	HRS is supported by the National Institute on Aging (NIA U01AG009740). The genotyping was funded separately by the National Institute on Aging (RC2 AG036495, RC4 AG039029). Our genotyping was conducted by the NIH Center for Inherited Disease Research (CIDR) at Johns Hopkins University. Genotyping quality control and final preparation of the data were performed by the Genetics Coordinating Center at the University of Washington.
INCHIANTI	Invecchiare in Chianti	The InCHIANTI study baseline (1998-2000) was supported as a "targeted project" (ICS110.1/RF97.71) by the Italian Ministry of Health and in part by the U.S. National Institute on Aging (Contracts: 263 MD 9164 and 263 MD 821336).
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KORA F3 / KORA F4	KORA F3 and F4: Cooperative Health Research in the Augsburg Region, Follow up for Study S3 and S4	The KORA study was initiated and financed by the Helmholtz Zentrum München – German Research Center for Environmental Health, which is funded by the German Federal Ministry of Education and Research (BMBF) and by the State of Bavaria. The KORA-Study Group consists of A. Peters (speaker), H. Schulz, R. Holle, R. Leidl, C. Meisinger, K. Strauch, and their co-workers, who are responsible for the design and conduct of the KORA studies. Furthermore, KORA research was supported within the Munich Center of Health Sciences (MC-Health), Ludwig-Maximilians-Universität, as part of LMUinnovativ. The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript. We thank all study participants and the study staff.
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NTR	The Netherlands Twin Register	The Netherland Twin Register: would like to thank all study participants for their contributions to our scientific efforts, the SURF SARA institute for computational resources and the Avera institute of Human Genetics for genotyping of samples. Funding was obtained from the Netherlands Organization for Scientific Research (NWO) and The Netherlands Organization for Health Research and Development (ZonMW) grants 904-61-090, 985-10-002, 912-10-020, 904-61-193,480-04-004, 463-06-001, 451-04-034, 400-05-717, Addiction-31160008, 016-115-035, 481-08-011, 400-07-080, 056-32-010, Middelgroot-911-09-032, OCW_NWO Gravity program –024.001.003, NWO-Groot 480-15-001/674, Center for Medical Systems Biology (CSMB, NWO Genomics), NBIC/BioAssist/RK(2008.024), Biobanking and Biomolecular Resources Research Infrastructure (BBMRI –NL, 184.021.007 and 184.033.111), X-Omics 184-034-019; Spinozapremie (NWO- 56-464-14192), KNAW Academy Professor Award (PAH/6635) and University Research Fellow grant (URF) to DIB; Amsterdam Public Health research institute (former EMGO+) , Neuroscience Amsterdam research institute (former NCA); Amsterdam Research & Development (AR&D) research institute; the European Community's Fifth and Seventh Framework Program (FP5- LIFE QUALITY-CT-2002-2006, FP7- HEALTH-F4-2007-2013, grant 01254: GenomEUtwin, grant 01413: ENGAGE and grant 602768: ACTION); the European Research Council (ERC Starting 284167, ERC Consolidator 771057, ERC Advanced 230374), Rutgers University Cell and DNA Repository (NIMH U24 MH068457-06), the National Institutes of Health (NIH, R01D0042157-01A1, R01MH58799-03, MH081802, DA018673, R01 DK092127-04, Grand Opportunity grants 1RC2 MH089951, and 1RC2 MH089995); the Avera Institute for Human Genetics, Sioux Falls, South Dakota (USA). Part of the genotyping and analyses were funded by the Genetic Association Information Network (GAIN) of the Foundation for the National Institutes of Health. Computing was supported by NWO through grant 2018/EW/00408559, BiG Grid, the Dutch e-Science Grid and SURFSARA.
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SHIP-Trend	Study of Health in Pomerania - Trend	SHIP is part of the Community Medicine Research net of the University of Greifswald, Germany, which is funded by the Federal Ministry of Education and Research (grants no. 01ZZ9603, 01ZZ0103, and 01ZZ0403), the Ministry of Cultural Affairs as well as the Social Ministry of the Federal State of Mecklenburg-West Pomerania. The University of Greifswald is a member of the Caché Campus program of the InterSystems GmbH.
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Study acronym	Full study name	Acknowledgments and sources of funding
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ABCFS	Australian Breast Cancer Family Study	ABCFS thank Maggie Angelakos, Judi Maskiell, Gillian Dite. The Australian Breast Cancer Family Study (ABCFS) was supported by grant UM1 CA164920 from the National Cancer Institute (USA). The content of this manuscript does not necessarily reflect the views or policies of the National Cancer Institute or any of the collaborating centers in the Breast Cancer Family Registry (BCFR), nor does mention of trade names, commercial products, or organizations imply endorsement by the USA Government or the BCFR. The ABCFS was also supported by the National Health and Medical Research Council of Australia, the New South Wales Cancer Council, the Victorian Health Promotion Foundation (Australia) and the Victorian Breast Cancer Research Consortium. J.L.H. is a National Health and Medical Research Council (NHMRC) Senior Principal Research Fellow. M.C.S. is a NHMRC Senior Research Fellow.
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CBCS	Canadian Breast Cancer Study	CBCS thanks study participants, co-investigators, collaborators and staff of the Canadian Breast Cancer Study, and project coordinators Agnes Lai and Celine Morissette. CBCS is funded by the Canadian Cancer Society (grant # 313404) and the Canadian Institutes of Health Research.
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Genome-wide analyses

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