

# A second update on mapping the human genetic architecture of COVID-19

<https://doi.org/10.1038/s41586-023-06355-3>

The COVID-19 Host Genetics Initiative\*

Received: 23 December 2022

Accepted: 21 June 2023

Published online: 6 September 2023

Open access

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ARISING FROM: COVID-19 Host Genetics Initiative. *Nature* <https://doi.org/10.1038/s41586-021-03767-x> (2021)

Investigating the role of host genetic factors in COVID-19 severity and susceptibility can inform our understanding of the underlying biological mechanisms that influence adverse outcomes and drug development<sup>1,2</sup>. Here we present a second updated genome-wide association study (GWAS) on COVID-19 severity and infection susceptibility to SARS-CoV-2 from the COVID-19 Host Genetic Initiative (data release 7). We performed a meta-analysis of up to 219,692 cases and over 3 million controls, identifying 51 distinct genome-wide significant loci—adding 28 loci from the previous data release<sup>2</sup>. The increased number of candidate genes at the identified loci helped to map three major biological pathways that are involved in susceptibility and severity: viral entry, airway defence in mucus and type I interferon.

We conducted a meta-analysis for 3 phenotypes across 82 studies from 35 countries, including 36 studies of individuals with non-European ancestry (Fig. 1, Supplementary Figs. 1 and 2 and Supplementary Table 1): critical illness (respiratory support or death; 21,194 cases), hospitalization (49,033 cases) and SARS-CoV-2 infection (219,692 cases). Most of the studies were collected before the widespread introduction of COVID-19 vaccination. We found 30, 40 and 21 loci that are associated with critical illness, hospitalization and infection due to SARS-CoV-2, respectively, for a total of 51 distinct genome-wide significant loci across all three phenotypes ( $P < 5 \times 10^{-8}$ ; Fig. 2, Supplementary Fig. 3 and Supplementary Table 2), adding 28 genome-wide significant loci to the 23 previously identified by the COVID-19 Host Genomics Initiative (HGI; data release 6)<sup>1,2</sup>. We observed a median increase of 2.9-fold in statistical power across lead variants owing to a median increase of 1.6-fold in effective sample sizes from the previous release (Supplementary Table 3). After correcting for the number of phenotypes examined, 46 loci remained significant ( $P < 1.67 \times 10^{-8}$ ). Of the 28 additional loci, 6 loci were originally reported by the GenOMICC study<sup>3</sup>, which also contributed to the current meta-analysis, and 9 other loci were identified by the new GenOMICC meta-analysis<sup>4</sup> during the preparation of this paper. We found nine more loci that reached genome-wide significance, but we excluded them as they were probably false positives, as determined using a leave-most-significant-biobank-out analysis (Supplementary Table 4 and Supplementary Note). Comparing the effect sizes and statistical significance between the previous<sup>2</sup> and current analysis indicated that all of the previously identified loci were replicated and showed an increase in statistical significance (Supplementary Fig. 4). Using our previously developed two-class Bayesian model for classifying loci as being more likely involved in infection susceptibility or severity<sup>2</sup>, we determined that 36 loci are substantially more likely (higher than 99% posterior probability) to affect disease severity (hospitalization) and 9 loci are substantially more likely to

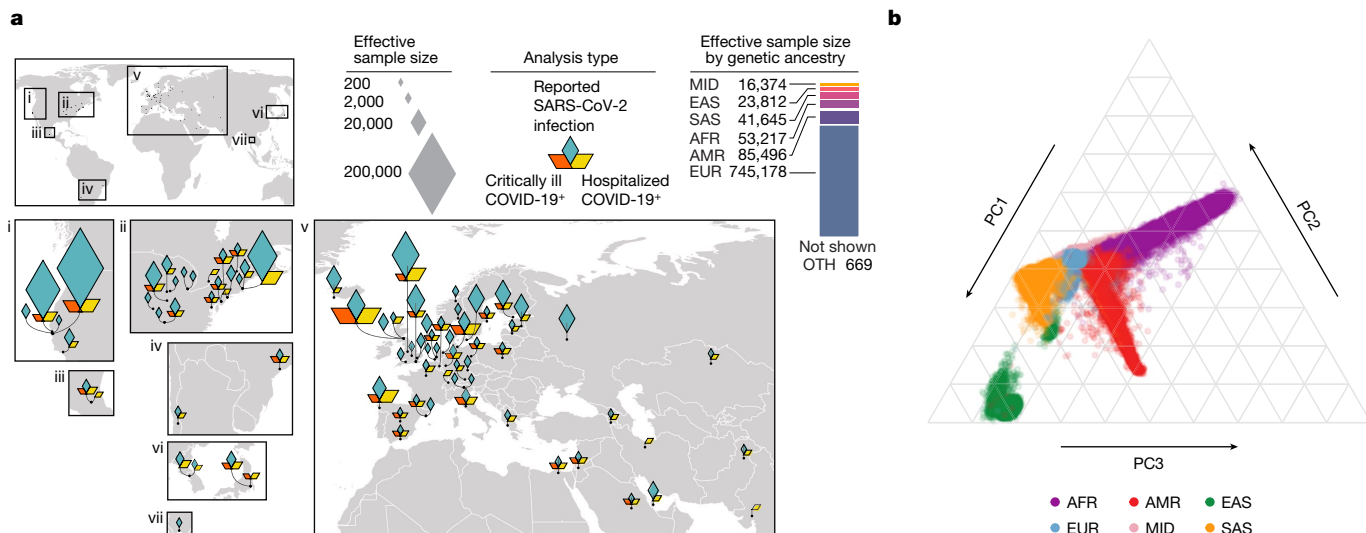
influence susceptibility to SARS-CoV-2 infection, while the remaining 6 loci could not be classified (Supplementary Fig. 5, Supplementary Table 5 and Supplementary Note). We observed that the 1q22 locus (lead variant: rs12752585:G>A) showed significant effect-size heterogeneity across ancestries ( $P_{\text{het}} < 9.80 \times 10^{-4} = 0.05/51$ ), whereas the previously reported heterogenous locus (*FOXP4*) remained at the same level of significance as before<sup>2</sup>, despite an increase in sample size ( $P_{\text{het}} = 2.01 \times 10^{-3}$ ; Supplementary Fig. 6 and Supplementary Table 6). We found significant observed-scale single-nucleotide polymorphism heritabilities of all the three phenotypes (1.2–8.2%,  $P < 0.0001$ ). We also estimated liability-scale heritabilities for a range of population prevalences (Supplementary Fig. 7, Supplementary Table 7 and Supplementary Note).

To better understand the biological mechanisms underlying COVID-19 susceptibility and severity, we further characterized candidate causal genes by mapping them onto biological pathways and performing a phenome-wide association analysis (Extended Data Fig. 1, Supplementary Fig. 8 and Supplementary Tables 2, 8 and 9). In total, 15 out of 51 loci could be linked to three major pathways involved in susceptibility and severity defined by expert-driven classification (Supplementary Note): (1) viral entry; (2) entry defence in airway mucus; and (3) type I interferon response. Moreover, the phenome-wide association analysis identified nine loci involved in the upkeep of healthy lung tissue.

First, five loci include candidate causal genes involved in the viral entry pathway (Extended Data Fig. 1a), such as previously reported *SLC6A20* (3p21.31), *ABO* (9q34.2), *SFTPD* (10q22.3) and *ACE2* (Xp22.2), as well as *TMPRSS2* (21q22.3), which was also identified in the data release 7. We found that the lead variant rs9305744:G>A, an intronic variant of *TMPRSS2*, is protective against critical illness (odds ratio (OR) = 0.92, 95% CI = 0.89–0.95,  $P = 1.4 \times 10^{-8}$ ) and is in linkage disequilibrium with the missense variant rs12329760:C>T (p.Val197Met;  $r^2 = 0.68$ ). SARS-CoV-2 uses the serine protease *TMPRSS2* for viral spike protein priming, as well as the previously reported *ACE2* for host cell entry which functionally interacts with *SLC6A20* (refs. 5,6). Notably, the previously reported association between ABO blood groups and susceptibility could be attributed to the interference of anti-A and anti-B antibodies with the spike protein, potentially interfering with viral entry<sup>7</sup>. Furthermore, the previously reported *SFTPD* encodes pulmonary surfactant protein D (SP-D), which contributes dually to the lung's innate immune molecules and viral-entry response in pulmonary epithelia<sup>8,9</sup> along with other genes for airway defence.

Second, four loci contain candidate causal genes for entry defence in the airway mucus (Extended Data Fig. 1b), such as previously reported *MUC1/THBS3* (1q22) and *MUC5B* (11p15.5) as well as novel *MUC4* (3q29) and *MUC16* (19p13.2). We found that the novel lead variants

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**Fig. 1 | Overview of the contributing studies in the HGI data release 7.**

**a**, Geographical overview of the studies contributing to the COVID-19 HGI and the composition by major ancestry groups. Populations are defined as Middle Eastern (MID), South Asian (SAS), East Asian (EAS), African (AFR), admixed American (AMR), European (EUR) and other (OTH). **b**, A principal component

analysis (PCA) highlights the population structure and the sample ancestry of the individuals participating in the COVID-19 HGI. Per-cohort PCA results are provided in Supplementary Fig. 2. This figure was reproduced from the original publication by the COVID-19 HGI<sup>1</sup> with modifications reflecting the updated analysis from data release 7.

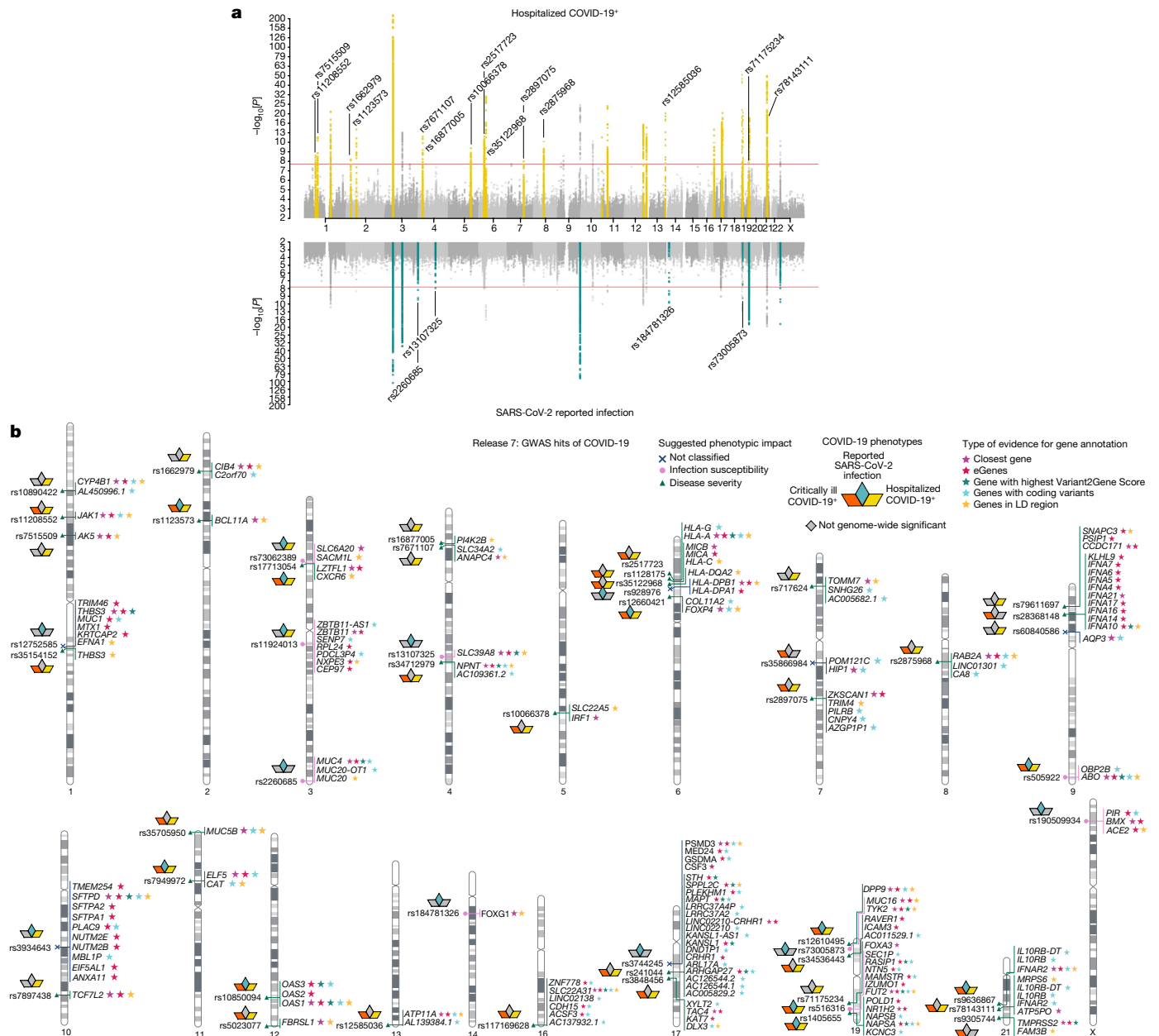
rs2260685:T>C in *MUC4* (intronic variant; in linkage disequilibrium ( $r^2 = 0.65$ ) with a missense variant rs2259292:C>T (p.Gly4324Asp)) and rs73005873:G>A in *MUC16* (intronic variant) increase the risk of SARS-CoV-2 infection (OR = 1.03 and 1.03, 95% CI = 1.02–1.04 and 1.02–1.04,  $P = 4.1 \times 10^{-8}$  and  $6.4 \times 10^{-10}$ , respectively). Moreover, the previously reported locus 1q22 contains an intergenic lead variant rs12752585:G>A that decreases the risk of infection (OR = 0.98, 95% CI = 0.97–0.98,  $P = 1.5 \times 10^{-11}$ ) and increases *MUC1* expression in the oesophagus mucosa in GTEx v8 ( $P = 5.2 \times 10^{-9}$ ). Notably, the 1q22 locus also contains an independent lead variant, rs35154152:T>C, a missense variant (p.Ser279Gly) of *THBS3*, that decreases the risk of hospitalization (OR = 0.88, 95% CI = 0.86–0.90,  $P = 5.6 \times 10^{-22}$ ) but not infection ( $P = 5.7 \times 10^{-4}$ ), suggesting potential distinct mechanisms in the locus. Consistent with these association patterns, *MUC1*, *MUC4* and *MUC16* are three known major transmembrane mucins of the respiratory tracts that prevent microbial invasion, whereas previously reported *MUC5B*, together with nearby *MUC5AC*, are primary structural components of airways mucus that enable mucociliary clearance of pathogens<sup>10</sup>.

Third, six loci contain candidate causal genes that are linked to the type I interferon pathway (Extended Data Fig. 1c), such as previously reported *IFNAR2* (21q22.11), *OAS1* (12q24.13) and *TYK2* (19p13.2), as well as additionally identified *JAK1* (1p31.3), *IRF1* (5q31.1) and *IFN $\alpha$* -coding genes (9p21.3). Previous studies have reported additional genes in this pathway: *TLR7* (refs. 11,12) and *DOCK2* (ref. 13). Here we found that the lead variant rs28368148:C>G, a missense variant (p.Trp164Cys) of *IFNA10* located within the *IFN $\alpha$*  gene cluster, increases the risk of critical illness (OR = 1.56, 95% CI = 1.38–1.77,  $P = 3.7 \times 10^{-12}$ ). *IFN $\alpha$*  is one of the type I interferons that binds specifically to the *IFN $\alpha$*  receptor consisting of *IFNAR1*–*IFNAR2* chains, in which mutations are also known to increase the risk of hospitalization and critical illness. In the genes that enable signalling downstream of *IFNAR*, we identified that the lead variant rs11208552:G>T, an intronic variant of *JAK1*, is protective against critical illness and hospitalization (OR = 0.92 and 0.95, 95% CI = 0.89–0.94 and 0.93–0.96,  $P = 5.5 \times 10^{-10}$  and  $2.2 \times 10^{-9}$ , respectively). This variant was previously reported to decrease lymphocyte counts<sup>14</sup> ( $\beta = -0.016$ ,  $P = 5.5 \times 10^{-15}$ ) and increase the *JAK1* expression in the thyroid in GTEx<sup>15</sup> ( $P = 6.1 \times 10^{-23}$ ). *JAK1* and previously reported *TYK2* are Janus kinases (JAKs) that are required for type I interferon-induced JAK–STAT signalling. JAK inhibitors are used to treat patients with severe

COVID-19 (ref. 16). Furthermore, downstream of JAK–STAT signalling, we found that the lead variant rs10066378:T>C, located 67 kb upstream of *IRF1*, increases the risk of critical illness and hospitalization (OR = 1.09 and 1.07, 95% CI = 1.06–1.13 and 1.05–1.09,  $P = 2.7 \times 10^{-9}$  and  $3.74 \times 10^{-10}$ , respectively).

Furthermore, the phenome-wide association analysis identified nine loci previously associated with lung function and respiratory diseases. These loci contain genes involved in the upkeep of healthy lung tissue such as previously reported *FOXP4* (6p21.1), *SFTPD* (10q22.3), *MUC5B* (11p15.5) and *DPP9* (19p13.3), as well as additionally identified *CIB4* (2p23.3), *NPNT* (4q24), *ZKSCAN1* (7q22.1), *ATP11A* (13q34) and *PSMD3* (17q21.1). For example, we found that three lead variants, rs1662979:G>T (intronic variant of *CIB4*), rs34712979:G>A (splice region variant of *NPNT*) and rs2897075:C>T (intronic variant of *ZKSCAN1*), are significantly associated with hospitalization (OR = 1.05, 0.94 and 1.05, 95% CI = 1.03–1.07, 0.92–0.96 and 1.03–1.07,  $P = 5.6 \times 10^{-9}$ ,  $3.8 \times 10^{-8}$  and  $8.9 \times 10^{-9}$ , respectively) and lung function (FEV1/FVC)<sup>17</sup>, similar to the previously reported lead variant rs3934643:G>A (intronic variant of *SFTPD*). Notably, whereas the alleles associated with increased risk of COVID-19 severity of rs1662979 and rs3934643 decrease lung function ( $\beta = -0.013$  and  $-0.025$ ,  $P = 5.3 \times 10^{-8}$  and  $6.3 \times 10^{-10}$ ), those of rs34712979 and rs2897075 increase lung function ( $\beta = 0.068$  and  $0.023$ ,  $P = 4.2 \times 10^{-134}$  and  $1.6 \times 10^{-20}$ , respectively). Likewise, we found lead variants that were significantly associated with hospitalization and idiopathic pulmonary fibrosis<sup>18,19</sup>, such as the aforementioned rs2897075 and rs12585036:C>T (intronic variant of *ATP11A*; OR = 1.10, 95% CI = 1.08–1.12,  $P = 3.2 \times 10^{-21}$ ), in addition to the previously reported rs35705950:G>T (promoter variant of *MUC5B*). Whereas the COVID-19 severity risk-increasing alleles of rs2897075 and rs12585036 increase the risk of idiopathic pulmonary fibrosis (OR = 1.12 and 1.27,  $P = 3.0 \times 10^{-14}$  and  $7.0 \times 10^{-9}$ , respectively), those of rs35705950 decreases the risk (OR = 0.50,  $P = 3.9 \times 10^{-80}$ ). These results highlight the complex pleiotropic relationships between COVID-19 severity, lung function and respiratory diseases.

We used genetic correlations and Mendelian randomization analyses to identify potential causal effects of risk factors on COVID-19 phenotypes (Supplementary Fig. 9 and Supplementary Tables 10 and 11). In total, 14 novel genetic correlations and 10 novel robust exposure-COVID-19 trait pairs showed evidence of causal associations



**Fig. 2 | GWAS results for COVID-19. a**, The results of a GWAS analysis of hospitalized individuals with COVID-19 ( $n = 49,033$  cases and  $n = 3,393,109$  controls) (top), and the results for individuals with reported SARS-CoV-2 infection ( $n = 219,692$  cases and  $n = 3,001,905$  controls) (bottom). The loci highlighted in yellow (top) represent regions that are associated with severity of COVID-19. The loci highlighted in green (bottom) are regions associated with susceptibility to SARS-CoV-2 infection. Lead variants for the loci that were identified in this data release are annotated with their respective rsID. The y axis is on the  $-\log_{10}(P)$  scale up to 10, after which it switches to a  $10 \times \log_{10}[-\log_{10}(P)]$  scale to aid presentation. **b**, Results of gene prioritization

using different evidence measures of gene annotation. For the genes in a linkage-disequilibrium (LD) region, genes with coding variants and eGenes (fine-mapped *cis*-expression quantitative trait locus (*cis*-eQTL) variant with posterior inclusion probability (PIP) > 0.1 in GTEx Lung) are annotated as such if they are in linkage disequilibrium with a COVID-19 lead variant ( $r^2 > 0.6$ ). V2G, the highest gene prioritized by OpenTargetGenetics V2G score. The pink circle indicates SARS-CoV-2 infection susceptibility, the green triangle indicates COVID-19 severity and the blue cross indicates unclassified. This figure was reproduced from the original publication by the COVID-19 HGI<sup>1</sup> with modifications reflecting the updated analysis from data release 7.

(Supplementary Note). In particular, smoking initiation and the number of cigarettes per day were positively correlated with severity and susceptibility phenotypes; Mendelian randomization indicated that smoking was causally associated with increased risk of COVID-19, further highlighting the role of the healthy lung tissue in COVID-19 severity. Moreover, genetically instrumented higher glomerular filtration rate (indicative of better kidney function) was associated with a lower risk of COVID-19 critical illness, whereas genetically predicted chronic kidney disease was associated with an increased risk of

COVID-19 critical illness, suggesting that better kidney function would be beneficial for a lower risk of COVID-19 severity.

In summary, we have substantially expanded the current knowledge of host genetics for COVID-19 susceptibility and severity by further doubling the case numbers from the previous data release<sup>2</sup> and identifying 28 additional loci. The increased number of loci enables us to map genes to pathways that are involved in viral entry, airway defence and immune system response. Notably, we observed severity loci mapped to type I interferon pathway, while susceptibility loci



# Matters arising

mapped to viral entry and airway defence pathways, with notable exceptions for severity-classified *TMPRSS2* and *MUC5B* loci. Further investigation of how such susceptibility and severity loci map to different pathways would provide mechanistic insights into the human genetic architecture of COVID-19.

## Online content

Any methods, additional references, Nature Portfolio reporting summaries, source data, extended data, supplementary information, acknowledgements, peer review information; details of author contributions and competing interests; and statements of data and code availability are available at <https://doi.org/10.1038/s41586-023-06355-3>.

## Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

## Data availability

Summary statistics generated by the COVID-19 HGI are available online, including per-ancestry summary statistics for African, admixed American, East Asian, European and South Asian ancestries (<https://www.covid19hg.org/results/r7/>). The analyses described here used the data release 7. If available, individual-level data can be requested directly from contributing studies, listed in Supplementary Table 1. We used publicly available data from GTEx (<https://gtexportal.org/home/>), the Neale laboratory (<http://www.nealelab.is/uk-biobank/>), the Finucane laboratory (<https://www.finucanelab.org>), the FinnGen Freeze 4 cohort ([https://www.finnngen.fi/en/access\\_results](https://www.finnngen.fi/en/access_results)) and the eQTL catalogue release 3 (<http://www.ebi.ac.uk/eQTL/>).

## Code availability

The code for summary statistics lift-over, the projection PCA pipeline including precomputed loadings and meta-analyses (<https://github.com/covid19-hg/>); for heritability estimation ([https://github.com/AndrewsLabUCSF/COVID19\\_heritability](https://github.com/AndrewsLabUCSF/COVID19_heritability)); for Mendelian randomization and genetic correlation (<https://github.com/marcoralab/MRcovid>); and subtype analyses ([https://github.com/mjpirinen/covid19-hgi\\_subtypes](https://github.com/mjpirinen/covid19-hgi_subtypes)) are available at GitHub.

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**Acknowledgements** We acknowledge M. O'Reilly and B. Cooley from the Pattern team at the Broad Institute of MIT and Harvard for designing the geographical map in Fig. 1. A full list of the members of the Genes & Health Research Team is available online (<https://www.genesandhealth.org/research/scientific-publications-authorship-and-acknowledgments>). A full list of acknowledgements is provided in Supplementary Table 12.

**Author contributions** Detailed author contributions are integrated in the authorship list.

**Competing interests** A full list of competing interests is provided in Supplementary Table 12.

## Additional information

**Supplementary information** The online version contains supplementary material available at <https://doi.org/10.1038/s41586-023-06355-3>.

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## Covid19g-CL

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# Matters arising

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Chapman<sup>543</sup>, Alexandre Eros<sup>543</sup>, Louise Cabrelli<sup>543</sup>, Stephen Cole<sup>543</sup>, Clare Whyte<sup>543</sup>, Matt Casey<sup>543</sup>, Vasileios Bafitis<sup>544</sup>, George Tsinaslanidis<sup>544</sup>, Cassandra George<sup>544</sup>, Reena Khade<sup>544</sup>, Christopher Black<sup>544</sup>, Sundar Raj Ashok<sup>544</sup>, Sean Farley<sup>545</sup>, Elaine Brinkworth<sup>545</sup>, Rachel Harford<sup>545</sup>, Carl Murphy<sup>545</sup>, Marie Williams<sup>545</sup>, Luke Newey<sup>545</sup>, Hannah Toghil<sup>545</sup>, Sophie Lewis<sup>545</sup>, Tabitha Rees<sup>545</sup>, Ceri Battle<sup>545</sup>, Mark Baker<sup>545</sup>, Jenny Travers<sup>545</sup>, Karen Chesters<sup>545</sup>, Nicola Baxter<sup>546</sup>, Andrew Arnett<sup>546</sup>, Gordan McCreath<sup>546</sup>, Christopher McParland<sup>546</sup>, Laura Rooney<sup>546</sup>, Malcolm Sim<sup>546</sup>, Steven Henderson<sup>546</sup>, Lynn Abel<sup>546</sup>, Carol Dalton<sup>546</sup>, Sophie Kennedy-Hay<sup>546</sup>, Lynn O'Donohoe<sup>546</sup>, Megan O'Hare<sup>546</sup>, Izabela Orlikowska<sup>546</sup>, Natasha Parker<sup>546</sup>, Fiona McNeela<sup>547</sup>, Amanda Lyle<sup>547</sup>, Alistair Hughes<sup>547</sup>, Jayachandran Radhakrishnan<sup>547</sup>, Sian Gibson<sup>547</sup>, Hollie Bancroft<sup>548</sup>, Mary Bellamy<sup>548</sup>, Jacqueline Daglish<sup>548</sup>, Salma Kadiri<sup>548</sup>, Faye Moore<sup>548</sup>, Joanne Rhodes<sup>548</sup>, Mirriam Sangombe<sup>548</sup>, Zhane Peterkin<sup>548</sup>, James Scriven<sup>548</sup>, Margaret Carmody<sup>548</sup>, Juliet Cottle<sup>548</sup>, Emily Peasgood<sup>549</sup>, Laura Ortiz-Ruiz de Gordoia<sup>549</sup>, Claire Phillips<sup>549</sup>, Denise Skinner<sup>549</sup>, Zoe Cinquina<sup>549</sup>, Kate Howard<sup>550</sup>, Rosie Joy<sup>550</sup>, Samantha Roche<sup>550</sup>, Isobel Birkinshaw<sup>550</sup>, Joseph Carter<sup>550</sup>, Jo Ingham<sup>550</sup>, Nicola Marshall<sup>550</sup>, Harriet Pearson<sup>550</sup>, Zoe Scott<sup>550</sup>, Jo Daggin<sup>551</sup>, Jaspreet Gill<sup>551</sup>, Annette Nilsson<sup>551</sup>, Amy Bamford<sup>551</sup>, Diana Hul<sup>551</sup>, Nafeesah Ahmadhaider<sup>551</sup>, Michelle Bates<sup>551</sup>, Christopher McGhee<sup>551</sup>, Hannah Ellis<sup>552</sup>, Gwenlian Sera Howe<sup>552</sup>, Jayaprakash Singh<sup>552</sup>, Natalie Stroud<sup>552</sup>, Lisa Roche<sup>552</sup>, Ceri Lynch<sup>552</sup>, Bethan Deacon<sup>552</sup>, Carla Potchary<sup>552</sup>, Justyna Smeaton<sup>552</sup>, Kevin Agravante<sup>552</sup>, Vinodh Krishnamurthy<sup>553</sup>, Cynthia Diaba<sup>553</sup>, Lincy John<sup>553</sup>, Lai Lim<sup>553</sup>, Rajeev Jha<sup>553</sup>, Jasmine Egan<sup>554</sup>, Timothy Felton<sup>554</sup>, Susannah Glasgow<sup>554</sup>, Grace Padden<sup>554</sup>, Ozerah Choudhri<sup>554</sup>, Joanne Bradley-Potts<sup>554</sup>, Stuart Moss<sup>554</sup>, Saejohn Lingeswaran<sup>554</sup>, Peter Alexander<sup>554</sup>, Craig Brandwood<sup>554</sup>, Sofia Fiouni<sup>554</sup>, Luke Ward<sup>554</sup>, Schvearn Allen<sup>554</sup>, Jane Shaw<sup>554</sup>, Christopher Smith<sup>554</sup>, Olurone Adanini<sup>555</sup>, Rebecca Collins<sup>555</sup>, Maines Msiska<sup>555</sup>, Linda Oforisi<sup>555</sup>, Nikhil Bhatia<sup>555</sup>, Hayley Dolan<sup>555</sup>, Mark Brunton<sup>555</sup>, Jess Caterson<sup>555</sup>, Holly Colles<sup>555</sup>, Liza Keating<sup>555</sup>, Emma Tilney<sup>556</sup>, Nicola Jacques<sup>556</sup>, Matthew Frise<sup>556</sup>, Jennifer Armistead<sup>556</sup>, Shauna Bartley<sup>556</sup>, Parminder Bhuie<sup>556</sup>, Sabi Ra<sup>556</sup>, Gabriela Tomkova<sup>556</sup>, Sandra Greer<sup>557</sup>, Karen Shuker<sup>557</sup>, Ascario Tridente<sup>557</sup>, Emma Dobson<sup>558</sup>, Jodie Hunt<sup>558</sup>, Redmond Tully<sup>558</sup>, Joy Dearden<sup>558</sup>, Andrew Drummond<sup>558</sup>, Prakash Kamath<sup>558</sup>, Emily Bullock<sup>558</sup>, Michelle Mulcahy<sup>558</sup>, Shelina Munt<sup>558</sup>, Grainne O'Connor<sup>558</sup>, Jennifer Philbin<sup>558</sup>, Chloe Rishon<sup>558</sup>, Chloe Scott<sup>558</sup>, Sarah Winnard<sup>558</sup>, Nurkamalia Hasni<sup>559</sup>, Rachel Gascoyne<sup>559</sup>, Joanne Hawes<sup>559</sup>, Kelly Pritchard<sup>559</sup>, Lesley Stevenson<sup>559</sup>, Amanda Whileman<sup>559</sup>, Sarah Beavis<sup>559</sup>, Lauren Bishop<sup>559</sup>, Cindy Carr<sup>559</sup>, Katie Dale<sup>559</sup>, Mary Kelly-Baxter<sup>559</sup>, Adam Mendelski<sup>559</sup>, Emma Moakes<sup>559</sup>, Rheanna Smith<sup>559</sup>, Jan Woodward<sup>559</sup>, Stephanie Wright<sup>559</sup>, Angela Allan<sup>560</sup>, Adriana Botello<sup>560</sup>, Jade Liew<sup>560</sup>, Jasmine Medhora<sup>560</sup>, Erin Trumper<sup>560</sup>, Felicity Savage<sup>560</sup>, Teresa Scott<sup>560</sup>, Marc Place<sup>560</sup>, Callum Kaye<sup>560</sup>, Sarah Benyon<sup>561</sup>, Suzie Marriott<sup>561</sup>, Linda Park<sup>561</sup>, Helen Quinn<sup>561</sup>, Daisy Skyes<sup>561</sup>, Lily Zitter<sup>561</sup>, Kizzy Baines<sup>561</sup>, Elizabeth Gordon<sup>561</sup>, Samantha Keenan<sup>561</sup>,

Andrew Pitt<sup>561</sup>, Katharine Duffy<sup>562</sup>, Jane Ireland<sup>562</sup>, Gary Semple<sup>562</sup>, Lynne Turner<sup>562</sup>, Susanne Cathcart<sup>562</sup>, Dominic Rimmer<sup>562</sup>, Alex Puxty<sup>562</sup>, Kathryn Puxty<sup>562</sup>, Andrew Hurst<sup>562</sup>, Jennifer Miller<sup>562</sup>, Susan Speirs<sup>562</sup>, Lauren Walker<sup>562</sup>, Zena Bradshaw<sup>563</sup>, Joanna Brown<sup>563</sup>, Sarah Melling<sup>563</sup>, Stephen Preston<sup>563</sup>, Nicola Slawson<sup>563</sup>, Scott Warden<sup>563</sup>, Alanna Beasley<sup>563</sup>, Emma Stoddard<sup>563</sup>, Leonie Benham<sup>563</sup>, Jason Cupitt<sup>563</sup>, Melanie Caswell<sup>563</sup>, Lisa Elawamy<sup>563</sup>, Ashleigh Wignall<sup>563</sup>, Belinda Roberts<sup>564</sup>, Hannah Golding<sup>564</sup>, Samantha Leggett<sup>564</sup>, Michelle Male<sup>564</sup>, Martyna Maran<sup>564</sup>, Kirsty Prager<sup>564</sup>, Toran Williams<sup>564</sup>, Kim Golde<sup>564</sup>, Oliver Jones<sup>564</sup>, Rebecca Cusack<sup>564</sup>, Clare Bolger<sup>564</sup>, Rachel Burnish<sup>564</sup>, Michael Carter<sup>564</sup>, Susan Jackson<sup>564</sup>, Karen Salmon<sup>564</sup>, Jonathan Biss<sup>564</sup>, Maia Aqno<sup>565</sup>, Maria Croft<sup>565</sup>, Victoria Fros<sup>565</sup>, Ian White<sup>565</sup>, Keshnie Govender<sup>565</sup>, Natasha Webb<sup>565</sup>, Liana Stapleton<sup>566</sup>, Colin Wells<sup>566</sup>, Nikitas Nikitas<sup>566</sup>, Ana Sanchez - Rodriguez<sup>566</sup>, Kayleigh Spencer<sup>566</sup>, Bethan Stowe<sup>566</sup>, Yvonne Izzard<sup>567</sup>, Michelle Poole<sup>567</sup>, Sonja Monney<sup>567</sup>, Sallyanne Trotman<sup>567</sup>, Valerie Beech<sup>567</sup>, Edward Combes<sup>567</sup>, Teishel Joefield<sup>567</sup>, Patrick Covernton<sup>568</sup>, Sarah Savage<sup>568</sup>, Elizabeth Woodward<sup>568</sup>, Julie Camsooksai<sup>568</sup>, Henrik Reschreiter<sup>568</sup>, Charlotte Barclay<sup>568</sup>, Yasmin DeAth<sup>568</sup>, Judith Dube<sup>568</sup>, Charlotte Humphrey<sup>568</sup>, Sarah Jenkins<sup>568</sup>, Emma Langridge<sup>568</sup>, Rebecca Milne<sup>568</sup>, Beverley Wadams<sup>568</sup>, Megan Woolcock<sup>568</sup>, Michael Brett<sup>569</sup>, Brian Digby<sup>569</sup>, Lisa Gemmill<sup>569</sup>, James Hornsby<sup>569</sup>, Patrick MacGoey<sup>569</sup>, Pauline O'Neil<sup>569</sup>, Richard Price<sup>569</sup>, Radha Sundaram<sup>569</sup>, Natalie Rodden<sup>569</sup>, Nicola Thomson<sup>569</sup>, Kevin Roone<sup>569</sup>, Susan Currie<sup>569</sup>, Philip Henderson<sup>569</sup>, Bethan Ogg<sup>570</sup>, Simon Whiteley<sup>570</sup>, Liz Wilby<sup>570</sup>, Kate Long<sup>570</sup>, Shailamma Matthew<sup>570</sup>, Sheila Salada<sup>570</sup>, Susan Trost<sup>570</sup>, Sarah Watts<sup>570</sup>, Zoe Friar<sup>570</sup>, Abigail Speight<sup>570</sup>, Victoria Bastion<sup>571</sup>, Humza Chandani<sup>571</sup>, Brice Djeugam<sup>571</sup>, Muhammad Haseeb<sup>571</sup>, Harriet Kent<sup>571</sup>, Gamu Lubimi<sup>571</sup>, Sophie Murdoch<sup>571</sup>, Alastair Thomas<sup>571</sup>, Mada David<sup>571</sup>, Rachel Lorusso<sup>571</sup>, Ana Vochin<sup>571</sup>, Melchizedek Penacerrada<sup>571</sup>, Retno Wulandari<sup>571</sup>, Charlotte Heath<sup>572</sup>, Srinivas Jakkula<sup>572</sup>, Anna Morris<sup>572</sup>, Ashar Ahmed<sup>572</sup>, Arvind Nune<sup>572</sup>, Claire Buttriss<sup>572</sup>, Emma Whitake<sup>572</sup>, Miriam Davey<sup>572</sup>, David Golden<sup>573</sup>, Amy Ackley<sup>573</sup>, Fabio Fernandes<sup>573</sup>, Bec Seaman<sup>573</sup>, Victoria Earl<sup>573</sup>, Amy Collins<sup>574</sup>, Waqas Khalid<sup>574</sup>, Rachel Adam<sup>574</sup>, Estefania Treus<sup>574</sup>, Sarah Holland<sup>575</sup>, Jordan Alfonso<sup>575</sup>, Bethan Blackledge<sup>575</sup>, Michelle Bruce<sup>575</sup>, Laura Jayne Durran<sup>575</sup>, Ayaa Eltayeb<sup>575</sup>, Jade Harris<sup>575</sup>, Samuel Hey<sup>575</sup>, Martin Hruska<sup>575</sup>, Thomas Lamb<sup>575</sup>, Joanne Rothwell<sup>575</sup>, Adele Fitzgerald<sup>575</sup>, Gabriella Lindergard<sup>575</sup>, Helen T-Michael<sup>575</sup>, Tracey Duncan<sup>575</sup>, Sharon Baxter-Dore<sup>575</sup>, Lisa Cooper<sup>575</sup>, Claire Fox<sup>575</sup>, Jacinta Guerin<sup>575</sup>, Tracey Hodgkiss<sup>575</sup>, Karen Connolly<sup>575</sup>, Paul McAlinden<sup>576</sup>, Victoria Bridgett<sup>576</sup>, Maggie Feary<sup>576</sup>, A. Gulati<sup>576</sup>, Helen Hanson<sup>576</sup>, Sinead Kelly<sup>576</sup>, Louise McCormack<sup>576</sup>, Rachel Nixon<sup>576</sup>, Philip Robinson<sup>576</sup>, Victoria Slater<sup>576</sup>, Elaine Stephenson<sup>576</sup>, Andrea Webster<sup>576</sup>, K. Webster<sup>576</sup>, Carole Hays<sup>576</sup>, Anne Hudson<sup>576</sup>, Bijal Patel<sup>576</sup>, Ian Clement<sup>576</sup>, John Davis<sup>576</sup>, Sarah Francis<sup>576</sup>, Douglas Jerry<sup>576</sup>, Caroline Abernathy<sup>577</sup>, Louise Foster<sup>577</sup>, Andrew Grant<sup>577</sup>, Lucia Cabral-Ortega<sup>577</sup>, Matthew Hines<sup>577</sup>, Victoria Martinson<sup>577</sup>, Elizabeth Stones<sup>577</sup>, Karen Winter<sup>577</sup>, Esther Barrow<sup>578</sup>, Katharine Wylie<sup>578</sup>, Deborah Baines<sup>578</sup>, Katie Birchall<sup>578</sup>, Laurel Kolakaluri<sup>578</sup>, Richard Clark<sup>578</sup>, Anila Sukumaran<sup>578</sup>, Melanie Barker<sup>578</sup>, Deborah Pariporanon<sup>578</sup>, Lara Smith<sup>578</sup>, Charlotte Taylor<sup>578</sup>, Charlotte Downes<sup>579</sup>, Melanie Hayman<sup>579</sup>, Katie Riches<sup>579</sup>, Priya Daniel<sup>579</sup>, Deepak Subramanian<sup>579</sup>, Kathleen Holding<sup>579</sup>, Mary Hilton<sup>579</sup>, Arly Mcdonald<sup>579</sup>, Georgina Richardson<sup>579</sup>, Georgia Hallada<sup>580</sup>, Peter Harding<sup>580</sup>, Carrie Reddy<sup>580</sup>, Ian Turner-Bone<sup>580</sup>, Laura Wilding<sup>580</sup>, Robert Parker<sup>580</sup>, Michaela Lloyd<sup>580</sup>, Leanne Smith<sup>580</sup>, Charlie Kelly<sup>580</sup>, Maria Lazo<sup>581</sup>, Alan Neal<sup>581</sup>, Olivia Walton<sup>581</sup>, Julie Melville<sup>581</sup>, Jay Naisbitt<sup>581</sup>, Rosane Jones<sup>581</sup>, Sara Callam<sup>582</sup>, Lisa Hudg<sup>582</sup>, Jocelyn Keshet-Price<sup>582</sup>, Katie Stammers<sup>582</sup>, Karen Convery<sup>582</sup>, Georgina Randel<sup>582</sup>, Deirdre Fottrell-gould<sup>582</sup>, Esther Mwaura<sup>583</sup>, Sara-Beth Sutherland<sup>583</sup>, Richard Stewart<sup>583</sup>, Louise Mew<sup>583</sup>, Lynn Wren<sup>583</sup>, Laura Thrasvoulou<sup>584</sup>, Heather Willis<sup>584</sup>, Bridget Hopkins<sup>584</sup>, Daniel Lenton<sup>584</sup>, Abigail Roberts<sup>584</sup>, Maria Bokhari<sup>585</sup>, Rachael Lucas<sup>585</sup>, Wendy McCormick<sup>585</sup>, Jenny Ritzema<sup>585</sup>, Vanessa Linnett<sup>585</sup>, Amanda Sanderson<sup>585</sup>, Helen Wild<sup>585</sup>, Rebecca Flanagan<sup>585</sup>, Robert Hull<sup>586</sup>, Kat Rhead<sup>586</sup>, Emma McKenna<sup>586</sup>, Gareth Hughes<sup>586</sup>, Jennifer Anderson<sup>586</sup>, Kelly Jones<sup>586</sup>, Scott Latham<sup>586</sup>, Heather Riley<sup>586</sup>, Martina Coulding<sup>587</sup>, Martyn Clark<sup>587</sup>, Jacqueline McCormick<sup>587</sup>, Oliver Mercer<sup>587</sup>, Darsh Pota<sup>587</sup>, Hafiz Rehman<sup>587</sup>, Heather Savill<sup>587</sup>, Victoria Turner<sup>587</sup>, Edward Jude<sup>587</sup>, Susan Kilroy<sup>587</sup>, Elena Apetri<sup>588</sup>, Cathrine Basikolo<sup>588</sup>, Laura Catlow<sup>588</sup>, Matthew Collis<sup>588</sup>, Reece Doonan<sup>588</sup>, Alice Harvey<sup>588</sup>, Karen Knowles<sup>588</sup>, Jessica Lee<sup>588</sup>, Diane Lomas<sup>588</sup>, Chloe Lyons<sup>588</sup>, Liam McMorrow<sup>588</sup>, Angiy Michael<sup>588</sup>, Stephanie Pentuberry<sup>588</sup>, Jane Perez<sup>588</sup>, Maria Poulaka<sup>588</sup>, Nicola Proudfoot<sup>588</sup>, Kathryn Slevin<sup>588</sup>, Vicky Thomas<sup>588</sup>, Danielle Walker<sup>588</sup>, Paul Dark<sup>588</sup>, Bethan Charles<sup>588</sup>, Danielle McLaughlan<sup>588</sup>, Melanie Slaughter<sup>588</sup>, Dan Horner<sup>588</sup>, Kathryn Cawley<sup>588</sup>, Tracy Marsden<sup>588</sup>, Jovann Andrews<sup>589</sup>, Emily Beech<sup>589</sup>, Olugbenga Akinkugbe<sup>589</sup>, Alasdair Bamford<sup>589</sup>, Holly Belfield<sup>589</sup>, Gareth A. L. Jones<sup>589</sup>, Tara McHugh<sup>589</sup>, Hamza Meghari<sup>589</sup>, Samiran Ray<sup>589</sup>, Ana Luisa Tomas<sup>589</sup>, Lauran O'Neill<sup>589</sup>, Mark Peters<sup>589</sup>, Michael Bell<sup>589</sup>, Sarah Benkenstein<sup>589</sup>, Catherine Chisholm<sup>589</sup>, Charlene Davies<sup>589</sup>, Klaudia Kupiec<sup>589</sup>, Caroline Payne<sup>589</sup>, Joanna Halls<sup>590</sup>, Hayley Blackmore<sup>590</sup>, Elizabeth Goff<sup>590</sup>, Kati Hayes<sup>590</sup>, Kerry Smith<sup>590</sup>, Deanna Stephens<sup>590</sup>, Ruth Worner<sup>590</sup>, Borislava Borislavova<sup>590</sup>, Beverley Faulkner<sup>590</sup>, Matt Thomas<sup>590</sup>, Ruth Cookson<sup>590</sup>, Emma Gendall<sup>590</sup>, Georgina Larmar<sup>590</sup>, Rebecca Pope<sup>590</sup>, Artur Smalira<sup>590</sup>, Victoria Priestley<sup>591</sup>, Tracey Cosier<sup>591</sup>, Gemma Millen<sup>591</sup>, James Rand<sup>591</sup>, Natasha Schumacher<sup>591</sup>, Roxana Sandhar<sup>591</sup>, Heather Weston<sup>591</sup>, Neil Richardson<sup>591</sup>, Lucy Cooper<sup>591</sup>, Cathy Jones<sup>592</sup>, Ya-Wen Jessica Huang<sup>592</sup>, Reni Jacob<sup>592</sup>, Craig Denmade<sup>592</sup>, Lewis McIntyre<sup>592</sup>, Dawn Trodd<sup>593</sup>, Jane Martin<sup>593</sup>, Geoff Watson<sup>593</sup>, Emily Bevan<sup>593</sup>, Caroline Wreybrow<sup>593</sup>, Shereen Bano<sup>594</sup>, Ruth Bellwood<sup>594</sup>, Michael Bentley<sup>594</sup>, Matt Bromley<sup>594</sup>, Amelia Gurf<sup>594</sup>, Camilla Ledgard<sup>594</sup>, Janet McGowan<sup>594</sup>, Kate Pye<sup>594</sup>, Kirsten Sellick<sup>594</sup>, Lucia Stacey<sup>594</sup>, Deborah Warren<sup>594</sup>, Brian Wilkinson<sup>594</sup>, Louise Akeroyd<sup>594</sup>, Huma Shafique<sup>594</sup>, James Morgan<sup>594</sup>, Susan Shorter<sup>594</sup>, Rachel Swinge<sup>594</sup>, Emily Waters<sup>594</sup>, Tom Lawton<sup>594</sup>, Elizabeth Allan<sup>595</sup>, Kate Darlington<sup>595</sup>, Fyfon Davies<sup>595</sup>, Llinos Davies<sup>595</sup>, Jack Easton<sup>595</sup>, Sumit Kumar<sup>595</sup>, Richard Lear<sup>595</sup>, Callum Mackay<sup>595</sup>, Richard Pugh<sup>595</sup>, Xinyi Qiu<sup>595</sup>, Stephanie Rees<sup>595</sup>, Jeremy Scanlon<sup>595</sup>, Joanne Lewis<sup>595</sup>, Daniel Menzies<sup>595</sup>, Annette Bolger<sup>595</sup>, Gwyneth Davies<sup>595</sup>, Jennifer Davies<sup>595</sup>, Esther Garrod<sup>595</sup>, Helen Jones<sup>595</sup>, Rachel Manley<sup>595</sup>, Hannah Williams<sup>595</sup>, Jordan Frankham<sup>596</sup>, Sally Pitts<sup>596</sup>, Nigel White<sup>596</sup>, Debbie Branney<sup>596</sup>, Heather Tiller<sup>596</sup>, Georgia Efford<sup>597</sup>, Zoe Garland<sup>597</sup>, Lisa Grimmer<sup>597</sup>, Bethany Gumbrell<sup>597</sup>, Rebekah Johnson<sup>597</sup>, Katie Sweet<sup>597</sup>, Jeremy Bewley<sup>597</sup>, Christina Coleman<sup>597</sup>, Katie Corcoran<sup>597</sup>, Eva Maria Hernandez Morano<sup>597</sup>, Rachel Shiel<sup>597</sup>, Denise Webster<sup>597</sup>, Josephine Bonnic<sup>597</sup>, Eleanor Daniel<sup>597</sup>, Abbie Dell<sup>597</sup>, Melanie Ken<sup>598</sup>, Ami Wilkinson<sup>598</sup>, Ellen Brown<sup>598</sup>, Andrea Kay<sup>598</sup>, Suzanne Campbell<sup>598</sup>, Amanda Cowton<sup>598</sup>, Mark Birr<sup>598</sup>, Vicki Greenaway<sup>598</sup>, Kathryn Potts<sup>598</sup>, Clare Hutton<sup>598</sup>, Andrew Shepperson<sup>598</sup>, Miranda Forsey<sup>600</sup>, Alice Nicholson<sup>600</sup>, Mark Vertue<sup>600</sup>, Joanne Riches<sup>600</sup>, Agilan Kaliappan<sup>600</sup>, Anne Nicholson<sup>600</sup>, Niall MacCallum<sup>601</sup>, Eamon Raith<sup>601</sup>, Georgia Berceades<sup>601</sup>, Ingrid Hass<sup>601</sup>, David Brealey<sup>601</sup>,



Gladys Martir<sup>601</sup>, Anna Reyes<sup>601</sup>, Deborah Smyth<sup>601</sup>, Maria Zapatamartinez<sup>601</sup>, Ana Alvaro<sup>602</sup>, Champa Jetha<sup>602</sup>, Louise Ma<sup>602</sup>, Lauren Booker<sup>602</sup>, Loreta Mostoles<sup>602</sup>, Anezka Pratley<sup>602</sup>, Abdelhakim Altabaibeh<sup>602</sup>, Chetan Parmar<sup>602</sup>, Kayleigh Gilbert<sup>602</sup>, Susie Ferguson<sup>603</sup>, Amy Shepherd<sup>603</sup>, Sheila Morris<sup>603</sup>, Rosie Baruah<sup>603</sup>, Georgina Lloyd<sup>604</sup>, Stephanie Bell<sup>604</sup>, Vanessa Rivers<sup>604</sup>, Bally Pureau<sup>605</sup>, Kate Hammerton<sup>605</sup>, Susan Anderson<sup>605</sup>, Janine Birch<sup>605</sup>, Emma Collins<sup>605</sup>, Ryan Oleary<sup>605</sup>, Sarah Cornell<sup>606</sup>, Jordan Jarman<sup>606</sup>, Kimberley Rogerson<sup>606</sup>, Fiona Wakinslaw<sup>606</sup>, Lindsey Woods<sup>606</sup>, Anthony Rostron<sup>606</sup>, Zeynep Elicioglu<sup>606</sup>, Alistair Roy<sup>606</sup>, Gillian Bell<sup>607</sup>, Holly Dickson<sup>607</sup>, Louise Wilcox<sup>607</sup>, Amro Katary<sup>607</sup>, Katy English<sup>607</sup>, Joanne Hutter<sup>608</sup>, Corinne Pawley<sup>608</sup>, Patricia Doble<sup>608</sup>, Charmaine Shovelton<sup>608</sup>, Marius Vaida<sup>608</sup>, Rebecca Purnell<sup>608</sup>, Ashly Thomas<sup>608</sup>, Lenka Cagova<sup>609</sup>, Adama Fofano<sup>609</sup>, Helen Holcombe<sup>609</sup>, Alice Michael Mitchell<sup>609</sup>, Lucy Mwaura<sup>609</sup>, Krithivasan A Praman<sup>609</sup>, Lucie Gann<sup>609</sup>, Sue Mephram<sup>609</sup>, Kitty Paques<sup>609</sup>, Alain Vuylsteke<sup>609</sup>, Jennifer Mackie<sup>609</sup>, Carmen Pearn<sup>609</sup>, Julie Zamikula<sup>609</sup>, Maggie Nyre<sup>610</sup>, Lisa Capozzi<sup>610</sup>, Rosie Reece-Antony<sup>610</sup>, Hazma Noor<sup>610</sup>, Alfa Cresia Nilo<sup>610</sup>, Michelle Grove<sup>611</sup>, Amelia Daniel<sup>611</sup>, Joanne Finn<sup>611</sup>, Nikki White<sup>611</sup>, Rajnish Sahra<sup>611</sup>, Bibi Bada<sup>611</sup>, Karen Ixer<sup>611</sup>, Donna Duffin<sup>612</sup>, Ben Playe<sup>612</sup>, Helen Hill<sup>612</sup>, Jade Cole<sup>612</sup>, Jenny Brooks<sup>612</sup>, Michelle Davies<sup>612</sup>, Rhys Davies<sup>612</sup>, Lauren Hunt<sup>612</sup>, Emma Thomas<sup>612</sup>, Angharad Williams<sup>612</sup>, Metod Oblak<sup>612</sup>, Mini Thankachen<sup>612</sup>, Jamie Irisari<sup>613</sup>, Amrinder Sayan<sup>613</sup>, Monica Popescu<sup>613</sup>, Cheryl Finch<sup>614</sup>, Andrew Jamieson<sup>614</sup>, Alison Quinn<sup>614</sup>, Joshua Cooper<sup>614</sup>, Sarah Litherth<sup>614</sup>, Natalia Waddington<sup>614</sup>, Iona Burn<sup>615</sup>, Katarina Manso<sup>615</sup>, Ruth Penn<sup>615</sup>, Julie Tebbutt<sup>615</sup>, Daniell Thornton<sup>615</sup>, James Winchester<sup>615</sup>, Geraldine Hambrook<sup>615</sup>, Pradeep Shanmugasundaram<sup>615</sup>, Jayne Craig<sup>616</sup>, Kerry Simpkin<sup>616</sup>, Andrew Higham<sup>616</sup>, Louise Sibbett<sup>616</sup>, Sheila Paine<sup>617</sup>, Annabel Reed<sup>617</sup>, Jo-Anna Conyngham<sup>617</sup>, McDonald Mupuzi<sup>617</sup>, Rachel Thomas<sup>617</sup>, Mary Wright<sup>617</sup>, Denise Griffin<sup>617</sup>, Richard Partridge<sup>617</sup>, Maria Alvarez Corral<sup>617</sup>, Nycola Muchenry<sup>617</sup>, Mildred Sitonik<sup>617</sup>, Aaron Butler<sup>618</sup>, Linda Folkes<sup>618</sup>, Heather Fox<sup>618</sup>, Amy Gardner<sup>618</sup>, David Helm<sup>618</sup>, Gillian Hobden<sup>618</sup>, Kirsten King<sup>618</sup>, Jordi Margalef<sup>618</sup>, Michael Margaron<sup>618</sup>, Tim Martindale<sup>618</sup>, Emma Meadows<sup>618</sup>, Dana Raynard<sup>618</sup>, Yvette Thirlwall<sup>618</sup>, Yolanda Baird<sup>618</sup>, Raquel Gomez<sup>618</sup>, Darren Martin<sup>618</sup>, Luke Hodgson<sup>618</sup>, Clinton Corin<sup>618</sup>, Erikka Sidall<sup>618</sup>, Densie Szabo<sup>618</sup>, Sharon Floyd<sup>618</sup>, Hannah Davies<sup>620</sup>, Karen Austin<sup>620</sup>, Olivia Kelsal<sup>620</sup>, Hannah Wood<sup>620</sup>, Thomas Cornell<sup>621</sup>, Kate Ralph<sup>621</sup>, Sarah Bean<sup>621</sup>, Karen Burr<sup>621</sup>, Michael Spivey<sup>621</sup>, Carol Richards<sup>621</sup>, Rachel Tedstone<sup>621</sup>, Siobhain Carmody<sup>622</sup>, Xiaobei Zhao<sup>622</sup>, Valerie Page<sup>622</sup>, Mark Louie Guanco<sup>622</sup>, Elvira Hoxha<sup>622</sup>, Camilla Zorloni<sup>622</sup>, Charlotte Dean<sup>623</sup>, Emma Jones<sup>623</sup>, Emma Carter<sup>623</sup>, Joshua Dunn<sup>623</sup>, Thomas Kong<sup>623</sup>, Mervin Mahenthiran<sup>623</sup>, Chris Marsh<sup>623</sup>, Maureen Holland<sup>623</sup>, Natalie Keenan<sup>623</sup>, Mohamed Mahmoud<sup>623</sup>, Marc Lyons<sup>623</sup>, Joanne Bradley-Potts<sup>623</sup>, Helen Wassall<sup>623</sup>, Meghan Young<sup>623</sup>, Paul Bradley<sup>624</sup>, Dorota Burda<sup>624</sup>, Sinead Donlon<sup>624</sup>, Lesley Harden<sup>624</sup>, Celia Harris<sup>624</sup>, Irving Mayangao<sup>624</sup>, Rugia Montaser<sup>624</sup>, Sheila Mtuwa<sup>624</sup>, Charles Piercy<sup>624</sup>, Eleanor Smith<sup>624</sup>, Sarah Stone<sup>624</sup>, Jerik Verula<sup>624</sup>, Helen Blackman<sup>624</sup>, Cheryl Marriott<sup>624</sup>, Natalia Michalak<sup>624</sup>, Ben Creagh-Brown<sup>624</sup>, Armored Salberg<sup>624</sup>, Naomi Boyer<sup>624</sup>, Veronika Pristopan<sup>624</sup>, Victoria Maynard<sup>625</sup>, Rachel Walker<sup>625</sup>, Anil Hormis<sup>625</sup>, Dawn Collier<sup>625</sup>, Cheryl Graham<sup>625</sup>, Jake McCormick<sup>625</sup>, Jake Warrington<sup>625</sup>, Denise Cosgrove<sup>625</sup>, Denise McFarland<sup>626</sup>, Judith Ratcliffe<sup>626</sup>, Rob Charnock<sup>626</sup>, Inez Wynter<sup>627</sup>, Mandy Gill<sup>627</sup>, Jill Kirk<sup>627</sup>, Paul Paul<sup>627</sup>, Valli Ratnam<sup>627</sup>, Sarah Shelton<sup>627</sup>, Catherine Jardine<sup>628</sup>, Alasdair Hay<sup>628</sup>, Dewi Williams<sup>628</sup>, Latha Durga<sup>629</sup>, Meg Hibbert<sup>629</sup>, Gareth Kennard-Holden<sup>629</sup>, Christopher Woodford<sup>629</sup>, Dariusz Tetla<sup>629</sup>, Alicia Price<sup>630</sup>, Alice Thomas<sup>630</sup>, Chris Thorpe<sup>630</sup>, Ellen Knights<sup>630</sup>, Donna Ward<sup>630</sup>, Shondipon Laha<sup>631</sup>, Mark Verlander<sup>631</sup>, Alexandra Williams<sup>631</sup>, Rachel Prout<sup>632</sup>, Helen Langton<sup>632</sup>, Malcolm Watters<sup>632</sup>, Charlotte Hunt<sup>632</sup>, Catherine Norris<sup>632</sup>, Sarwat Arif<sup>633</sup>, Amy Cunningham<sup>633</sup>, Claire Hewitt<sup>633</sup>, Julia Hindale<sup>633</sup>, Karen Jackson-Lawrence<sup>633</sup>, Sarah Shepardson<sup>633</sup>, Maryanne Wills<sup>633</sup>, Susie Butle<sup>633</sup>, Silvia Tavares<sup>633</sup>, Russell Barber<sup>633</sup>, Annette Hilldrith<sup>633</sup>, Kelly Hubbard<sup>633</sup>, Dawn Egginton<sup>634</sup>, Michele Clark<sup>634</sup>, Sarah Purvis<sup>634</sup>, Simon Sinclair<sup>634</sup>, Vicky Collins<sup>634</sup>, Bethan Landeg<sup>635</sup>, Craig Sell<sup>635</sup>, Samantha Coetzee<sup>635</sup>, Alistair Gales<sup>635</sup>, Igor Otahal<sup>635</sup>, Becky Icke<sup>635</sup>, Meena Raj<sup>635</sup>, Caroline Williams<sup>635</sup>, Jill Williams<sup>635</sup>, Lucy Hill<sup>635</sup>, Abdul Kayani<sup>636</sup>, Bridgett Masunda<sup>636</sup>, Prisca Gondo<sup>636</sup>, Nigara Atayeva<sup>636</sup>, Carina Cruz<sup>636</sup>, Natalie Pattison<sup>637</sup>, Caroline Burnett<sup>638</sup>, Jonathan Hatton<sup>638</sup>, Elaine Heeney<sup>638</sup>, Maria Newton<sup>638</sup>, Hassan Al-Moassel<sup>638</sup>, Teresa Behan<sup>638</sup>, Jasmine Player<sup>638</sup>, Rachael Stead<sup>638</sup>, Atideb Mitra<sup>638</sup>, Kirsty Nauyokas<sup>638</sup>, Sally Humphreys<sup>639</sup>, Helen Cockerill<sup>639</sup>, Ruth Tamspeit<sup>639</sup>, Evgeniya Postovalova<sup>640</sup>, Tina Coventry<sup>640</sup>, Amanda McGregor<sup>640</sup>, Susan Fowler<sup>640</sup>, Mike Macmahon<sup>640</sup>, Patricia Cochrane<sup>640</sup>, Sandra Pirie<sup>640</sup>, Sarah Hanley<sup>641</sup>, Asifa Ali<sup>641</sup>, Megan Brady<sup>641</sup>, Sam Dale<sup>641</sup>, Annalisa Dance<sup>641</sup>, Lisa Gledhill<sup>641</sup>, Jill Greig<sup>641</sup>, Kathryn Hanson<sup>641</sup>, Kelly Holdroyd<sup>641</sup>, Marie Home<sup>641</sup>, Tahira Ishaq<sup>641</sup>, Diane Kelly<sup>641</sup>, Lear Matapure<sup>641</sup>, Deborah Melia<sup>641</sup>, Samantha Mellor<sup>641</sup>, Ekta Merwaha<sup>641</sup>, Tonicha Nortcliffe<sup>641</sup>, Lisa Shaw<sup>641</sup>, Tracy Wood<sup>641</sup>, Lee-Ann Bayo<sup>641</sup>, Miranda Usher<sup>641</sup>, Alison Wilson<sup>641</sup>, Ross Kitson<sup>641</sup>, Jez Pinnell<sup>641</sup>, Matthew Robinson<sup>641</sup>, Kaitlin Boltwood<sup>641</sup>, Jenny Birch<sup>643</sup>, Laura Bough<sup>643</sup>, Rebecca Tutton<sup>643</sup>, Barbara Winter-Goodwin<sup>643</sup>, Josie Goodsell<sup>643</sup>, Kate Taylor<sup>643</sup>, Patricia Williams<sup>643</sup>, Sarah Williams<sup>643</sup>, Ashleigh Cave<sup>643</sup>, James Rees<sup>643</sup>, Janet Imeson-Wood<sup>644</sup>, Jacqueline Smith<sup>644</sup>, Vishal Amin<sup>644</sup>, Komala Karthik<sup>644</sup>, Rizwana Kausa<sup>644</sup>, Elena Anastasescu<sup>644</sup>, Karen Reid<sup>644</sup>, Vikram Anumakonda<sup>644</sup>, Ella Stoddart<sup>644</sup>, Carrie Demetriou<sup>645</sup>, Charlotte Eckbad<sup>645</sup>, Lucy Howie<sup>645</sup>, Sarah Hitchard<sup>645</sup>, Lidia Ramos<sup>645</sup>, Katie White<sup>645</sup>, Sarah Hierons<sup>645</sup>, Fiona Kelly<sup>645</sup>, Alfredo Serrano-Ruiz<sup>645</sup>, Gabrielle Evans<sup>645</sup>, Liz Nicol<sup>646</sup>, Joy Wilkins<sup>646</sup>, Kim Hulacka<sup>646</sup>, Gabor Debrenceni<sup>646</sup>, Alison Brown<sup>646</sup>, Vikki Crickmore<sup>646</sup>, Kay Hill<sup>647</sup>, Thogulava Kannan<sup>647</sup>, Zenaida Dagutao<sup>648</sup>, Kate Beesley<sup>648</sup>, Alison Lewis<sup>648</sup>, Jess Perry<sup>648</sup>, Sheryl Antony<sup>648</sup>, Sarah Board<sup>648</sup>, Clare Buckley<sup>648</sup>, Lucy Pippard<sup>648</sup>, Alfonso Tanate<sup>648</sup>, Diane Wood<sup>648</sup>, Agnieska Kubisz-Pudelok<sup>648</sup>, Ayman Gouda<sup>648</sup>, Fiona Auld<sup>649</sup>, Joanne Donnachie<sup>649</sup>, Euan Murdoch<sup>649</sup>, Lynn Prentice<sup>649</sup>, Nikole Runciman<sup>649</sup>, Dhaneesha Senaratne<sup>649</sup>, Abigail Short<sup>649</sup>, Laura Sweeney<sup>649</sup>, Lesley Symon<sup>649</sup>, Anne Todd<sup>649</sup>, Patricia Turner<sup>649</sup>, Erin McCann<sup>649</sup>, Dario Salutous<sup>649</sup>, Ian Edmond<sup>649</sup>, Lesley Whitelaw<sup>649</sup>, Yvonne Bland<sup>650</sup>, Istvan Kajtor<sup>650</sup>, Lisa Kavanagh<sup>650</sup>, Karen Singler<sup>650</sup>, George Linfield-Brown<sup>650</sup>, Luke Stephen Prockter Moore<sup>651</sup>, Marcela Viczaychipi<sup>651</sup>, Laura Martins<sup>651</sup>, Luke Moore<sup>651</sup>, Rhian Bul<sup>651</sup>, Jaime Carungcong<sup>651</sup>, Louise Allen<sup>652</sup>, Eva Beranova<sup>652</sup>, Alicia Knight<sup>652</sup>, Carly Price<sup>652</sup>, Sorrell Tilbey<sup>652</sup>, Sharon Turner<sup>652</sup>, Tracy Hazelton<sup>652</sup>, Gabriella Tut<sup>652</sup>, Mansi Arora<sup>652</sup>, Salah Turki<sup>652</sup>, Emily Sinfield<sup>652</sup>, Joanne Deer<sup>652</sup>, Hazel Ramos<sup>652</sup>, Daniele Cristiano<sup>653</sup>, Natalie Dormand<sup>653</sup>, Zohreh Farzad<sup>653</sup>, Mahitha Gummadi<sup>653</sup>, Sara Salmi<sup>653</sup>, Geraldine Sloane<sup>653</sup>, Mathew Varghese<sup>653</sup>, Vicky Thwaites<sup>653</sup>, Brijesh Patel<sup>653</sup>, Livanage Kamal<sup>653</sup>, Anelise Catealan Zborowski<sup>653</sup>, Ryan Coe<sup>654</sup>, Madeleine Anderson<sup>654</sup>, Jane Beadle<sup>654</sup>, Charlotte Coates<sup>654</sup>, Katy Collins<sup>654</sup>, Maria Crowley<sup>654</sup>, Laura Johnson<sup>654</sup>, Laura King<sup>654</sup>, Remi Paramsothy<sup>654</sup>, Janet Sargeant<sup>654</sup>, Pedro Silva<sup>654</sup>, Carmel Stuart<sup>654</sup>, June Taylor<sup>654</sup>, David Ty<sup>654</sup>, Philippa Wakefield<sup>654</sup>, Charlotte Kamund<sup>654</sup>, Olumide Olufuwa<sup>654</sup>, Zakoulla Belagoda<sup>654</sup>, Anca Gherman<sup>654</sup>, Naomi Oakley<sup>654</sup>, John Allan<sup>655</sup>, Tim Geary<sup>655</sup>, Alistair Meikle<sup>655</sup>, Peter O'Brien<sup>655</sup>, Stephen Wood<sup>655</sup>, Andrew Clark<sup>655</sup>, Gordon Houston<sup>655</sup>, Karen Black<sup>656</sup>, Michelle Clarkson<sup>656</sup>, Stuart D'Sylva<sup>656</sup>, Alan Morrison<sup>656</sup>, Kathryn Norman<sup>656</sup>, Margaret Taylor<sup>656</sup>, Suzanne Clements<sup>656</sup>, Catriona Cochrane<sup>656</sup>, Nora Gonzalez<sup>656</sup>, Dominic Strachan<sup>656</sup>, Claire Beith<sup>656</sup>, Kirsten Moar<sup>656</sup>, Peter Anderson<sup>656</sup>, Katie Archer<sup>656</sup>, Andrew Burtenshaw<sup>656</sup>, Sarah Clayton<sup>656</sup>, Naiara Cothe<sup>656</sup>, Nicholas Cowley<sup>656</sup>, Caroline Davis<sup>656</sup>, Stephen Digby<sup>656</sup>, Alison Durie<sup>656</sup>, Alison Harrison<sup>656</sup>, Emma Low<sup>656</sup>, Michael McAlindon<sup>656</sup>, Alex McCurdy<sup>656</sup>, Aled Morgan<sup>656</sup>, Tobias Rankin<sup>656</sup>, Jessica Thrush<sup>656</sup>, Helen Tranter<sup>656</sup>, Charlie Vigurs<sup>656</sup>, Laura Wild<sup>656</sup>, Lorna Murphy<sup>656</sup>, Michelle Smythe<sup>656</sup>, Kathy Brickell<sup>657</sup>, Intahkab Ali Mohamed Ali<sup>658</sup>, Karen Beaumont<sup>658</sup>, Mohamed Elsaadany<sup>658</sup>, Kay Fernandes<sup>658</sup>, Sameena Mohamed Ally<sup>658</sup>, Harini Rangarajan<sup>658</sup>, Varun Sarathy<sup>658</sup>, Sivapuram Selvanayagam<sup>658</sup>, Dave Vedage<sup>658</sup>, Matthew White<sup>658</sup>, Zoe Coton<sup>658</sup>, Aricsa Joshy<sup>658</sup>, Mark Blunt<sup>658</sup>, Hollie Curgenvin<sup>658</sup>, Liam Botfield<sup>659</sup>, Catherine Dexter<sup>659</sup>, Aditya Kuravi<sup>659</sup>, Joanne Butler<sup>659</sup>, Robert Chadwick<sup>659</sup>, Pooman Ranga<sup>659</sup>, Lisa Richardson<sup>659</sup>, Emma Virgilio<sup>659</sup>, Maddhina Anwe<sup>659</sup>, Atul Garg<sup>659</sup>, Donna Botfield<sup>659</sup>, Xana Marriott<sup>659</sup>, Keely Stewart<sup>660</sup>, Dee Mullan<sup>660</sup>, Jane Gaylard<sup>660</sup>, Justyna Nowal<sup>660</sup>, Sian Jones<sup>661</sup>, Rikki Crawley<sup>661</sup>, Abigail Crew<sup>661</sup>, Mishell Cunningham<sup>661</sup>, Allison Daniels<sup>661</sup>, Laura Harrison<sup>661</sup>, Susan Hope<sup>661</sup>, Nicola Lancaster<sup>661</sup>, Jamie Matthews<sup>661</sup>, Gemma Wray<sup>661</sup>, Ken Inwergbu<sup>661</sup>, Sarah Cutts<sup>661</sup>, Katharine Miller<sup>661</sup>, Ailbhe Brady<sup>662</sup>, Rebekah Chan<sup>662</sup>, Shane McIvor<sup>662</sup>, Helena Prady<sup>662</sup>, Bijoy Mathew<sup>662</sup>, Jeff Little<sup>662</sup>, Tim Furniss<sup>662</sup>, Chris Wright<sup>662</sup>, Bernadette King<sup>663</sup>, Christopher Wasson<sup>663</sup>, Aisling O'Neill<sup>663</sup>, Christine Turley<sup>663</sup>, Peter McGuigan<sup>663</sup>, Erin Collins<sup>663</sup>, Stephanie Finn<sup>663</sup>, Jackie Green<sup>663</sup>, Julie McAuley<sup>663</sup>, Abitha Nair<sup>663</sup>, Charlotte Quinn<sup>663</sup>, Suzanne Tauro<sup>663</sup>, Kathryn Ward<sup>663</sup>, Michael McGinlay<sup>663</sup>, Kiran Reddy<sup>663</sup>, Norfaizan Ahmad<sup>664</sup>, Samantha Anderson<sup>664</sup>, Joann Barker<sup>664</sup>, Kris Bachmuller<sup>664</sup>, Kathryn Birchall<sup>664</sup>, Sarah Birch<sup>664</sup>, Kay Cawthron<sup>664</sup>, Luke Chetam<sup>664</sup>, Joby Cole<sup>664</sup>, Ben Dono<sup>664</sup>, David Foote<sup>664</sup>, Amber Ford<sup>664</sup>, Helena Hanratty<sup>664</sup>, Kate Harrington<sup>664</sup>, Lisa Hesselton<sup>664</sup>, Kay Housley<sup>664</sup>, Yvonne Jackson<sup>664</sup>, Claire Jarman<sup>664</sup>, Faith Kibutu<sup>664</sup>, Becky Lenagh<sup>664</sup>, Irene Macharia<sup>664</sup>, Shamiso Masuku<sup>664</sup>, Leanne Milner<sup>664</sup>, Helen Newell<sup>664</sup>, Lorenza Nwafor<sup>664</sup>, Simon Oxspring<sup>664</sup>, Patrick Phillips<sup>664</sup>, Ajay Raithatha<sup>664</sup>, Sarah Rowland-Jones<sup>664</sup>, Jacqui Smith<sup>664</sup>, Roger Thompson<sup>664</sup>, Helen Trowe<sup>664</sup>, Sara Walker<sup>664</sup>, James Watson<sup>664</sup>, Michael Wilkes<sup>664</sup>, Alison Lye<sup>664</sup>, Jayne Willson<sup>664</sup>, Gary Mills<sup>664</sup>, Sansha Harris<sup>664</sup>, Eleanor Hartill<sup>664</sup>, Anthony Barron<sup>665</sup>, Ciara Collins<sup>665</sup>, Sundeeep Kaul<sup>665</sup>, Claire Nolan<sup>665</sup>, Oliver Polgar<sup>665</sup>, Claire Prendergast<sup>665</sup>, Paula Rogers<sup>665</sup>, Rajvinder Shokkar<sup>665</sup>, Meriel Woodruff<sup>665</sup>, Kanta Mahay<sup>665</sup>, Anna Reed<sup>665</sup>, Hayley Meyrick<sup>665</sup>, Heather Passmore<sup>665</sup>, James Farwell<sup>665</sup>, Susan O'Connell<sup>666</sup>, Jane Gregory<sup>666</sup>, Luigi Barberis<sup>666</sup>, Rosemary Harper<sup>666</sup>, Tim Smith<sup>666</sup>, Diane Armstrong<sup>666</sup>, Angie Bowey<sup>666</sup>, Anne Cowley<sup>666</sup>, Andrew Corner<sup>666</sup>, Judith Highgate<sup>666</sup>, Claire Rutherford<sup>666</sup>, Jo-Anne Taylor<sup>666</sup>, Sarah Goodwin<sup>666</sup>, Beena Eaper<sup>666</sup>, Fiona Trim<sup>666</sup>, Phil Donnison<sup>666</sup>, Lisa Armstrong<sup>666</sup>, Hayley Bates<sup>666</sup>, Emma Dooks<sup>666</sup>, Fiona Farquhar<sup>666</sup>, Amy Kitching<sup>666</sup>, Chantal McParland<sup>666</sup>, Sophie Packham<sup>666</sup>, Bridgid Hairsine<sup>666</sup>, Premetie Androu<sup>666</sup>, Dawn Hales<sup>666</sup>, Megha Mathews<sup>666</sup>, Rekha Patel<sup>666</sup>, Peter Barry<sup>666</sup>, Neil Flint<sup>666</sup>, Jessica Hailstone<sup>666</sup>, Navneet Ghuman<sup>666</sup>, Bethany Leonard<sup>666</sup>, Rachel Lees<sup>666</sup>, Deborah Butcher<sup>666</sup>, Katy Leng<sup>666</sup>, Nicola Butterworth-Cowin<sup>666</sup>, Susie O'Sullivan<sup>666</sup>, Alison Ghosh<sup>666</sup>, Emma Williams<sup>666</sup>, Colene Adams<sup>666</sup>, Anita Agasou<sup>666</sup>, Tracie Arden<sup>666</sup>, Mandy Beekes<sup>666</sup>, Amy Bowes<sup>666</sup>, Pauline Boyle<sup>666</sup>, Heather Button<sup>666</sup>, Mandy Carnahan<sup>666</sup>, Anne Carter<sup>666</sup>, Danielle Childs<sup>666</sup>, Fran Hurford<sup>666</sup>, Yasmin Hussain<sup>666</sup>, Ayesha Javid<sup>666</sup>, James Jones<sup>666</sup>, Michael Leigh<sup>666</sup>, Terry Martin<sup>666</sup>, Helen Millward<sup>666</sup>, Nichola Motherwell<sup>666</sup>, Julie Newman<sup>666</sup>, Rachel Rikunen<sup>666</sup>, Jo Stickley<sup>666</sup>, Julie Summers<sup>666</sup>, Louise Ting<sup>666</sup>, Helen Tivenan<sup>666</sup>, Denise Donaldson<sup>666</sup>, Nigel Capps<sup>666</sup>, Emily Cales<sup>666</sup>, Sanal Jose<sup>666</sup>, Wendy Osbourne<sup>666</sup>, Susie Pajak<sup>666</sup>, Jayne Rankin<sup>666</sup>, Louise Tonks<sup>666</sup>, Tracy Baird<sup>666</sup>, Margaret Harkins<sup>666</sup>, Jim Ruddy<sup>666</sup>, Joe West<sup>666</sup>, Joseph Duffield<sup>666</sup>, Lewis Mallon<sup>666</sup>, Oliver Smith<sup>666</sup>, Sara Smuts<sup>666</sup>, Andy Campbell<sup>666</sup>, Cate Davies<sup>666</sup>, Sarah Davis<sup>666</sup>, Rachel Hughes<sup>666</sup>, Lisa Jobs<sup>666</sup>, Victoria Whitehead<sup>666</sup>, Clare Watkins<sup>666</sup>, Fiona Bowman<sup>666</sup>, Barry Milligan<sup>666</sup>, Liane McPherson<sup>666</sup>, Stella Metherell<sup>666</sup>, Nichola Harris<sup>666</sup>, Victoria Lake<sup>666</sup>, Elizabeth Radford<sup>666</sup>, Andy Smallwood<sup>666</sup>, Shameer Gopal<sup>666</sup>, Katherine Vassel<sup>666</sup>, Dina Bell<sup>666</sup>, Rosalind Boyle<sup>666</sup>, Katie Douglas<sup>666</sup>, Lynn Glass<sup>666</sup>, Liz Lennon<sup>666</sup>, Austin Rattray<sup>666</sup>, Emma Lee<sup>666</sup>, Danielle Jones<sup>666</sup>, Penny Parsons<sup>666</sup>, Ben Atwood<sup>666</sup>, Paul Jefferson<sup>666</sup>, Mohan Ranganathan<sup>666</sup>, Inderjit Atwal<sup>666</sup>, Bridget Campbell<sup>666</sup>, Angela Day<sup>666</sup>, Camilla Stagg<sup>666</sup>, Emma Haynes<sup>666</sup>, Cecilia Ahmed<sup>666</sup>, Sarah Clamp<sup>666</sup>, Julie Colley<sup>666</sup>, Risna Haq<sup>666</sup>, Anne Hayes<sup>666</sup>, Sibet Joseph<sup>666</sup>, Zahira Maqsood<sup>666</sup>, Samia Hussain<sup>666</sup>, Jonathan Hulme<sup>666</sup>, Patience Domingos<sup>666</sup>, Rita Kumar<sup>666</sup>, Manjit Pureau<sup>666</sup>, Becky Taylor<sup>666</sup>, Lara Bunn<sup>666</sup>, Monica Latif<sup>666</sup>, Claire Jennings<sup>666</sup>, Shilu Jose<sup>666</sup>, Rebecca Marshall<sup>666</sup>, Aleksandra Metryka<sup>666</sup>, Gayathri Subramanian<sup>666</sup>, Adam Burgoyne<sup>666</sup>, Amanda Tyler<sup>666</sup>, Joanne Waldron<sup>666</sup>, Paula Hillout<sup>666</sup>, Jayne Evitts<sup>666</sup>, Geraldine Ward<sup>666</sup>, Pamela Bremmer<sup>666</sup>, Carl Hawkins<sup>666</sup>, Sophie Jackson<sup>666</sup>, Michal Ogorek<sup>666</sup>, Kylie Ashby<sup>666</sup>, Lorraine Thornton<sup>666</sup>, Pauline Mercer<sup>666</sup>, Matthew Halkes<sup>666</sup>, Adam Revill<sup>666</sup>, Bryony Saint<sup>666</sup>, Jo Fletcher<sup>666</sup>, Kimberley Netherton<sup>666</sup>, Manish Chhabani<sup>666</sup>, Amy Kirkby<sup>666</sup>, Amanda Roper<sup>666</sup>, Kinga Szymiczek<sup>666</sup>, Isobel Sutherland<sup>666</sup>, Linda O'Brien<sup>666</sup>, Joanne Connel<sup>666</sup>, Kim Davies<sup>666</sup>, Tracy Lewis<sup>666</sup>, Zohra Omar<sup>666</sup>, Emma Perkins<sup>666</sup>, Sonia Sathe<sup>666</sup>, Ellie Davies<sup>666</sup>, Alex Lyon<sup>666</sup>, Ishesuone Mafunde<sup>666</sup>, Charlotte Willis<sup>666</sup>, Rachael Hitchcock<sup>666</sup>, Kathryn Hall<sup>666</sup>, Christopher King<sup>666</sup>, Andrew Fagan<sup>666</sup>, Roonak Nazari<sup>666</sup>, Lucy Worsley<sup>666</sup>, Suzanne Allibone<sup>666</sup>, Vidya Kasipandian<sup>666</sup>, Amit Patel<sup>666</sup>, Parisa Cutting<sup>666</sup>, Roman Genetu<sup>666</sup>, Ainhí Mac<sup>666</sup>, Anthony Murphy<sup>666</sup>, Sinead Ward<sup>666</sup>, Fatima Butt<sup>666</sup>, Amanda Ayers<sup>666</sup>, Wendy Harrison<sup>666</sup>, Katherine Mackintosh<sup>666</sup>, Julie North<sup>666</sup>, Lydia Ashton<sup>666</sup>, Rehana Bi<sup>666</sup>, Samantha Owen<sup>666</sup>, Helen Winnill<sup>666</sup>, Barney Scholefield<sup>666</sup>, Hannah Blowing<sup>666</sup>, Erin Williams<sup>666</sup>, Michaela Duskova<sup>666</sup>, Michelle Edwards<sup>666</sup>, Alun Rees<sup>666</sup>, Helen Thomas<sup>666</sup>, Rachel Hughes<sup>666</sup>, Jolene Brooks<sup>666</sup>, Janet Phipps<sup>666</sup>, Suzanne Brooks<sup>666</sup>, Catherine Dennis<sup>666</sup>, Vicki Parris<sup>666</sup>, Sinduya Srikanan<sup>666</sup>, Anisha Sukha<sup>666</sup>, Alistair McGregor<sup>666</sup>, Gerlynn Tiongson<sup>666</sup>, Katie Adams<sup>666</sup>, Benedict Andrew<sup>666</sup>, Adam Brayne<sup>666</sup>, Sasha Carter<sup>666</sup>, Louise Finlay<sup>666</sup>, Emma Fisher<sup>666</sup>, Peter Jackson<sup>666</sup>, Duncan Kaye<sup>666</sup>, Juliet Parkin<sup>666</sup>, Victoria Tuckey<sup>666</sup>, Jane Hunt<sup>666</sup>, Nicholas Love<sup>666</sup>, Lynne van Koutrick<sup>666</sup>, Ashley Hanson<sup>666</sup>, Kathy Dent<sup>666</sup>, Elizabeth Horsley<sup>666</sup>, Sandra Pearson<sup>666</sup>, Sue Spence<sup>666</sup>, Dorothy Hutchinson<sup>666</sup>, Dorota Potoczna<sup>666</sup>, Muhammad Nauman Akhtar<sup>666</sup>, Lisa-Jayne Cottam<sup>666</sup>, Jack Sanders<sup>666</sup>, Sara Mingo Garcia<sup>666</sup>, Glykeria pakou<sup>666</sup>, Helder Filipe<sup>666</sup>, Amita Maharajh<sup>666</sup>, Mark de Neef<sup>666</sup>, Daniel Martin<sup>666</sup>, Christine Eastgate<sup>666</sup>, Poh Choo Teoh<sup>666</sup>, Fiona Barrett<sup>666</sup>, Clare Bradley<sup>666</sup>, Avril Donaldson<sup>666</sup>, Mairi Mascarenhas<sup>666</sup>, Marianne O'Hara<sup>666</sup>, Laura Okeefe<sup>666</sup>

# Matters arising

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**Variability in Immune Response Genes and Severity of SARS-CoV-2 Infection (INMUNGEN-CoV2 study)**

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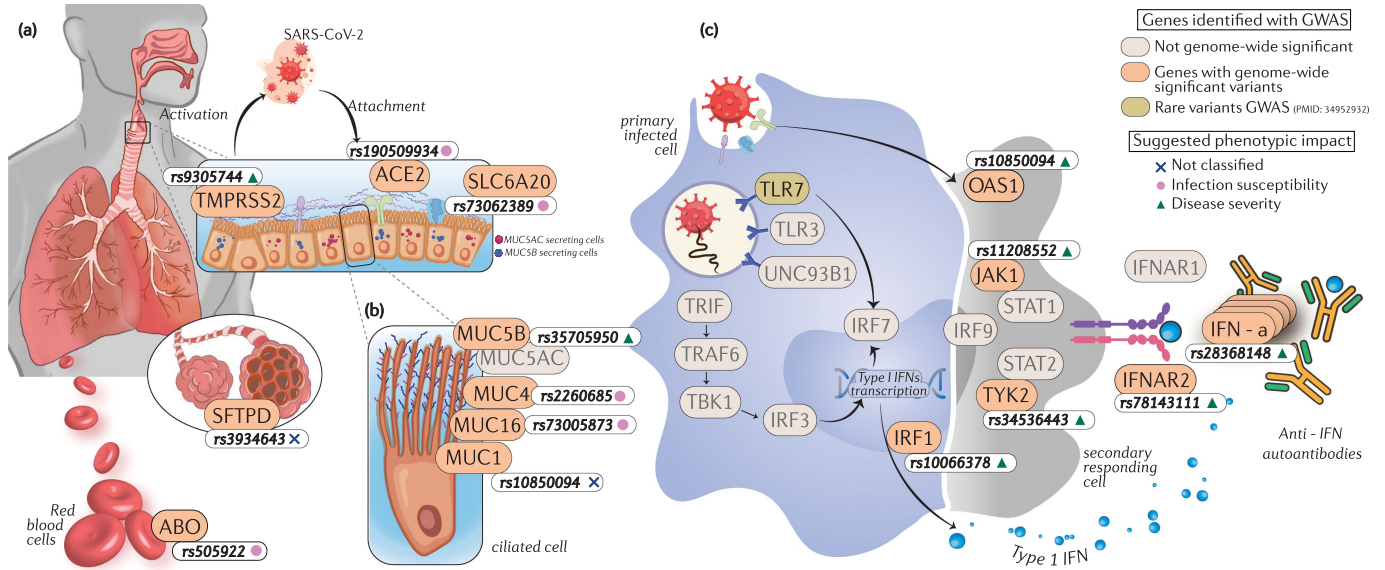
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# Matters arising



**Extended Data Fig. 1 | Major COVID-19 biological pathways mapped with susceptibility and severity GWAS loci.** Genome-wide significant variants associated with COVID-19 (white boxes) and the annotated genes (peach boxes) are mapped on to pathways known to be involved in (a) viral entry and innate immunity, (b) entry defence in airway mucus, and (c) type I interferon. The suggested phenotypic impact of the significant variants using the Bayesian

approach<sup>2</sup> are denoted with shapes; COVID-19 susceptibility (pink circles), COVID-19 disease severity (green triangles), and unclassified (blue cross). Other genes known to be involved in the aforementioned pathways are shown using grey boxes. Detailed list of references to studies used to design this pathway can be found in Supplementary Note.

## Reporting Summary

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### Statistics

For all statistical analyses, confirm that the following items are present in the figure legend, table legend, main text, or Methods section.

n/a | Confirmed

- The exact sample size ( $n$ ) for each experimental group/condition, given as a discrete number and unit of measurement
- A statement on whether measurements were taken from distinct samples or whether the same sample was measured repeatedly
- The statistical test(s) used AND whether they are one- or two-sided  
*Only common tests should be described solely by name; describe more complex techniques in the Methods section.*
- A description of all covariates tested
- A description of any assumptions or corrections, such as tests of normality and adjustment for multiple comparisons
- A full description of the statistical parameters including central tendency (e.g. means) or other basic estimates (e.g. regression coefficient) AND variation (e.g. standard deviation) or associated estimates of uncertainty (e.g. confidence intervals)
- For null hypothesis testing, the test statistic (e.g.  $F$ ,  $t$ ,  $r$ ) with confidence intervals, effect sizes, degrees of freedom and  $P$  value noted  
*Give  $P$  values as exact values whenever suitable.*
- For Bayesian analysis, information on the choice of priors and Markov chain Monte Carlo settings
- For hierarchical and complex designs, identification of the appropriate level for tests and full reporting of outcomes
- Estimates of effect sizes (e.g. Cohen's  $d$ , Pearson's  $r$ ), indicating how they were calculated

*Our web collection on [statistics for biologists](#) contains articles on many of the points above.*

### Software and code

Policy information about [availability of computer code](#)

Data collection

No code was used to collect data in the study.

Data analysis

Each individual study that contributed genetic-phenotype association summary statistics to the consortium carried out their association analyses independently of the consortium (study-specific information outlined in Supplementary Table 1). However, the consortium released phenotyping and analysis guidelines as a recommendation (<https://www.covid19hg.org/>). For quality control of genotype data we recommended using the Ricopili pipeline (PMID: 31393554). For genotype phasing and imputation we recommended the TopMed Imputation Server (PMID: 27571263) or Michigan Imputation Server (PMID: 27571263). For genome-wide association study (GWAS), we recommended SAIGE (PMID: 30104761), but some studies used PLINK (PMID: 17701901). Each study then submitted their GWAS summary statistics to the consortium for meta-analysis. No version was specified in the recommendation—each study used the best available version for them. LD score regression v 1.0.1 (PMID: 25642630) was used for heritability and partitioned heritability analyses. Variants for Mendelian randomization instruments were selected using PLINK version 1.90b6.18 (PMID: 17701901). Exposure and outcome datasets were harmonized, and MR statistical analysis conducted using R version 4.0.3. with the R-package TwoSampleMR version 0.5.5 (PMID: 29846171) (which included a fixed-effect IVW analysis [PMID: 24114802], weighted median estimator [WME] [PMID: 27061298], weighted mode based estimator [WMBE] and MR Egger regression [PMID: 26050253]) and additionally MR-PRESSO version 1.0 (PMID: 29686387). Code availability statement: The code for summary statistics lift-over, the projection PCA pipeline including precomputed loadings and meta-analyses are available at <https://github.com/covid19-hg/>; heritability estimation at <https://github.com/AndrewsLabUCSF/> COVID19\_heritability; Mendelian randomization and genetic correlation at <https://github.com/marcoralab/MRcovid/>; and subtype analyses at [https://github.com/mjpirinen/covid19-hgi\\_subtypes](https://github.com/mjpirinen/covid19-hgi_subtypes).

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## Data

Policy information about [availability of data](#)

All manuscripts must include a [data availability statement](#). This statement should provide the following information, where applicable:

- Accession codes, unique identifiers, or web links for publicly available datasets
- A description of any restrictions on data availability
- For clinical datasets or third party data, please ensure that the statement adheres to our [policy](#)

Summary statistics generated by COVID-19 HGI are available online, including per-ancestry summary statistics for African, Admixed American, East Asian, European, and South Asian ancestries (<https://www.covid19hg.org/results/r7/>). The analyses described here utilize the data release 7. If available, individual-level data can be requested directly from contributing studies, listed in Supplementary Table 1. We used publicly available data from GTEx v8 (<https://gtexportal.org/home/>; dbGaP Accession phs000424.v8.p2), the Neale lab (<http://www.nealelab.is/uk-biobank/>), Finucane lab (<https://www.finucanelab.org>), FinnGen Freeze 4 cohort ([https://www.finnngen.fi/en/access\\_results](https://www.finnngen.fi/en/access_results)), and eQTL catalogue release 3 (<http://www.ebi.ac.uk/eQTL/>).

## Human research participants

Policy information about [studies involving human research participants and Sex and Gender in Research](#).

Reporting on sex and gender

Biological sex was collected by each study. The consortium recommended using biological sex as one of the covariates to correct for potential confounding effects (full recommended covariates are: age + age<sup>2</sup> + sex + age\*sex + 20 principal components obtained using genetic data). No sex or gender specific analysis was reported in this study. The consortium did not collect gender information.

Population characteristics

Summary statistics from 82 independent studies were included in consortium meta-analyses. The sample size for genetic ancestry populations for Sars-CoV2 infection was: n=17,898 Middle Eastern; n=53,116 South Asian; 40,580 East Asian; 148,891 African; 129,629 Ad-mixed American; 2,824,391 European. Population characteristics regarding age, sex and exact case and control sample numbers for each contributing study are given in Supplementary Table 1.

Recruitment

The consortium pre-defined phenotype criteria for cases and controls, but the specific recruitment was carried out independently by each contributing study. COVID-19 disease status (critical illness, hospitalization status) was assessed following the Diagnosis and Treatment Protocol for Novel Coronavirus Pneumonia (PMID: 32358325). The critically ill COVID-19 group included patients who were hospitalized due to symptoms associated with laboratory-confirmed SARS-CoV-2 infection and who required respiratory support or whose cause of death was associated with COVID-19. The hospitalized COVID-19 group included patients who were hospitalized due to symptoms associated with laboratory confirmed SARS-CoV-2 infection. The reported infection cases group included individuals with laboratory-confirmed SARS-CoV-2 infection or electronic health record, ICD coding or clinically confirmed COVID-19, or self-reported COVID-19 (e.g. by questionnaire), with or without symptoms of any severity. Genetic ancestry-matched controls for the three case definitions were sourced from population-based cohorts, including individuals whose exposure status to SARS-CoV-2 was either unknown or infection-negative for questionnaire/electronic health record based cohorts.

Ethics oversight

Ethical statements for each contributing study are given in Supplementary Table 1.

Note that full information on the approval of the study protocol must also be provided in the manuscript.

## Field-specific reporting

Please select the one below that is the best fit for your research. If you are not sure, read the appropriate sections before making your selection.

- Life sciences       Behavioural & social sciences       Ecological, evolutionary & environmental sciences

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## Life sciences study design

All studies must disclose on these points even when the disclosure is negative.

Sample size

The consortium meta-analysed genome-wide association study (GWAS) summary statistics from any individual study that had included a minimum of 100 cases and 100 controls in their analysis. The cutoff was aimed at reducing noise for the meta-analysis, but also to be inclusive of studies that had not yet accumulated large numbers of COVID-19 patient data. The consortium aimed to reach the largest possible sample size for the study and meta-analyzed all the submitted summary statistics. No statistical calculation for adequate sample size was performed, but the results identifying multiple genomic regions at genome-wide significance threshold indicates adequate power for genetic discovery.

Data exclusions

Individual level phenotype and genotype data exclusions were performed by each individual study, following the consortium analysis plan recommendations ([www.covid19hg.org](https://www.covid19hg.org)). Possible reasons for sample exclusion included removing genetic ancestry outliers within a study

(using principal components analysis), poor quality of genetic data or lack of phenotypic data for a sample. The consortium manually examined GWAS summary statistics data submitted by each study (for each submitted analysis separately), including sample size used for analysis, allele frequency check against Gnomad reference panel, and distribution of test statistics. After meta-analysis, the results were checked for heterogeneity variant effects between contributing studies in Supplementary Table 2

## Replication

No replication was performed. The consortium meta-analysed GWAS summary statistics, bringing together as many studies as possible to achieve the largest possible sample size and statistical power for association. This meant that the consortium included most large studies of COVID-19 host genetics that have been performed to date, so it was not possible to perform replication analyses in external cohorts. Therefore we performed manual checks on each study contributing summary statistics before entering them into the meta-analysis. In addition, after meta-analysis, we performed a check for heterogeneity between variant association estimates across studies contributing data. This allowed us to better understand whether the variant effects differed much between individual studies.

## Randomization

No randomization was performed because there was no allocation of samples to experimental groups

## Blinding

Blinding was not relevant to the study because no intervention was implemented in the study. The case status and severity of symptoms was evaluated for each sample by investigators from each study respectively. The consortium recommended using covariates to control for confounding: age + age<sup>2</sup> + sex + age\*sex + 20 principal components (obtained using genetic data) + study specific covariates (if any). The consortium meta-analysed summary statistics from these case/control studies, not individual level data. Details of which variables each study used and how the calculated PCs for their analysis are available in Supplementary Table 1.

## Reporting for specific materials, systems and methods

We require information from authors about some types of materials, experimental systems and methods used in many studies. Here, indicate whether each material, system or method listed is relevant to your study. If you are not sure if a list item applies to your research, read the appropriate section before selecting a response.

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### Methods

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