

Mapping the human genetic architecture of COVID-19

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COVID-19 Host Genetics Initiative*

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The genetic make-up of an individual contributes to the susceptibility and response to viral infection. Although environmental, clinical and social factors have a role in the chance of exposure to SARS-CoV-2 and the severity of COVID-19^{1,2}, host genetics may also be important. Identifying host-specific genetic factors may reveal biological mechanisms of therapeutic relevance and clarify causal relationships of modifiable environmental risk factors for SARS-CoV-2 infection and outcomes. We formed a global network of researchers to investigate the role of human genetics in SARS-CoV-2 infection and COVID-19 severity. Here we describe the results of three genome-wide association meta-analyses that consist of up to 49,562 patients with COVID-19 from 46 studies across 19 countries. We report 13 genome-wide significant loci that are associated with SARS-CoV-2 infection or severe manifestations of COVID-19. Several of these loci correspond to previously documented associations to lung or autoimmune and inflammatory diseases^{3–7}. They also represent potentially actionable mechanisms in response to infection. Mendelian randomization analyses support a causal role for smoking and body-mass index for severe COVID-19 although not for type II diabetes. The identification of novel host genetic factors associated with COVID-19 was made possible by the community of human genetics researchers coming together to prioritize the sharing of data, results, resources and analytical frameworks. This working model of international collaboration underscores what is possible for future genetic discoveries in emerging pandemics, or indeed for any complex human disease.

The COVID-19 pandemic, caused by infection with SARS-CoV-2, has resulted in an enormous health and economic burden worldwide. One of the most remarkable features of SARS-CoV-2 infection is the variation in consequences, which range from asymptomatic to life-threatening, viral pneumonia and acute respiratory distress syndrome⁸. Although established host factors correlate with disease severity (for example, increasing age, being a man and higher body-mass index¹), these risk factors alone do not explain all of the variability in disease severity observed across individuals.

Genetic factors contributing to COVID-19 susceptibility and severity may provide new biological insights into disease pathogenesis and identify mechanistic targets for therapeutic development or drug repurposing, as treating the disease remains a highly important goal despite the recent development of vaccines. Further supporting this line of inquiry, rare loss-of-function variants in genes involved in the type I interferon response may be involved in severe forms of COVID-19^{9–11}. At the same time, several genome-wide association studies that investigate the contribution of common genetic variation^{12–15} to COVID-19 have provided robust support for the involvement of several genomic loci associated with COVID-19 severity and susceptibility, with the strongest and most robust finding for severity being at the 3p21.31 locus^{12–16}. However, much remains unknown about the genetic basis of susceptibility to SARS-CoV-2 and severity of COVID-19.

The COVID-19 Host Genetics Initiative (COVID-19 HGI) (<https://www.covid19hg.org/>)¹⁷ is an international, open-science collaboration to share scientific methods and resources with research groups across the world with the goal to robustly map the host genetic determinants of SARS-CoV-2 infection and the severity of the resulting COVID-19 disease. Here, we report the latest results of meta-analyses of 46 studies from 19 countries (Fig. 1) for COVID-19 host genetic effects.

Meta-analyses of COVID-19

Overall, the COVID-19 HGI combined genetic data from 49,562 cases and 2 million controls across 46 distinct studies (Fig. 1). The data included studies from populations of different genetic ancestries, including European, admixed American, African, Middle Eastern, South Asian and East Asian individuals (Supplementary Table 1). An overview of the study design is provided in Extended Data Fig. 1. We performed case-control meta-analyses in three main categories of COVID-19 disease according to predefined and partially overlapping phenotypic criteria. These included (1) critically ill cases of COVID-19 defined as those individuals who required respiratory support in hospital or who died due to the disease; (2) cases of moderate or severe COVID-19 defined as those participants who were hospitalized due to symptoms associated with the infection; and (3) all cases with reported SARS-CoV-2 infection

*Lists of authors and their affiliations appear in the online version of the paper.

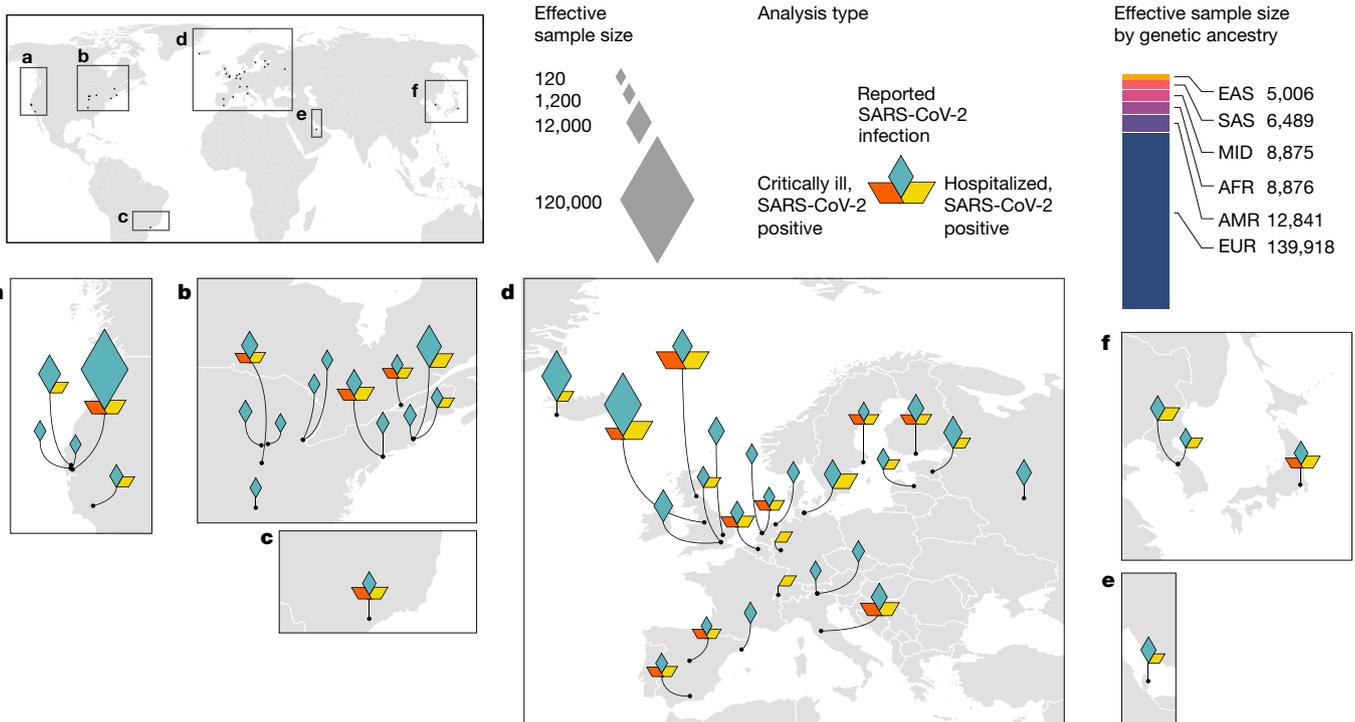


Fig. 1 | Geographical overview of the contributing studies to the COVID-19 HGI and composition by major ancestry groups. Populations are defined as African (AFR), admixed American (AMR), East Asian (EAS), European (EUR), Middle Eastern (MID) and South Asian (SAS).

regardless of symptoms (Methods). Controls for all three analyses were selected as genetically ancestry-matched samples without known SARS-CoV-2 infection, if that information was available (Methods). The average age of the participants with COVID-19 across studies was 55 years (Supplementary Table 1). We report quantile–quantile plots in Supplementary Fig. 1 and ancestry principal component plots for contributing studies in Extended Data Fig. 2.

Across our three analyses, we reported a total of 13 independent genome-wide significant loci associated with COVID-19 (the threshold of $P < 1.67 \times 10^{-8}$ is adjusted for multiple trait testing) (Supplementary Table 2), most of which were shared between two or more COVID-19 phenotypes. Two of these loci are in very close proximity within the 3p21.31 region, which was previously reported as a single locus associated with COVID-19 severity^{12–16} (Extended Data Fig. 3). Overall, we find six genome-wide significant associations for critical illness due to COVID-19, using data from 6,179 cases and 1,483,780 controls from 16 studies (Extended Data Fig. 4). Nine genome-wide significant loci were detected for moderate to severe hospitalized COVID-19 (including five of the six critical illness loci) from an analysis of 13,641 cases of COVID-19 and 2,070,709 controls across 29 studies (Fig. 2a, top). Finally, seven loci reached genome-wide significance in the analysis using data for all available 49,562 reported cases of SARS-CoV-2 infection and 1,770,206 controls, using data from a total of 44 studies (Fig. 2a, bottom). The proportion of cases with non-European genetic ancestry for each of the three analyses was 23%, 29% and 22%. We report the results for the lead variants at the 13 loci in different ancestry-group meta-analyses in Supplementary Table 3. We note that two loci, tagged by lead variants rs1886814 and rs72711165, had higher allele frequencies in southeast Asian (rs1886814; 15%) and East Asian genetic ancestry (rs72711165; 8%) whereas the minor allele frequencies in European populations were less than 3%. This highlights the value of including data from diverse populations for genetic discovery. We discuss the replication of previous findings and the new discoveries from these three analyses in the Supplementary Note.

Variant effects on severity and susceptibility

We found no genome-wide significant sex-specific effects at the 13 loci. However, we did identify significant heterogeneous effects ($P < 0.004$) across studies for 3 out of the 13 loci (Methods), which probably reflects the differential ascertainment of cases (Supplementary Table 2). There was a small number of overlapping samples ($n = 8,380$ European ancestry; $n = 745$ East Asian ancestry) between controls from the genOMICC and the UK Biobank studies, but leave-one-out sensitivity analyses did not reveal any bias in the corresponding effect sizes or P values (Extended Data Fig. 5 and Supplementary Information).

We next wanted to better understand whether the 13 significant loci were acting through mechanisms that increased the susceptibility to infection or that affected the progression of symptoms towards more severe disease. For all 13 loci, we compared the lead variant (strongest association P value) odds ratios (ORs) for the risk-increasing allele across our different COVID-19 phenotype definitions.

Focusing on the two better powered analyses: all cases with a reported SARS-CoV-2 infection and all cases hospitalized due to COVID-19, we find that four of the loci have similar odds ratios between these two analyses (Methods and Supplementary Table 2). Such consistency suggests a stronger link to susceptibility to SARS-CoV-2 infection rather than to the development of severe COVID-19. The strongest susceptibility signal was the previously reported *ABO* locus (rs912805253)^{12,13,15,16}. Notably, and in agreement with a previously reported study¹⁵, we also report a locus within the 3p21.31 region that was more strongly associated with susceptibility to SARS-CoV-2 than progression to more severe COVID-19 phenotypes. rs2271616 showed a stronger association with a reported SARS-CoV-2 infection ($P = 1.79 \times 10^{-34}$; OR (95% confidence interval (CI)) = 1.15 (1.13–1.18)) than hospitalization ($P = 1.05 \times 10^{-5}$; OR (95% CI) = 1.12 (1.06–1.19)). For this locus—which contains additional independent signals—the linkage-disequilibrium (LD) pattern is discordant with the P -value expectation (Extended Data Fig. 6 and Supplementary Note), pointing to a key missing causal variant or to a potentially undiscovered multi-allelic or structural variant in this locus.

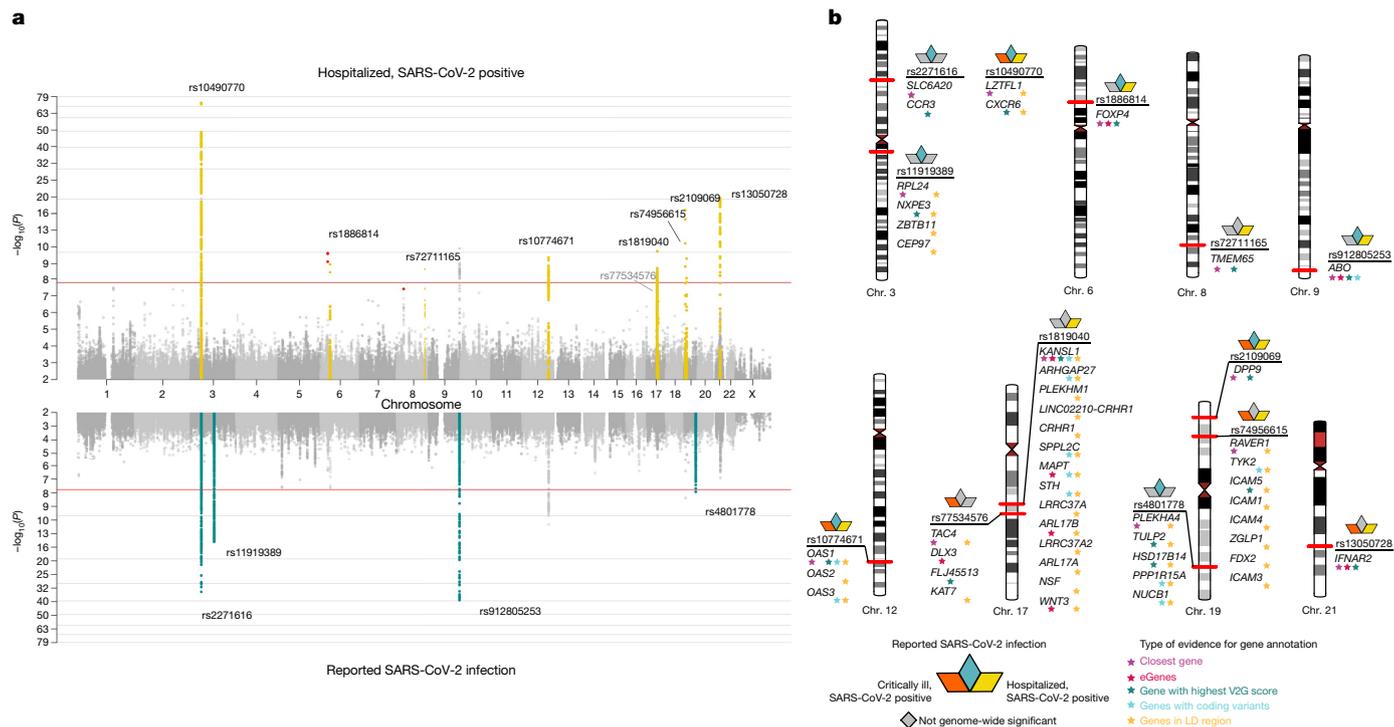


Fig. 2 | Genome-wide association results for COVID-19. **a**, Top, results of a genome-wide association study of hospitalized cases of COVID-19 ($n = 13,641$ cases and $n = 2,070,709$ controls). Bottom, the results of reported SARS-CoV-2 infections ($n = 49,562$ cases and $n = 1,770,206$ controls). Loci highlighted in yellow (top) represent regions associated with the severity of the COVID-19 manifestation—that is, increased odds of more severe COVID-19 phenotypes. Loci highlighted in green (bottom) are regions associated with susceptibility to a SARS-CoV-2 infection—that is, the effect is the same across mild and severe

By contrast, 9 out of the 13 loci were associated with increased risk of severe symptoms with significantly larger odds ratios for hospitalized COVID-19 compared with the mildest phenotype of reported SARS-CoV-2 infection (eight loci were below the threshold of $P < 0.004$ (test for effect size difference) and, in addition, the lead variant rs10774671 had a clear increase in odds ratios despite not passing this threshold) (Supplementary Table 2). We further compared the odds ratios for these nine loci for critical illness due to COVID-19 versus hospitalized due to COVID-19, and found that these loci exhibited a general increase in effect risk for critical illness (Methods, Extended Data Fig. 7a and Supplementary Table 4), but the lower power for association analysis of critically ill COVID-19 means that these results should be considered as suggestive. Overall, these results indicated that these nine loci were more likely to be associated with progression of the disease and worse outcome from SARS-CoV-2 infection compared to being associated with susceptibility to SARS-CoV-2 infection.

For some of these analyses, the controls were simply existing population controls without knowledge of SARS-CoV-2 infection or COVID-19 status, which may bias effect size estimates as some of these individuals may have either become infected with SARS-CoV-2 or developed COVID-19. We perform several sensitivity analyses (Extended Data Fig. 7b, Supplementary Note and Supplementary Table 4) in which we show that using population controls can be a valid and powerful strategy for host genetic discovery of infectious disease, and particularly those that are widespread and with rare severe outcomes.

Gene prioritization and association with other traits

To better understand the potential biological mechanism of each locus, we applied several approaches to prioritize candidate causal genes and

COVID-19 phenotypes. We highlight in red genome-wide significant variants that had high heterogeneity across contributing studies and that were therefore excluded from the list of loci found. **b**, Results of gene prioritization using different evidence measures of gene annotation. Genes in the LD region, genes with coding variants and eGenes (fine-mapped *cis*-eQTL variant $PIP > 0.1$ in GTEx Lung) are annotated if in LD with a COVID-19 lead variant ($r^2 > 0.6$). V2G, highest gene prioritized by the V2G score of Open Target Genetics.

explore additional associations with other diseases and traits. Of the 13 genome-wide significant loci, we found that nine loci implicated biologically plausible genes (Supplementary Tables 2, 5). Protein-altering variants in LD with lead variants implicated genes at six loci, including *TYK2* (chromosome and cytogenetic band (chr.) 19p13.2) and *PPP1R15A* (chr. 19q13.33). The COVID-19 lead variant rs74956615T>A in *TYK2*, which confers risk for critical illness (OR (95% CI) = 1.43 (1.29–1.59), $P = 9.71 \times 10^{-12}$) and hospitalization due to COVID-19 (OR (95% CI) = 1.27 (1.18–1.36), $P = 5.05 \times 10^{-10}$) is correlated with the missense variant rs34536443:G>C (p.Pro1104Ala; $r^2 = 0.82$). This is consistent with the primary immunodeficiency described with complete *TYK2* loss of function³ as this variant is known to reduce function^{18,19}. By contrast, this missense variant was previously reported to be protective against autoimmune diseases (Extended Data Fig. 8 and Supplementary Table 6), including rheumatoid arthritis (OR = 0.74, $P = 3.0 \times 10^{-8}$; UK Biobank SAIGE) and hypothyroidism (OR = 0.84, $P = 1.8 \times 10^{-10}$; UK Biobank). At the 19q13.33 locus, the lead variant rs4801778, which was significantly associated with a reported SARS-CoV-2 infection (OR (95% CI) = 0.95 (0.93–0.96), $P = 2.1 \times 10^{-8}$), is in LD ($r^2 = 0.93$) with a missense variant rs11541192:G>A (p.Gly312Ser) in *PPP1R15A*.

A lung-specific *cis*-expression quantitative trait loci (*cis*-eQTLs) from GTEx v.8²⁰ ($n = 515$) and the Lung eQTL Consortium²¹ ($n = 1,103$) provided further support for a subset of loci (Supplementary Table 7), including *FOXP4* (chr. 6p21.1) and *ABO* (chr. 9q34.2), *OAS1/OAS3/OAS2* (chr. 12q24.13) and *IFNAR2/IL10RB* (21q22.11), where the COVID-19-associated variants modify gene expression in lung. Furthermore, our phenome-wide association study (PheWAS) analysis (Supplementary Table 6) implicated three additional loci related to lung function, with modest lung eQTL evidence—that is, the lead variant was not fine-mapped but significantly associated. An intronic variant

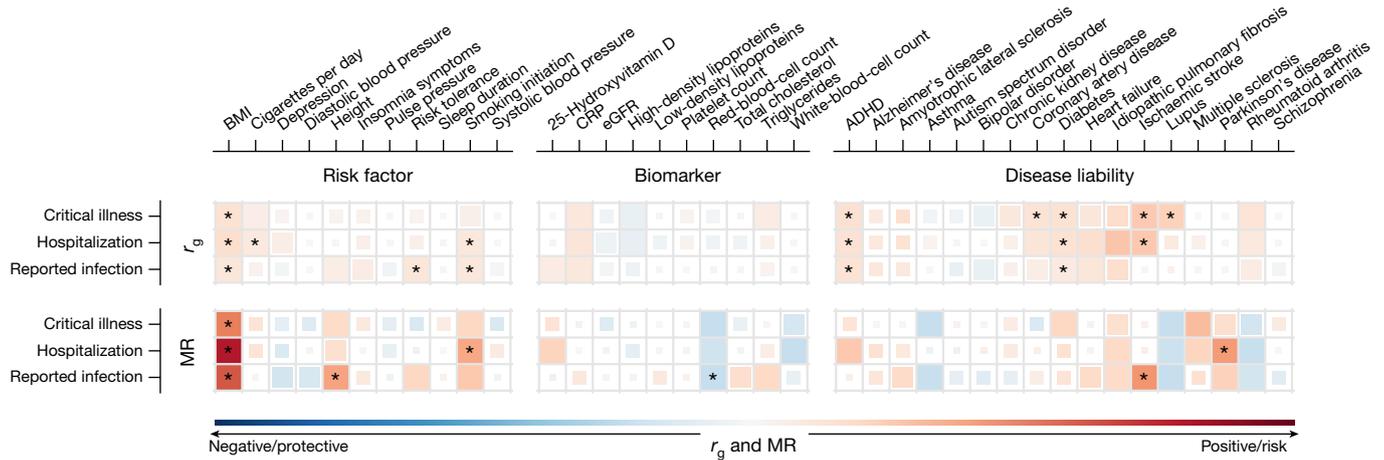


Fig. 3 | Genetic correlations and Mendelian randomization causal estimates between 38 traits and COVID-19 critical illness, hospitalization and reported SARS-CoV-2 infection. Larger squares correspond to P values with higher significance, with genetic correlations (r_g) or Mendelian randomization (MR) causal estimates significantly different from zero. The size of each coloured square indicates the magnitude of the P value, with $P < 0.05$ shown as a full-sized square, $P = 0.05-0.1$ as a large square, $P = 0.1-0.5$

as a medium square and $P > 0.5$ as a small square. Genetic correlations or causal estimates that are significantly different from zero at an FDR of 5% are marked with an asterisk. Two-sided P values were calculated using LDSC for genetic correlations and inverse-variance-weighted analysis for Mendelian randomization. ADHD, attention-deficit hyperactivity disorder; BMI, body mass index; CRP, C-reactive protein; eGFR, estimated glomerular filtration rate.

rs2109069:G>A in *DPP9* (chr. 19p13.3), which is positively associated with critical illness, was previously reported to be risk-increasing for interstitial lung disease (tag lead variant rs12610495:A>G (p.Leu8Pro); OR = 1.29, $P = 2.0 \times 10^{-12}$)⁵. The COVID-19 lead variant rs1886814:A>C in the *FOXP4* locus is correlated ($r^2 = 0.64$) with a lead variant of lung adenocarcinoma (tag variant is rs7741164; OR = 1.2, $P = 6.0 \times 10^{-13}$)^{6,22} and similarly with a lead variant reported for subclinical interstitial lung disease²³. In severe COVID-19, lung cancer and interstitial lung disease, the minor, expression-increasing allele is associated with increased risk. We also found that intronic variants (chr. 1q22) and rs1819040:T>A in *KANSL1* (chr. 17q21.31), associated with protection against hospitalization due to COVID-19, were previously reported for reduced lung function (for example, tag lead variant rs141942982:G>T; OR (95% CI) = 0.96 (0.95–0.97), $P = 1.00 \times 10^{-20}$)⁷. Notably, the 17q21.31 locus is a well-known locus for structural variants containing a megabase inversion polymorphism (H1 and inverted H2 forms) and complex copy-number variations, in which the inverted H2 forms were shown to be positively selected in European individuals^{24,25}.

Lastly, there are two loci in the 3p21.31 region with varying genes prioritized by different methods for different independent signals. For the severity lead variant rs10490770:T>C, we prioritized *CXCR6* with the Variant2Gene (V2G) algorithm²⁶, although *LZTFL1* is the closest gene. The *CXCR6* has a role in chemokine signalling²⁷ and *LZTFL1* has been implicated in lung cancer²⁸. rs2271616:G>T, which is associated with susceptibility, tags a complex region including several independent signals (Supplementary Note) that are all located within the gene body of *SLC6A20*, which encodes a protein that is known to functionally interact with the SARS-CoV-2 receptor ACE2²⁹. However, none of the lead variants in the 3p21.31 region has been previously associated with other traits or diseases in our PheWAS analysis. Although these results provide supporting in silico evidence for candidate causal gene prioritization, further functional characterization is needed. Detailed locus descriptions and LocusZoom plots are provided in Supplementary Fig. 2.

Polygenic architecture of COVID-19

To further investigate the genetic architecture of COVID-19, we used results from meta-analyses including samples from European ancestries

(sample sizes are described in the Methods and Supplementary Table 1) to estimate the heritability explained by common single-nucleotide polymorphisms—that is, the proportion of variation in the two phenotypes that was attributable to common genetic variants—and to determine whether heritability of COVID-19 phenotypes was enriched in genes that were specifically expressed in certain tissues³⁰ from the GTEx dataset³¹. We detected low, but significant, heritability across all three analyses (<1% on observed scale, all P values were $P < 0.0001$) (Supplementary Table 8). The values are low compared to previously published studies¹⁴, but may be explained by differences in the reported estimate scale (observed versus liability), the specific method used, disease-prevalence estimates, phenotypic differences between patient cohorts or ascertainment of controls. Despite the low reported values, we found that heritability of a reported SARS-CoV-2 infection was significantly enriched in genes that were specifically expressed in the lung ($P = 5.0 \times 10^{-4}$) (Supplementary Table 9). These findings, together with the genome-wide significant loci identified in the meta-analyses, suggest that there is a significant polygenic architecture that can be better leveraged with future, larger, sample sizes.

Genetic correlation and Mendelian randomization

Genetic correlations (r_g) between the three COVID-19 phenotypes was high, although lower correlations were observed between hospitalized COVID-19 and reported SARS-CoV-2 infection (critical illness versus hospitalized: r_g (95% CI) = 1.37 (1.08–1.65), $P = 2.9 \times 10^{-21}$; critical illness versus reported SARS-CoV-2 infection, r_g (95% CI) = 0.96 (0.71–1.20), $P = 1.1 \times 10^{-14}$; hospitalized versus reported SARS-CoV-2 infection: r_g (95% CI) = 0.85 (0.68–1.02), $P = 1.1 \times 10^{-22}$). To better understand which traits are genetically correlated and/or potentially causally associated with COVID-19 hospitalization, critical illness and reported SARS-CoV-2 infection, we chose a set of 38 disease, health and neuropsychiatric phenotypes as potential COVID-19 risk factors based on their clinical correlation with disease susceptibility, severity or mortality (Supplementary Table 10).

We found evidence (false-discovery rate (FDR) < 0.05) of significant genetic correlations between nine traits and hospitalized COVID-19 and reported SARS-CoV-2 infection (Fig. 3, Extended Data Fig. 9 and Supplementary Table 11). Notably, genetic liability to ischaemic

stroke was only significantly positively correlated with critical illness or hospitalization due to COVID-19, but not with a higher likelihood of reported SARS-CoV-2 infection (infection $r_g = 0.019$ versus hospitalization $r_g = 0.41$, $z = 2.7$, $P = 0.006$; infection $r_g = 0.019$ versus critical illness $r_g = 0.40$, $z = 2.49$, $P = 0.013$).

We next used two-sample Mendelian randomization to infer potentially causal relationships between these traits. After correcting for multiple testing (FDR < 0.05), eight exposure–COVID-19 trait pairs showed suggestive evidence of a causal association (Fig. 3, Extended Data Fig. 10, Supplementary Table 12 and Supplementary Fig. 3). Five of these associations were robust to potential violations of the underlying assumptions of Mendelian randomization. Corroborating our genetic correlation results and evidence from epidemiological studies, genetically predicted higher body-mass index (OR (95% CI) = 1.4 (1.3–1.6), $P = 8.5 \times 10^{-11}$) and smoking (OR (95% CI) = 1.9 (1.3–2.8), $P = 0.0012$) were associated with increased risk of COVID-19 hospitalization, with body-mass index also being associated with increased risk of SARS-CoV-2 infection (OR (95% CI) = 1.1 (1.1–1.2), $P = 4.8 \times 10^{-7}$). Genetically predicted increased height (OR (95% CI) = 1.1 (1–1.1), $P = 8.9 \times 10^{-4}$) was associated with an increased risk of reported SARS-CoV-2 infection, whereas a genetically predicted higher red-blood-cell count (OR (95% CI) = 0.93 (0.89–0.96), $P = 5.7 \times 10^{-5}$) was associated with a reduced risk of reported SARS-CoV-2 infection. Despite evidence of a genetic correlation between type II diabetes and COVID-19 outcomes, there was no evidence of a causal association in the Mendelian randomization analyses, which suggests that the observed genetic correlations are due to pleiotropic effects between body-mass index and type 2 diabetes. Further sensitivity analyses relating to sample overlap are discussed in the Supplementary Information.

Discussion

The COVID-19 HGI has brought together investigators from across the world to advance genetic discovery for SARS-CoV-2 infection and severe COVID-19 disease. We report 13 genome-wide significant loci associated with some aspect of SARS-CoV-2 infection or COVID-19. Many of these loci overlap with previously reported associations with lung-related phenotypes or autoimmune or inflammatory diseases, but some loci have no obvious candidate gene.

Four out of the thirteen genome-wide significant loci showed similar effects in the reported SARS-CoV-2 infection analysis (a proxy for disease susceptibility) and all-hospitalized COVID-19 (a proxy for disease severity). Of these, one locus was in close proximity to, yet independent of, the major genetic signal for COVID-19 severity at the 3p21.31 locus. Notably, this locus was associated with COVID-19 susceptibility rather than severity. The locus overlaps *SLC6A20*, which encodes an amino acid transporter that interacts with ACE2. Nonetheless, we caution that more data are needed to resolve the nature of the relationship between genetic variation and COVID-19 at this locus, particularly as the physical proximity, LD structure and patterns of association suggest that untagged genetic variation could drive the association signal in the region. Our findings support the notion that some genetic variants, most notably at the *ABO* and *PPP1R15A* loci, in addition to *SLC6A20*, can indeed affect susceptibility to infection rather than progression to severe COVID-19 once infected.

Several of the loci reported here—as noted in previous publications^{12,14}—intersect with well-known genetic variants that have established genetic associations. Examples of these include variants at *DPP9* and *FOXP4*, which show previous evidence of increasing risk for interstitial lung disease⁵, and missense variants within *TYK2* that show a protective effect on several autoimmune-related diseases^{32–35}. Together with the heritability enrichment observed in genes expressed in lung tissues, these results highlight the involvement of lung-related biological pathways in the development of severe COVID-19. Several other loci show no previously documented genome-wide significant

associations, despite the high significance and attractive candidate genes for COVID-19 (for example, *CXCR6*, *LZTFL1*, *IFNAR2* and *OAS1/OAS2/OAS3* loci). The previously reported associations for the strongest association for COVID-19 severity at the 3p21.31 locus and monocytes count are likely to be due to proximity and not a true co-localization.

Increasing the global representation in genetic studies enhances the ability to detect novel associations. Two of the loci that affect disease severity were only discovered by including the four studies of individuals with East Asian ancestry. One of these loci—close to *FOXP4*—is common particularly in East Asian participants (32%) as well as admixed American participants in the Americas (20%) and Middle Eastern participants (7%), but has a low frequency in most European ancestries (2–3%) in our data. Although we cannot be certain of the mechanism of action, the *FOXP4* association is an attractive biological target, as it is expressed in the proximal and distal airway epithelium³⁶ and has been shown to have a role in controlling epithelial cell fate during lung development³⁷. The COVID-19 HGI continues to pursue expansion of the datasets included in the analyses of the consortium to populations from underrepresented populations in upcoming data releases. We plan to release ancestry-specific results in full once the sample sizes allow for a well-powered meta-analysis.

Care should be taken when interpreting the results from a meta-analysis because of challenges with case and control ascertainment and collider bias (see Supplementary Note for a more detailed discussion on study limitations). Drawing a comprehensive and reproducible map of the host genetics factors associated with COVID-19 severity and SARS-CoV-2 requires a sustained international effort to include diverse ancestries and study designs. To accelerate downstream research and therapeutic discovery, the COVID-19 HGI regularly publishes meta-analysis results from periodic data freezes on the website <https://www.covid19hg.org/> and provides an interactive explorer through which researchers can browse the results and the genomic loci in more detail. Future work will be required to better understand the biological and clinical value of these findings. Continued efforts to collect more samples and detailed phenotypic data should be endorsed globally, allowing for more thorough investigation of variable, heritable symptoms, particularly in light of the newly emerging strains of SARS-CoV-2, which may provoke different host responses that lead to disease.

Online content

Any methods, additional references, Nature Research 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/s41586-021-03767-x>.

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Article

COVID-19 Host Genetics Initiative

Leadership

Mari E. K. Niemi^{1,280}, Juha Karjalainen^{1,280}, Rachel G. Liao², Benjamin M. Neale^{4,1280} , Mark Daly^{1,2,3,1280} & Andrea Ganna^{1,2,3,1280}

Writing group

Writing group leaders

Mari E. K. Niemi^{1,280}, Gita A. Pathak⁶, Shea J. Andrews⁷ & Masahiro Kanai²

Writing group members

Kumar Veerapen², Israel Fernandez-Cadenas⁸, Eva C. Schulte^{9,10,11}, Pasquale Striano^{12,13}, Minttu Marttila⁷⁵, Camelia Minica², Eirini Marouli¹⁴, Mohd Anisul Karim^{15,38}, Frank R. Wendt⁴, Jeanne Savage¹⁶, Laura Sloofman⁷, Guillaume Butler-Laporte^{17,53}, Han-Na Kim¹⁸, Stavroula Kanoni¹⁴, Yukinori Okada¹⁹, Jinyoung Byun²⁰, Younghun Han²⁰, Mohammed Jashim Uddin²¹, George Davey Smith²², Cristen J. Willer^{23,24,25} & Joseph D. Buxbaum²⁶

Analysis group

Manuscript analyses team leader

Juha Karjalainen^{1,280}

Manuscript analyses team member: meta-analysis

Juha Mehtonen¹

Manuscript analyses team member: heritability, methods and supplements

Mari E. K. Niemi^{1,280}

Manuscript analyses team member: PHEWAS

Gita A. Pathak⁶

Manuscript analyses team member: Mendelian randomization

Shea J. Andrews⁷

Manuscript analyses team member: PC projection and gene prioritization

Masahiro Kanai²

Manuscript analyses team member: gene prioritization

Hilary Finucane^{5,29}

Manuscript analyses team member: sensitivity analysis

Mattia Cordioli¹

Manuscript analyses team members: PC projection

Alicia R. Martin^{3,29} & Wei Zhou^{3,29}

In silico analysis team members

Mattia Cordioli¹, Bogdan Pasaniuc³², Hanna Julienne³³, Hugues Aschard³³, Huwenbo Shi³⁴, Loic Yengo³⁵, Renato Polimanti⁶, Maya Ghousaini^{15,38}, Jeremy Schwartzentruber^{15,38}, Ian Dunham^{15,40} & Joseph D. Buxbaum²⁶

Project management group

Project management leader

Rachel G. Liao²

Project management support

Karolina Chwialkowska⁴², Margherita Francescatto⁴³, Amy Trankiem² & Mary K. Balaconis²

Phenotype steering group

Lea Davis⁴⁴, Andrea Ganna^{1,2,3}, Sulggi Lee⁴⁵, James Priest⁴⁶, Alessandra Renieri^{47,65}, Vijay G. Sankaran⁴⁹, David van Heel⁵⁰, Patrick Deelen^{51,52}, J. Brent Richards^{17,53,55,56}, Tomoko Nakanishi^{17,56,57}, Les Biesecker⁵⁹, V. Eric Kerchberger⁴⁴ & J. Kenneth Baillie^{60,61,62}

Data dictionary

Alessandra Renieri^{47,65}, Francesca Mari^{63,64,65}, Anna Bernasconi⁶⁶, Stefano Ceri⁶⁷ & Arif Canakoglu⁶⁷

Scientific communication group

Scientific communication leaders

Kumar Veerapen² & Brooke Wolford⁶⁸

Scientific communication members

Amy Trankiem², Annika Faucon⁶⁹, Atanu Kumar Dutta⁷⁰, Claudia Schurmann⁷¹, Emi Harry⁷², Ewan Birney⁷³, Gita A. Pathak⁶, Huy Nguyen², Jamal Nasir⁷⁴, James Priest⁴⁶, Mari Kaunisto¹, Minttu Marttila⁷⁵, Matthew Solomonson², Nicole Dueker⁷⁶, Nirmal Vadgama⁴⁶, Shea J. Andrews⁷, Sophie Limou⁷⁸, Rachel G. Liao² & Andrea Ganna^{1,2,3}

Translators

Souad Rahmouni⁷⁹, Hamdi Mbarek⁸⁰, Dima Darwish⁸⁰, Atanu Kumar Dutta⁷⁰, Md Mesbah Uddin^{82,83}, Israel Fernandez-Cadenas⁸, Raquel Albertos⁸⁴, Jordi Pérez-Tur^{85,86,87}, Ruolin Li⁸⁸, Lasse Folkersen⁸⁹, Ida Moltke⁹⁰, Nils Koelling⁹¹, Eva C. Schulte^{91,11}, Claudia Schurmann⁷¹, Alexander Teumer^{93,94}, Athanasios Kousathanas⁹⁵, Eirini Marouli¹⁴,

Alicia Utrilla⁹⁶, Ricardo A. Verdugo⁹⁷, Ruth Zárate⁹⁸, Carolina Medina-Gómez⁹⁸, David Gómez-Cabrero^{100,101}, Elena Carnero-Montoro¹⁰², Jordi Pérez-Tur^{85,86,87}, Israel Fernandez-Cadenas⁸, Carmen L. Cadilla¹⁰³, Andrés Moreno-Estrada¹⁰⁴, Adriana Garmendia¹⁰⁴, Leire Moya¹⁰⁵, Bahar Sedaghati-Khayat⁸⁸, Minttu Marttila⁷⁵, Palwendé Romuald Boua¹⁰⁶, Guillaume Butler-Laporte^{17,53}, Marie-Julie Favé¹⁰⁷, Laurent Francioli², Audrey Lemaçon¹⁰⁸, Sophie Limou⁷⁹, Isabelle Migeotte¹⁰⁹, Atanu Kumar Dutta⁷⁰, Sanjay Patel⁷⁰, Reka Varnai¹¹², Jozsef L. Szentpeteri¹¹², Csilla Sipeky¹¹³, Francesca Colombo¹¹⁴, Margherita Francescatto⁴³, Kathrin von Hohenstaufen¹¹⁵, Pietro Lio¹¹⁶, Costanza Vallergera⁸⁸, Pasquale Striano^{12,13}, Qingbo Wang², Masahiro Kanai², Yosuke Tanigawa⁴⁶, Tomoko Nakanishi^{17,56,57}, Hogune Im¹¹⁷, Chulho Han¹¹⁷, Han Song¹¹⁷, Jiwoo Lim¹¹⁷, Younhe Lee¹¹⁷, Sugyeong Kim¹¹⁷, Sangyoon Im¹²⁸¹, Biljana Atanasovska¹¹⁹, Hajar Fauzan Ahmad¹²⁰, Kumar Veerapen², Cindy Boer⁸⁸, Philip Jansen¹²², Lude Franke¹²³, Karolina Chwialkowska⁴², Elżbieta Kaja¹²⁴, Dorota Pasko⁹⁵, Ingrid Kennis-Szilagy⁸⁸, Sergey A. Kornilov²⁵, Vid Prijatelj⁸⁸, Ivana Prokić⁸⁸, Ilankumaran Sivanadhan¹²⁶, Sarala Perumal¹²⁷, Sahar Esmaeeli¹²⁸, Nathaniel M. Pearson¹²⁹, Ruth Zárate⁹⁸ & Mohd Anisul Karim^{15,38}

Website Development

Website development leaders

Huy Nguyen² & Matthew Solomonson²

23andMe

Analysis team leader

Adam Auton¹³⁰

Data collection leaders

23andMe COVID-19 Team*, Janie F. Shelton¹³⁰ & Anjali J. Shastri¹³⁰

Analysis team members

Teresa Filshtein-Sonmez¹³⁰, Daniella Coker¹³⁰, Antony Symons¹³⁰, Jorge Esparza-Gordillo¹³¹, Stella Aslibekyan¹³⁰ & Jared O'Connell¹³⁰

Data collection members

Chelsea Ye¹³⁰ & Catherine H. Weldon¹³⁰

23andMe COVID-19 Team

Adam Auton¹³⁰

ACCOuNT

Analysis team leader

Minoli Perera¹³²

Data collection leaders

Kevin O'Leary¹³³, Matthew Tuck¹³⁴, Travis O'Brien¹³⁵, David Meltzer¹³⁶, Peter O'Donnell¹³⁷ & Edith Nutescu¹³⁸

Analysis team members

Guang Yang¹³²

Data collection members

Cristina Alarcon¹³², Stefanie Herrmann¹³², Sophia Mazurek¹³³, Jeff Banagan¹³⁴, Zacharia Hamidi¹³⁴, April Barbour¹⁴⁴, Noora Raffat¹³⁶ & Diana Moreno¹³⁸

Admin team member

Paula Friedman¹³²

Amsterdam UMC COVID Study Group

Analysis team leader

Bart Ferwerda¹⁴⁸

Data collection leaders

Diederik van de Beek¹⁴⁸, Matthijs C. Brouwer¹⁴⁸, Alexander P. J. Vlaar¹⁴⁹ & W. Joost Wiersinga¹⁵⁰

Analysis team members

Danielle Posthuma¹⁶, Elleke Tisink¹⁶, A. H. Koos Zwinderman¹⁵¹ & Emil Uffelmann¹⁶

Data collection members

Michiel van Agtmael¹⁵⁰, Anne Geke Algera¹⁴⁹, Frank van Baarle¹⁴⁹, Diane Bax¹⁵², Martijn Beudel¹⁴⁸, Harm Jan Bogaard¹⁵³, Marije Bomers¹⁵⁰, Peter I. Bonta¹⁵³, Lieuwe Bos¹⁴⁹, Michela Botta¹⁴⁹, Justin de Brabander¹⁵⁰, Godelieve de Bree¹⁵⁰, Sanne de Bruin¹⁴⁹, Marianna Bugiani¹⁵⁴, Esther Bulle¹⁴⁹, Osoul Chouchane¹⁵⁰, Alex Cloherty¹⁵², Dave Dongelmans¹⁴⁹, Paul Elbers¹⁴⁹, Lucas Fleuren¹⁴⁹, Suzanne Geerlings¹⁵⁰, Bart Geerts¹⁵⁵, Theo Geijtenbeek¹⁵², Armand Girbes¹⁴⁹, Bram Goorhuis¹⁵⁰, Martin P. Grobusch¹⁵⁰, Florianne Hafkamp¹⁵², Laura Hagens¹⁴⁹, Jorg Hamann¹⁵⁶, Vanessa Harris¹⁵⁰, Robert Hemke¹⁵⁷, Sabine M. Hermans¹⁵⁰, Leo Heunks¹⁴⁹, Markus Hollmann¹⁵⁵, Janneke Horn¹⁴⁹, Joppe W. Hovius¹⁵⁰, Menno D. de Jong¹⁵⁸, Rutger Koning¹⁴⁸, Niels van Mourik¹⁴⁹, Jeannine Nellen¹⁵⁰, Esther J. Nossent¹⁵³, Frederique Paulus¹⁴⁹, Edgar Peters¹⁵⁰, Tom van der Poll¹⁵⁰, Bennedikt Preckel¹⁵², Jan M. Prins¹⁵⁰, Jorinde Raasveld¹⁴⁹, Tom Reijnders¹⁵⁰, Michiel Schinkel¹⁵⁰, Marcus J. Schultz¹⁴⁹, Alex Schuurman¹⁵⁰, Kim Sigaloff¹⁵⁰, Marry Smit¹⁴⁹, Cornelis S. Stjinis¹⁵⁰, Willelme Stilma¹⁵⁹, Charlotte Teunissen¹⁴⁹, Patrick Thora¹⁴⁹, Anissa Tsonas¹⁵⁰, Marc van der Valk¹⁵⁰, Denise Veelo¹⁵⁵, Heder de Vries¹⁴⁹, Michèle van Vugt¹⁵⁰, Dorien Wouters¹⁵⁹, René P. Minnaar¹⁶⁰, Adrie Kromhout¹⁶⁰, Kees W. J. van Uffelen¹⁶⁰ & Ruud A. Wolterman¹⁶¹

AncestryDNA COVID-19 Research Study

Analysis team leader

Genevieve Roberts¹⁶²

Data collection leader

Danny Park¹⁶²

Admin team leader

Catherine A. Ball¹⁶²

Analysis team members

Marie Coignet¹⁶², Shannon McCurdy¹⁶², Spencer Knight¹⁶², Raghavendran Partha¹⁶² & Brooke Rhead¹⁶²

Data collection members

Miao Zhang¹⁶², Nathan Berkowitz¹⁶², Michael Gaddis¹⁶², Keith Noto¹⁶², Luong Ruiz¹⁶² & Milos Pavlovic¹⁶²

Admin team members

Eurie L. Hong¹⁶², Kristin Rand¹⁶², Ahna Girshick¹⁶², Harendra Guturu¹⁶² & Asher Haug Baltzell¹⁶²

BelCovid

Analysis team leader

Mari E. K. Niemi^{1,2,180}

Data collection leaders

Isabelle Migeotte¹⁰⁹, Souad Rahmouni¹⁶³ & Julien Guntz¹⁶⁴

Admin team leader

Yves Beguin¹⁶⁵

Analysis team members

Mattia Cordioli¹, Sara Pigazzini¹ & Lindokuhle Nkambule^{3,29,167}

Data collection members

Youssef Bouysran¹⁶⁸, Adeline Busson¹⁶⁸, Xavier Peyrassot¹⁶⁸, Françoise Wilkin¹⁶⁸, Bruno Pichon¹⁶⁸, Guillaume Smits¹⁶⁸, Isabelle Vandernoot¹⁶⁸, Jean-Christophe Goffard¹⁶⁹, Michel Georges¹⁶³, Michel Moutschen¹⁷⁰, Benoit Misset¹⁷⁰, Gilles Darcis¹⁷⁰, Julien Guiot¹⁷⁰, Laurent Jadot¹⁶⁴, Samira Azarzar¹⁷⁰, Patricia Dellot¹⁷⁰, Stéphanie Gofflot¹⁶⁵, Sabine Claassen¹⁶⁴, Axelle Bertrand¹⁷⁰, Gilles Parzibut¹⁷⁰, Mathilde Clarinval¹⁷⁰, Catherine Moermans¹⁷⁰, Olivier Malaise¹⁷⁰, Kamilia El Kandoussi¹⁶⁵, Raphaël Thonon¹⁶⁵, Pascale Huynen¹⁷⁰, Alyssia Mesdagh¹⁷⁰, Sofia Melo¹⁶³, Nicolas Jacques¹⁶³, Emmanuel Di Valentin¹⁶³, François Giroule¹⁶³, Alice Collignon¹⁶³, Coraline Radermecker¹⁶³, Marielle Lebrun¹⁶³, Alice Collignon¹⁶³, Hélène Perée¹⁶³, Samuel Latour¹⁶³, Olivia Barada¹⁶³, Judit Sanchez¹⁶³, Claire Josse¹⁷⁰, Bouchra Boujemla¹⁷⁰, Margot Meunier¹⁶³, Emeline Mariavelle¹⁶³, Sandy Anania¹⁶³, Hélène Gazon¹⁶³, Danusia Juszcak¹⁷⁰, Marjorie Fadeur¹⁷⁰, Séverine Camby¹⁷⁰, Christelle Meuris¹⁷⁰, Marie Thys¹⁷⁰, Jessica Jacques¹⁷⁰, Monique Henket¹⁷⁰, Philippe Léonard¹⁷⁰, Frederic Fripiat¹⁷⁰, Jean-Baptiste Giot¹⁷⁰, Anne-Sophie Sauvage¹⁷⁰, Christian Von Frenckel¹⁷⁰, Myriam Mni¹⁶³, Marie Wéry¹⁶³, Alicia Staderoli¹⁷⁰, Yasmine Belhaj¹⁶³ & Bernard Lambermont¹⁷⁰

Biobanque Quebec COVID-19

Analysis team leader

Tomoko Nakanishi^{17,56,57}

Data collection leader

David R. Morrison¹⁷

Admin team leaders

Vincent Mooser^{56,174} & J. Brent Richards^{17,53,55,56}

Analysis team members

Guillaume Butler-Laporte^{17,53}, Vincenzo Forgetta¹⁷ & Rui Li^{56,174}

Data collection members

Biswarup Ghosh¹⁷, Laetitia Laurent¹⁷, Alexandre Belisle^{56,174}, Danielle Henry¹⁷, Tala Abdullah¹⁷, Olumide Adeleye¹⁷, Noor Mamlouk¹⁷, Nofar Kimchi¹⁷, Zaman Afrasiabi¹⁷, Nardin Rezk¹⁷, Branka Vulesevic¹⁷, Meriem Bouab¹⁷, Charlotte Guzman¹⁷, Louis Petitjean¹⁷, Chris Tselios¹⁷, Xiaoping Xue¹⁷, Jonathan Afilalo¹⁷, Marc Afilalo^{17,178}, Maureen Oliveira¹⁷⁹, Bluma Brenner¹⁸⁰, Nathalie Brassard¹⁸¹ & Madeleine Durand^{182,183}

Admin team members

Erwin Schurr¹⁸⁴, Pierre Lepage^{56,174}, Jiannis Ragoussis^{56,174}, Daniel Auld^{4,56,174}, Michaël Chassé^{183,185}, Daniel E. Kaufmann^{83,186}, G. Mark Lathrop^{56,174} & Darin Adra¹⁷

BioVU

Analysis team leaders

Lea K. Davis^{187,188}, Nancy J. Cox^{187,188} & Jennifer E. Below^{187,188}

Analysis team members

Julia M. Sealock^{187,188}, Annika B. Faucon^{187,188}, Megan M. Shuey^{187,188}, Hannah G. Polikowsky^{187,188}, Lauren E. Petty^{187,188}, Douglas M. Shaw^{187,188}, Hung-Hsin Chen^{187,188} & Wanying Zhu^{187,188}

Bonn Study of COVID-19 Genetics

Data collection leader

Kerstin U. Ludwig¹⁸⁹

Analysis team members

Julia Schröder¹⁸⁹ & Carlo Maj¹⁹⁰

Data collection members

Selina Rolke¹⁸⁹, Markus M. Nöthen¹⁸⁹, Julia Fazaal¹⁸⁹, Verena Keitel¹⁹¹, Björn-Erik Ole Jensen¹⁹¹, Torsten Feldt¹⁹¹, Ingo Kurth¹⁹², Nikolaus Marx¹⁹³, Michael Dreher¹⁹⁴, Isabell Pink¹⁹⁵, Markus Cornberg¹⁹⁶, Thomas Illig¹⁹⁷, Clara Lehmann^{198,199,200}, Philipp Schommers^{198,199,200}, Max Augustin¹⁸⁸, Jan Rybniker¹⁹⁶, Lisa Knopp¹⁹¹, Thomas Eggemann¹⁹², Sonja Volland¹⁹⁷, Janine Altmüller²⁰², Marc M. Berger²⁰³, Thorsten Brenner²⁰³, Anke Hinney²⁰⁴, Oliver Witzke²⁰⁵, Robert Bals²⁰⁶, Christian Herr²⁰⁶, Nicole Ludwig²⁰⁷ & Jörn Walter²⁰⁸

CHRIS

Analysis team leader

Christian Fuchsberger²⁰⁹

Data collection leaders

Cristian Pattaro²⁰⁹ & Alessandro De Grandi²⁰⁹

Admin team leader

Peter Pramstaller²⁰⁹

Analysis team members

David Emmert²⁰⁹, Roberto Melotti²⁰⁹ & Luisa Foco²⁰⁹

Admin team members

Deborah Mascalonzi²⁰⁹, Martin Gögele²⁰⁹, Francisco Domingues²⁰⁹ & Andrew Hicks²⁰⁹

Colorado Center for Personalized Medicine (CCPM)

Analysis team leader

Christopher R. Gignoux²¹⁰

Data collection leaders

Stephen J. Wicks²¹⁰ & Kristy Crooks²¹⁰

Admin team leader

Kathleen C. Barnes²¹⁰

Analysis team members

Michelle Daya²¹⁰, Jonathan Shortt²¹⁰, Nicholas Rafaels²¹⁰ & Sameer Chavan²¹⁰

Columbia University COVID-19 Biobank

Analysis team leaders

David B. Goldstein²¹¹ & Krzysztof Kiryluk²¹²

Data collection leaders

Soumitra Sengupta²¹³, Wendy Chung²¹⁴ & Muredach P. Reilly²¹⁵

Analysis team members

Atlas Khan²¹⁵, Chen Wang²¹⁵, Gundula Povysil²¹⁶, Nitin Bhardwaj²¹⁶, Ali G. Gharavi²¹⁵ & Luliana Ionita-Laza²¹⁷

Data collection members

Ning Shang²¹⁵, Sheila M. O'Byrne²¹⁵, Renu Nandakumar²¹⁵, Amritha Menon²¹³, Yat S. So²¹³ & Eldad Hod²¹⁸

Admin team member

Danielle Pendrick²¹⁸

Corea (Genetics of COVID-19-related Manifestation)

Analysis team leader

Han-Na Kim^{219,220}

Data collection leaders

Soo-Kyung Park²²¹, Hyung-Lae Kim²²², Chang Kyung Kang²²³, Hyo-Jung Lee²²⁴ & Kyoung-Ho Song²²⁵

Admin team leaders

Kyung Jae Yoon^{226,227,228} & Nam-Jong Paik^{229,230}

Analysis team members

Woojin Seok²³¹ & Heejun Yoon²³²

Data collection members

Eun-Jeong Joo²³³, Yoosoo Chang^{234,235}, Seunggho Ryu^{234,235}, Wan Beom Park²²³, Jeong Su Park²³⁶, Kyoung Un Park²³⁶, Sin Young Ham²²⁵, Jongtak Jung²²⁵, Eu Suk Kim²²⁵ & Hong Bin Kim²²⁵

Article

COVID-19-Hostage

Analysis team leaders

David Ellinghaus^{237,239}, Frauke Degenhardt²³⁷, Mario Cáceres^{239,240}, Simonas Juzenas²³⁷ & Tobias L. Lenz^{241,242}

Data collection leaders

Agustín Albillos^{243,244}, Antonio Juliá²⁴⁵, Bettina Heidecker²⁴⁶, Eva C. Schulte^{9,10,11}, Federico García^{249,250}, Florian Kurth²⁴⁶, Florian Tran²³⁷, Frank Hanses^{251,252}, Heinz Zoller²⁵³, Jan C. Holter^{254,255}, Javier Fernández^{256,257}, Leif Erik Sande²⁴⁶, Philip Rosenstiel²³⁷, Philipp Koehler^{198,259,260}, Rafael de Cid²⁶¹, Rosanna Asselta^{262,263}, Stefan Schreiber^{237,265}, Ute Hehr²⁶⁶, Daniele Prati²⁸⁵, Guido Baselli²⁸⁵, Luca Valenti^{285,316}, Luis Bujanda^{244,322,329}, Jesus M. Banales^{244,321,322}, Stefano Duga^{262,263}, Mauro D'Amato^{321,322,344}, Manuel Romero-Góm ez^{1241,244}, Maria Buti^{244,292,298} & Pietro Invernizzi^{286,287}

Admin team leaders

Andre Franke^{237,267}, Johannes R. Hov^{254,268,269,270}, Tom H. Karlsen^{254,268,269,270}, Trine Følseraas^{254,268,269,270} & Douglas Maya-Miles^{1244,1245,244}

Analysis team members

Ana Teles^{241,242}, Clinton Azuure²⁴¹, Eike Matthias Wacker²³⁷, Florian Uellendahl-Werth²³⁷, Hesham ELAbd²³⁷, Jatin Arora^{29,272,273,274,275}, Jon Lerga-Jaso²³⁹, Lars Wienbrandt²³⁷, Malte Christoph Rühlemann²³⁷, Mareike Wendorff²³⁷, May Sissel Vadla²⁷⁷, Ole Bernt Lenning²⁷⁶, Onur Özer^{241,242}, Ronny Myhre²⁷⁸, Soumya Raychaudhuri²⁷⁸, Anja Tanck²³⁷, Christoph Gassner^{237,1240}, Georg Hemmrich-Stanisak²³⁷, Jan Kässens²³⁷, Maria E. Figuera Basso²³⁷, Martin Schulzky²³⁷, Michael Wittig²³⁷, Nicole Braun^{237,267}, Tanja Wesse²³⁷, Wolfgang Albrecht²³⁷ & Xiaoli Yi²³⁷

Data collection members

Aaron Blandino Ortiz²⁸⁰, Adolfo Garrido Chercoles²⁸¹, Agustín Ruiz^{282,283}, Alberto Mantovani^{262,263}, Aleksander Rygh Holten^{254,284}, Alena Mayer²⁴⁶, Alessandro Cherubini²⁸⁵, Alessandro Protti^{262,263}, Alessio Aghemo^{262,263}, Alessio Gerussi^{286,287}, Alfredo Ramirez^{288,289,290,291}, Alice Braun²⁴⁶, Ana Barreira²⁹², Ana Lleo^{262,263}, Anders Benjamin Kildal²⁹³, Andrea Ganna^{1,2,3,1280}, Andreas Glück²⁹⁴, Anna Carreras Nolla²⁶¹, Anna Latiano²⁹⁵, Anne Ma Dyrholm-Riise^{254,296}, Antonio Muscatello²⁸⁵, Antonio Voza²⁶², Ariadna Rando-Segura^{297,298}, Aurora Solier^{299,1226}, Banasik Karina²³⁸, Beatriz Cortes²⁶¹, Beatriz Mateos^{243,244}, Beatriz Nafria-Jimenez²⁸¹, Benedikt Schaefer²⁵³, Carla Bellinghausen³⁰⁰, Carlos Ferrando²⁵⁶, Carmen Quereda³⁰¹, Carsten Skurk²⁴⁶, Charlotte Thibault²⁴⁶, Christoph D. Spinner³⁰², Christoph Lange^{303,304,305}, Cinzia Hu²⁸⁵, Claudio Cappadona²⁶³, Cristiana Bianco²⁸⁵, Cristina Sancho³⁰⁶, Dag Arne Lihaug Hoff^{307,308}, Daniela Galimberti²⁸⁵, David Jiménez^{299,1226}, David Pestaña³⁰⁹, David Toapanta^{310,313}, Elena Azzolini^{262,263}, Elio Scarpin²⁸⁵, Elisa T. Helbig²⁴⁶, Eloisa Urrechaga³¹¹, Elvezia Maria Paraboschi^{262,263}, Emanuele Pontali³¹², Enric Reverter^{256,313}, Enrique Navas³⁰¹, Eunata Arana³¹⁴, Félix García Sánchez³¹⁵, Ferruccio Ceriotti²⁸⁵, Francesco Malvestiti³¹⁶, Francisco Mesonero^{243,244}, Gianni Pezzoli³¹⁷, Giuseppe Lamorte²⁸⁵, Holger Neb³¹⁸, Ilaria My²⁶², Isabel Hernández^{282,283}, Itziar de Rojas^{282,283}, Iván Galván-Femenia²⁶¹, Jan Heyckendorf^{303,304,305}, Jan Rybníker^{198,260,319}, Joan Ramon Badia²⁵⁶, Jochen Schneider³⁰², Josune Goikoetxea³²³, Julia Kraft²⁴⁶, Karl Erik Müller³²⁴, Karoline I. Gaede^{325,326,327}, Koldo Garcia-Etxebarria^{244,322,329}, Kristian Tonby^{254,330}, Lars Heggelund^{324,331}, Laura Izquierdo-Sanchez^{244,322}, Lauro Sumoy³³³, Lena J. Lipper²⁴⁶, Leonardo Terranova²⁸⁵, Lindokuhle Nkambule^{3,291,67}, Lucia Garbarino³¹², Luis Téllez^{243,244}, Luisa Roadó²⁹⁸, Mahnoosh Ostadreza²⁸⁵, Maider Intxausti³⁰⁶, Manolis Kogevinas^{335,336,337,338}, Mari E. K. Nieminen¹²⁸⁰, María A. Gutiérrez-Stampa³³⁹, Maria J. G. T. Vehreschild³⁴⁰, Marta Marqué^{282,283}, Massimo Castoldi³⁴¹, Mattia Cordioli¹, Maurizio Ceconi^{262,263}, Mercè Boada^{282,283}, Michael J. Seilmaier³⁴⁵, Michela Mazzocco³¹², Miguel Rodríguez-Gandía^{243,244}, Natale Imaz Ayo³¹⁴, Natalia Blay²⁶¹, Nilda Martínez³⁴⁶, Norwegian SARS-CoV-2 Study Group³, Oliver A. Cornely^{198,259,319,349}, Orazio Palmieri²⁹⁵, Paolo Tentorio²⁶², Pedro M. Rodrigues^{244,322,332}, Pedro P. España³¹¹, Per Hoffmann³⁵¹, Petra Bacher^{352,353,354}, Phillip Suwalski²⁴⁶, Raúl de Pablo²⁸⁰, Rosa Nieto^{299,1226}, Salvatore Badalamenti²⁶², Sandra Ciesek^{355,356}, Sara Bombace²⁶², Sara Pigazzini¹, Sibylle Wilfling^{262,266,357}, Søren Brunak²³⁸, Stefanie Heilmann-Heimbach³⁵¹, The Humanitas COVID-19 Task Force³, The Humanitas Gavazzeni COVID-19 Task Force³, Stephan Ripke²⁴⁶, Thomas Bahmer²⁹⁴, Ulf Landmesser³⁵⁹, Ulrike Protze^{9,360}, Valeria Rimoldi²⁶³, Vegard Skogen^{361,362}, Victor Andrade^{289,291}, Victor Moreno^{336,363,364,365}, Wolfgang Poller²⁴⁶, Xavier Farre²⁶¹, Xiaomin Wang²⁴⁶, Yascha Khodamoradi³⁴⁰, Zehra Karadeniz²⁴⁶, Adolfo de Salazar^{249,50}, Adriana Palom^{245,292}, Alba-Estela Garcia-Fernandez¹²⁴², Albert Blanco-Grau¹²⁴², Alberto Zanella^{285,316}, Alessandra Bandera^{285,316}, Almut Nebel²³⁷, Andrea Biondi¹²⁶⁴, Andrea Caba llero-Garralda¹²⁴², Andrea Gori^{285,316}, Andreas Lind^{254,255}, Anna Ludovica Fracanzani^{285,316}, Anna Peschuck²³⁷, Antonio Pesenti^{285,316}, Carmen de la Horra^{36,1244,1245,336,1246}, Chiara Milani^{286,287}, Cinzia Paccapelo²⁸⁵, Claudio Angelini¹²⁴⁷, Cristina Cea¹²⁴², Eduardo Muñoz-Díaz¹²⁴⁸, Elena Sandova¹²⁴⁹, Enrique J. Calderón^{1243,1244,1245,366,1246}, Erik Solligård^{1265,1266}, Fátima Aziz¹²⁴⁹, Filippo Martinelli-Boneschi^{285,316}, Flora Peyvand^{285,316}, Francesco Blasi^{285,1250}, Francisco J. Medrano^{1251,1243,1244,366,1246}, Francisco Rodríguez-Frias^{245,298,244,1242}, Fredrik Mülle^{254,255}, Giacomo Grasselli^{285,316}, Giorgio Costantino^{285,316}, Giulia Cardamone¹²⁵², Giuseppe Foti¹²⁵³, Giuseppe Matullo¹²⁵⁴, Hayato Kurihara¹²⁴⁷, Jan Egil Afset^{307,1255}, Jan Kristian Damås^{1256,1257}, Javier Ampuero^{1243,1244,1245,369}, Javier Martín¹²⁵⁹, Jeanette Erdmann^{1260,1261,1262}, Jonas Bergan¹²⁶³, Siegfried Goerg²⁶⁴, Jose Ferrusquía-Acosta¹²⁴⁷, Jose Hernández Quero^{249,250}, Juan Delgado^{1243,1244,1245,366,1246}, Juan M. Guerrero^{243,1244,1245}, Kari Risnes^{1257,1258}, Laura Rachele Bettini^{1257,1258}, Leticia Moreira¹²⁴⁹, Lise Tuset Gustad^{1265,1267}, Luigi Santoro²⁸⁵, Luigia Scudeller²⁸⁵, Mar Riveiro-Barciela^{292,298,244}, Marco Schaefer¹²⁶⁸, Maria Carrabba²⁸⁵, Maria G. Valsecchi¹²⁶⁹, María Hernandez-Tejero²⁵⁶, Marialbert Acosta-Herrera¹²⁵⁹, Mariella D'Angio¹²⁶⁴, Marina Baldini²⁸⁵, Marina Cazzaniga¹²⁷⁰, Michele Ciccarelli¹²⁴⁷, Monica Bocciolone¹²⁴⁷, Monica Miozzo^{285,316}, Natalia Chueca²⁴⁹, Nicola Montano^{285,316}, Paola Faverio¹²⁷¹, Paoletta Preatoni¹²⁴⁷, Paolo Bonfanti^{1272,1273}, Paolo Omodei¹²⁴⁷, Pedro Castro²⁶⁶, Ricard Ferrer^{84,1274}, Roberta Gualtierotti^{285,316}, Rocío Gallego-Durán^{144,1245,244}, Rubén Morilla^{1243,1244,1245,366,1246}, Samra Haider³⁰⁸, Sara Marsal²⁴⁵, Serena Anelli¹²⁵⁴, Serena Pelusi^{285,316}, Silvano Bosari^{285,316}, Stefano Aliberti^{285,1250}, Susanne Dudman^{254,255}, Tenghao Zheng³⁴⁴, Tomas Pumarola²⁹⁷, Trinidad Gonzalez Cejudo²⁴⁹, Valter Monzani²⁸⁵, Vicente Friaza^{1243,1244,1245,366,1246}, Wolfgang Peter²⁶⁸ & Ximo Dopazo¹²⁷⁵

Norwegian SARS-CoV-2 Study Group

Tom H. Karlsen^{254,268,269,270}

Humanitas COVID-19 Task Force

Stefano Duga^{262,263,341}

The Humanitas Gavazzeni COVID-19 Task Force

Stefano Duga^{262,263,341}

Admin team members

Sandra May²³⁷ & Marit M. Grimsrud^{254,269,270}

deCODE

Analysis team leader

Daniel F. Gudbjartsson³⁶⁶

Data collection leader

Kari Stefansson³⁶⁶

Analysis team members

Patrick Sulem³⁶⁶, Gardar Sveinbjornsson³⁶⁶, Pall Melsted³⁶⁶, Gudmundur Norddahl³⁶⁶ & Kristjan Helgi Swerford Moore³⁶⁶

Data collection members

Unnur Thorsteinsdóttir³⁶⁶ & Hilma Holm³⁶⁶

Determining the Molecular Pathways & Genetic Predisposition of the Acute Inflammatory Process Caused by SARS-CoV-2

Analysis team leader

Marta E. Alarcón-Riquelme¹⁰²

Data collection leader

David Bernardo^{368,369}

Analysis team member

Manuel Martínez-Bueno¹⁰²

Data collection member

Silvia Rojo Rello³⁷⁰

Estonian Biobank

Analysis team leader

Reedik Mägi³⁷¹

Data collection leader

Lili Milani³⁷¹

Admin team leader

Andres Metspalu³⁷¹

Analysis team members

Triin Laisk³⁷¹, Kristi Läll³⁷¹ & Maarja Lepamets³⁷¹

Data collection members

Tõnu Esko³⁷¹, Ene Reimann³⁷¹, Paul Naaber³⁷², Edward Laane^{373,374}, Jaana Pesukova³⁷⁴, Pärt Peterson³⁷⁵, Kai Kisand³⁷⁵, Jekaterina Tabri³⁷⁷, Raili Allos³⁷⁷, Kati Hensen³⁷⁷, Joel Starkopf³⁷⁸, Inge Ringmets³⁷⁹, Anu Tamm³⁸⁰ & Anne Kallaste³⁸⁰

Admin team members

Helene Alavere³⁷¹, Kristjan Metsalu³⁷¹ & Mairo Puusepp³⁷¹

FinnGen

Data collection members

Kati Kristiansson³⁸², Juha Karjalainen¹, Sami Koskelainen³⁸², Markus Perola^{382,383}, Kati Donner¹, Katja Kivinen¹ & Aarno Palotie¹

Admin team member

Mari Kaunisto¹

FinnGen Admin team leader

Aarno Palotie³⁸¹

Functional Host Genomics in Infectious Diseases (FHOiD)

Analysis team leader

Carlo Rivolta^{384,385}

Data collection leaders

Pierre-Yves Bochud³⁸⁶, Stéphanie Bibert³⁸⁶, Noémie Boillat³⁸⁶, Semira Gonseth Nussle³⁸⁸ & Werner Albrich³⁸⁹

Analysis team members

Mathieu Quinodoz^{384,385} & Dhryata Kamdar^{384,385}

Data collection members

Neémie Suh³⁹⁰, Dionysios Neofytos³⁹¹, Véronique Erard³⁹², Cathy Voide³⁹³, FHoGID*, RegCOVID*, P-PredictUs*, SeroCOVID* & CRIPSI*

FHoGID

P. Y. Bochud^{394,395,398}, C. Rivolta³⁹⁴, S. Bibert³⁹⁴, M. Quinodoz³⁹⁴, D. Kamdar³⁹⁴, D. Neofytos³⁹⁴, V. Erard³⁹⁴, C. Voide³⁹⁴, R. Friolet³⁹⁴, P. Vollenweider^{394,395}, J. L. Pagani^{394,395}, M. Oddo³⁹⁴, F. Meyer zu Bentrup³⁹⁴, A. Conen³⁹⁴, O. Clerc³⁹⁴, O. Marchetti³⁹⁴, A. Guillet³⁹⁴, C. Guyat-Jacques³⁹⁴, S. Foucras³⁹⁴, M. Rime³⁹⁴, J. Chassot³⁹⁴, M. Jaquet³⁹⁴, R. Merlet Viollet³⁹⁴, Y. Lannepoudenx³⁹⁴ & L. Portopena³⁹⁴

RegCOVID

P. Y. Bochud^{394,395,398}, P. Vollenweider^{394,395}, J. L. Pagani^{394,395}, F. Desgranges³⁹⁵, P. Filippidis³⁹⁵, B. Guéry³⁹⁵, D. Haefliger³⁹⁵, E. E. Kampouri³⁹⁵, O. Manuel³⁹⁵, A. Munting³⁹⁵, M. Papadimitriou-Olivgeris³⁹⁵, J. Regina³⁹⁵, L. Rochat-Stettler³⁹⁵, V. Suttels³⁹⁵, E. Tadini³⁹⁵, J. Tschopp³⁹⁵, M. Van Singer³⁹⁵ & B. Viala³⁹⁵

P-PredictUs

N. Boillat-Blanco³⁹⁶, T. Brahier³⁹⁶, O. Hügli³⁹⁶, J. Y. Meuwly³⁹⁶ & O. Pantet³⁹⁶

SérocoVID

S. Gonseth Nussle³⁹⁷, M. Bochud³⁹⁷, V. D'Acremont³⁹⁷ & S. Estoppey Younes³⁹⁷

CRIPSI

W. C. Albrich³⁹⁸, N. Suh³⁹⁸, A. Cerny³⁹⁸, L. O'Mahony³⁹⁸, C. von Mering, P. Y. Bochud^{394,395,398}, M. Frischknecht³⁹⁸, G.-R. Kleger³⁹⁸, M. Filipovic³⁹⁸, C. R. Kahlert³⁹⁸, H. Wozniak³⁹⁸, T. Rochat Negro³⁹⁸, J. Pugin³⁹⁸, K. Bouras³⁹⁸, C. Knapp³⁹⁸, T. Egger³⁹⁸, A. Perret³⁹⁸, P. Montillier³⁹⁸, C. di Bartolomeo³⁹⁸ & B. Barda³⁹⁸

GCAT Genomes For Life

Analysis team leader

Rafael de Cid³⁹⁹

Data collection leaders

Anna Carreras³⁹⁹, Victor Moreno⁴⁰⁰ & Manolis Kogevinas^{335,336,337,338}

Analysis team members

Iván Galván-Femenía³⁹⁹, Natalia Blay³⁹⁹, Xavier Farré³⁹⁹ & Lauro Sumoy³⁹⁹

Data collection members

Beatriz Cortés³⁹⁹, Josep Maria Mercader^{401,1276,1277,1278,1279}, Marta Guindo-Martinez⁴⁰¹, David Torrents⁴⁰¹, Judith Garcia-Aymerich^{335,336,337}, Gemma Castaño-Vinyals^{335,336,337,338} & Carlota Dobaño^{335,336}

GEN-COVID Multicenter Study

Analysis team leaders

Marco Gori^{404,405} & Mari E. K. Niemi¹²⁸⁰

Data collection leaders

Alessandra Renieri^{63,64,65}, Francesca Mari^{63,64,65}, Mario Umberto Mondelli^{408,409}, Francesco Castellì⁴¹⁰, Massimo Vaghi⁴¹¹, Stefano Rusconi^{412,413}, Francesca Montagnani^{65,414}, Elena Bargagli⁴¹⁵, Federico Franchi⁴¹⁶, Maria Antonietta Mazzei⁴¹⁷, Luca Cantarini⁴¹⁸, Danilo Tacconi⁴¹⁹, Marco Feri⁴²⁰, Raffaele Scala⁴²¹, Genni Spargi⁴²², Cesira Nencioni⁴²³, Maria Bandini⁴²⁴, Gian Piero Caldarelli⁴²⁵, Maurizio Spagnesi⁴²⁴, Anna Canaccini⁴²⁶, Agostino Ognibene⁴²⁷, Antonella D'Arminio Monforte⁴²⁸, Massimo Girardis⁴²⁹, Andrea Antinori⁴³⁰, Daniela Francisci^{431,432}, Elisabetta Schiaroli^{431,432}, Pier Giorgio Scotton⁴³³, Sandro Panese⁴³⁴, Renzo Scaggiante⁴³⁵, Matteo Della Monica⁴³⁶, Mario Capasso^{437,438,439}, Giuseppe Fiorentino⁴⁴⁰, Marco Castori⁴⁴¹, Filippo Aucella⁴⁴², Antonio Di Biagio⁴⁴³, Luca Masucci^{444,445}, Serafina Valente⁴⁴⁶, Marco Mandalà⁴⁴⁷, Patrizia Zucchi⁴⁴⁸, Ferdinando Giannattasio⁴⁴⁹, Domenico A. Coviello^{12,450}, Cristina Mussini⁴⁵¹, Giancarlo Bosio⁴⁵², Luisa Tavecchia⁴⁵³, Lia Crotti^{454,455,456,457}, Marco Rizzi⁴⁵⁸, Maria Teresa La Rovere⁴⁵⁹, Simona Sarzi-Braga⁴⁶⁰, Maurizio Bussotti⁴⁶¹, Sabrina Ravaglia⁴⁶², Rosangela Artuso⁴⁶³, Antonio Perrella⁴⁶⁴, Davide Romani⁴⁶⁵, Paola Bergomi⁴⁶⁶, Emanuele Catena⁴⁶⁶, Antonella Vincenti¹²³¹, Claudio Feri¹²³², Davide Grassi¹²³², Gloria Pessina¹²³³, Mario Tumbarello^{65,414}, Massimo Di Pietro¹²³⁴, Ravaglia Sabrina⁴⁶², Sauro Luchi¹²³⁵, Chiara Barbieri¹²³⁵, Donatella Acquilini¹²³⁵, Elena Andreucci¹²³⁵, Francesco Paciosi¹²³⁵, Francesco Vladimiro Segala¹²³⁸, Giusy Tiseo¹²³⁶, Marco Falcone¹²³⁶, Mirjam Lista^{63,65}, Monica Poscente¹²³⁵, Oreste De Vivo⁴⁴⁶, Paola Petrocelli¹²³⁵, Alessandra Guarnaccia^{444,445}, Silvia Baroni¹²³⁹ & Valentina Perticaroli^{63,64,65}

Admin team leaders

Simone Furini⁶⁵ & Simona Dei⁴⁶⁷

Analysis team members

Elisa Benetti⁶⁵, Nicola Picchiotti^{404,468}, Maurizio Sanarico⁴⁶⁹, Stefano Ceri⁶⁶, Pietro Pinoli⁶⁶, Francesco Raimondi⁴⁷⁰, Filippo Biscarini⁴⁷¹, Alessandra Stella⁴⁷¹, Mattia Bergomi⁴⁷³,

Kristina Zguro⁶⁵, Katia Capitanì^{65,475}, Mattia Cordioli¹, Sara Pigazzini¹, Lindokuhle Nkambule^{3,29,167} & Marco Tanfoni⁴⁶⁸

Data collection members

Chiara Fallerini^{63,65}, Sergio Daga^{63,65}, Margherita Baldassarri^{63,65}, Francesca Fava^{63,64,65}, Elisa Frullanti^{63,65}, Floriana Valentino^{63,65}, Gabriella Doddato^{63,65}, Annarita Giliberti^{63,65}, Rossella Tita⁶⁴, Sara Amitrano⁶⁴, Mirella Bruttini^{63,65,64}, Susanna Croci^{63,65}, Ilaria Meloni^{63,65}, Maria Antonietta Mencarelli⁶⁴, Caterina Lo Rizzo⁶⁴, Anna Maria Pinto⁶⁴, Giada Beligni^{63,65}, Andrea Tommasi^{63,64,65}, Laura Di Sarno^{63,65}, Maria Palmieri^{63,65}, Miriam Lucia Carriero^{63,65}, Diana Alaverdian^{63,65}, Nicola Iuso^{63,65}, Gabriele Inchingolo^{63,65}, Stefano Busani⁴²⁹, Raffaele Bruno^{408,409}, Marco Vecchia⁴⁷⁶, Mary Ann Belli⁴⁵³, Stefania Mantovani⁴⁷⁸, Serena Ludovisi^{408,409}, Eugenia Quiros-Roldan⁴¹⁰, Melania Degli Antoni⁴¹⁰, Isabella Zanella^{479,480}, Matteo Siano⁴¹³, Arianna Emiliozzi⁴³⁰, Massimiliano Fabbiani⁴¹⁴, Barbara Rossetti⁴¹⁴, Giacomo Zanelli^{65,414}, Laura Bergantini⁴¹⁵, Miriana D'Alessandro⁴¹⁵, Paolo Cameli⁴¹⁵, David Benet⁴¹⁵, Federico Anedda⁴¹⁶, Simona Marcantonio⁴¹⁶, Sabino Scolletta⁴¹⁶, Susanna Guerrini⁴¹⁷, Edoardo Conticini⁴¹⁸, Bruno Frediani⁴¹⁸, Chiara Spertilli⁴¹⁹, Alice Donati⁴²⁰, Luca Guidelli⁴²¹, Marta Corridi⁴²², Leonardo Croci⁴²³, Paolo Piacentini⁴²⁴, Elena Desanctis⁴²⁴, Silvia Cappelli⁴²⁴, Agnese Verzuri⁴²⁶, Valentina Anemoli⁴²⁶, Alessandro Pancrazi⁴²⁷, Maria Lorubbio⁴²⁷, Esther Merlini⁴²⁸, Federica Gaia Miraglia⁴²⁸, Sophie Venturilli⁴²⁹, Andrea Cossarizza⁴³¹, Alessandra Vergori⁴³⁰, Arianna Gabrieli⁴¹³, Agostino Riva^{412,413}, Francesco Paciosi⁴³², Francesca Andretta⁴³³, Francesca Gatti⁴³⁵, Saverio Giuseppe Parisi⁴⁸², Stefano Barattì⁴⁸², Carmelo Piscopo⁴³⁶, Roberta Russo^{437,438}, Immacolata Andolfo^{437,438}, Achille Iolascon^{437,438}, Massimo Carella⁴⁴¹, Giuseppa Merla^{437,483}, Gabriella Maria Squeo⁴⁸³, Pamela Raggi⁴⁸⁴, Carmen Marciano⁴⁸⁴, Rita Perna⁴⁸⁴, Matteo Bassetti^{443,485}, Maurizio Sanguinetti^{444,445}, Alessia Giorli⁴⁴⁷, Lorenzo Salerni⁴⁴⁷, Pierpaolo Parravicini⁴⁴⁸, Elisabetta Menatti⁴⁶⁶, Tullio Trotta⁴⁴⁹, Gabriella Coiro⁴⁴⁹, Fabio Lena⁴⁸⁷, Enrico Martinelli⁴⁵², Sandro Mancarella⁴⁵³, Chiara Gabbi⁴⁸⁸, Franco Maggiolo⁴⁵⁸, Diego Ripamonti⁴⁵⁸, Tiziana Bachetti⁴⁸⁹, Claudia Suardi⁴⁹⁰, Gianfranco Parati^{454,455}, Giordano Bottà⁴⁹¹, Paolo Di Domenico⁴⁹¹, Ilaria Rancan⁴¹⁴, Francesco Bianchi^{65,484}, Riccardo Colombo⁴⁶⁹, Chiara Barbieri¹²³⁵, Donatella Acquilini¹²³⁵, Elena Andreucci¹²³⁵, Francesco Paciosi¹²³⁵, Francesco Vladimiro Segala¹²³⁸, Giusy Tiseo¹²³⁶, Marco Falcone¹²³⁶, Mirjam Lista^{63,65}, Monica Poscente¹²³⁵, Oreste De Vivo⁴⁴⁶, Paola Petrocelli¹²³⁵, Alessandra Guarnaccia^{444,445}, Silvia Baroni¹²³⁹ & Valentina Perticaroli^{63,64,65}

Genes & Health

Analysis team leader

David A. van Heel⁵⁰

Data collection leader

Karen A. Hunt⁵⁰

Admin team leader

Richard C. Trembath⁴⁹³

Analysis team members

Qin Qin Huang⁴⁹⁴ & Hilary C. Martin⁴⁹⁴

Data collection members

Dan Mason⁴⁹⁵, Bhavi Trivedi⁵⁰⁰ & John Wright⁴⁹⁵

Admin team members

Sarah Finer⁴⁹⁷, Genes & Health Research Team* & Christopher J. Griffiths⁴⁹⁹

Genes & Health Research Team

Shaheen Akhtar⁴⁹⁸, Mohammad Anwar⁴⁹⁸, Elena Arciero⁴⁹⁸, Samina Ashraf⁴⁹⁸, Gerome Breen⁴⁹⁸, Raymond Chung⁴⁹⁸, Charles J. Curtis⁴⁹⁸, Maharun Chowdhury⁴⁹⁸, Grainne Colligan⁴⁹⁸, Panos Deloukas⁴⁹⁸, Ceri Durham⁴⁹⁸, Sarah Finer⁴⁹⁸, Chris Griffiths⁴⁹⁸, Qin Qin Huang⁴⁹⁸, Matt Hurler⁴⁹⁸, Karen A. Hunt⁴⁹⁸, Shapna Hussain⁴⁹⁸, Kamrul Islam⁴⁹⁸, Ahsan Khan⁴⁹⁸, Amara Khan⁴⁹⁸, Cath Lavery⁴⁹⁸, Sang Hyuck Lee⁴⁹⁸, Robin Lerner⁴⁹⁸, Daniel MacArthur⁴⁹⁸, Bev MacLaughlin⁴⁹⁸, Hilary Martin⁴⁹⁸, Dan Mason⁴⁹⁸, Shefa Miah⁴⁹⁸, Bill Newman⁴⁹⁸, Nishat Safa⁴⁹⁸, Farah Tahmasebi⁴⁹⁸, Richard C. Trembath⁴⁹⁸, Bhavi Trivedi⁴⁹⁸, David A. van Heel⁴⁹⁸ & John Wright⁴⁹⁸

Genes for Good

Analysis team leader

Albert V. Smith⁵⁰⁰

Data collection members

Andrew P. Boughton⁵⁰⁰, Kevin W. Li⁵⁰⁰, Jonathon LeFaive⁵⁰⁰ & Aubrey Annis⁵⁰⁰

Genetic determinants of COVID-19 complications in the Brazilian population

Analysis team leader

Mari E. K. Niemi¹²⁸⁰

Data collection leader

Cinthia E. Janes⁵⁰¹

Admin team leaders

Jose E. Krieger⁵⁰¹ & Alexandre C. Pereira⁵⁰¹

Analysis team members

Mariliza Velho⁵⁰¹, Emanuele Marques⁵⁰¹, Mattia Cordioli¹, Sara Pigazzini¹ & Lindokuhle Nkambule^{3,29,167}

Article

Data collection members

Isabella Ramos Lima⁵⁰¹, Mauricio Teruo Tada⁵⁰¹ & Karina Valino⁵⁰¹

Genetic influences on severity of COVID-19 illness in Korea

Analysis team leaders

Mark McCarthy⁵⁰² & Carrie Rosenberger⁵⁰²

Data collection leader

Jong Eun Lee⁵⁰³

Analysis team members

Diana Chang⁵⁰², Christian Hammer⁵⁰², Julie Hunkapiller⁵⁰², Anubha Mahajan⁵⁰², Sarah Pendergrass⁵⁰², Lara Sucheston-Campbell⁵⁰² & Brian Yaspan⁵⁰²

Data collection members

Hyun Soo Lee⁵⁰³, Eunsoon Shin⁵⁰³, Hye Yoon Jang⁵⁰³, Sunmie Kim⁵⁰⁴, Sungmin Kym⁵⁰⁵, Yeon-Sook Kim⁵⁰⁵, Hyeongseok Jeong⁵⁰⁵, Ki Tae Kwon⁵⁰⁷, Shin-Woo Kim⁵⁰⁷, Jin Yong Kim⁵⁰⁸, Young Rock Jang⁵⁰⁸, Hyun ah Kim⁵⁰⁹, Ji Yeon Lee⁵⁰⁹, Jeong Eun Lee⁵¹⁰, Shinwon Lee⁵¹⁰, Kang-Won Choe⁵¹¹, Yu Min Kang⁵¹¹, Sun Ha Jee⁵¹² & Keum Ji Jung⁵¹²

Genomic epidemiology of SARS-CoV-2 host genetics in coronavirus disease 2019

Data collection leaders

Victoria Parikh⁵¹³, Euan Ashley^{514,515}, Matthew Wheeler⁵¹³, Manuel Rivas⁵¹⁶, Carlos Bustamante^{515,516}, Benjamin Pinksy⁵¹⁸, Phillip Febbo⁵¹⁹, Kyle Farh⁵¹⁹, Gary P. Schroth⁵¹⁹ & Francis deSouza⁵¹⁹

Admin team leaders

Karen Dalton⁵¹³ & Jeff Christle⁵¹³

Analysis team members

Christopher Deboever⁵²⁰, Sándor Szalma⁵²⁰, Yosuke Tanigawa⁵¹⁶, Simone Rubinacci⁵²¹ & Olivier Delaneau⁵²¹

Data collection members

John Gorzynski⁵¹³, Hannah de Jong⁵¹³, Shirley Sutton⁵¹³, Nathan Youtlon⁵¹³, Ruchi Josh⁵¹³, David Jimenez-Morales⁵¹³, Christopher Hughes⁵¹³, David Amar⁵¹³, Alex Ioannidis⁵¹⁶, Steve Hershman⁵¹³, Anna Kirillova⁵¹³, Kinya Seo⁵¹³, Yong Huang⁵¹³, Massa Shoura⁵¹⁸, Nathan Hammond⁵¹⁸, Nathaniel Watson⁵¹⁸, Archana Raja⁵¹³, ChunHong Huang⁵¹⁸, Malaya Sahoo⁵¹⁸ & Hannah Wang⁵¹⁸

Admin team member

Jimmy Zhen⁵¹³

Genotek COVID-19 study

Analysis team leader

Alexander Rakitov⁹⁷⁴

Admin team leader

Valery Ilinsky⁹⁷⁴

Analysis team members

Danat Yermakovich⁹⁷⁴, Iaroslav Popov⁹⁷⁴, Alexander Chernitsov⁹⁷⁴, Elena Kovalenko⁹⁷⁴, Anna Krasnenko⁹⁷⁴, Nikolay Plotnikov⁹⁷⁴, Ivan Stetsenko⁹⁷⁴ & Anna Kim⁹⁷⁴

Helix & Healthy Nevada Project Exome+ COVID-19 Phenotypes

Analysis team leader

Elizabeth T. Cirulli⁹⁷⁵

Analysis team members

Kelly M. Schiabor Barrett⁹⁷⁵, Alexandre Bolze⁹⁷⁵, Simon White⁹⁷⁵, Nicole L. Washington⁹⁷⁵ & James T. Lu⁹⁷⁵

Data collection members

Stephen Riffle⁹⁷⁵, Francisco Tanudjaja⁹⁷⁵, Xueqing Wang⁹⁷⁵, Jimmy M. Ramirez III⁹⁷⁵, Nicole Leonetti⁹⁷⁵, Efen Sandoval⁹⁷⁵, Iva Neveux⁹⁷⁶, Shaun Dabe⁹⁷⁷ & Joseph J. Grzymalski⁹⁷⁶

24Genetics & IdiPaz Genomic Variants associated to COVID-19 infection outcome

Analysis team leader

Juan Ignacio Esteban Miñano⁹⁷⁸

Data collection leader

Luis A. Aguirre⁹⁷⁹

Admin team leader

Eduardo López-Collazo⁹⁷⁹

Analysis team members

Manuel de la Mata Pazos⁹⁷⁸, Luciano Cerrato⁹⁷⁸ & Lasse Folkersen⁹⁷⁸

Data collection members

Roberto Lozano-Rodríguez⁹⁷⁹, José Avendaño-Ortiz⁹⁷⁹, Verónica Terrón Arcos⁹⁷⁹, Karla Marina Montalbán-Hernández⁹⁷⁹, Jaime Valentín Quiroga⁹⁷⁹ & Alejandro Pascual-Iglesias⁹⁷⁹

Admin team members

Charbel Maroun-Eid⁹⁷⁹ & Alejandro Martín-Quirós⁹⁷⁹

Japan Coronavirus Taskforce

Analysis team leaders

Ho Namkoong⁹⁸⁰, Yukinori Okada^{981,982,983} & Seiya Imoto⁹⁸⁴

Data collection leaders

Kazuhiko Katayama⁹⁸⁵, Koichi Fukunaga⁹⁸⁰, Yuku Kitagawa⁹⁸⁶, Toshiro Sato⁹⁸⁷, Naoki Hasegawa⁹⁸⁸, Atsushi Kumanogoh^{983,989,990}, Akinori Kimura⁹⁹¹, Masumi Ai⁹⁹² & Katsushi Tokunaga⁹⁹³

Admin team leaders

Takanori Kanai⁹⁹⁴, Satoru Miyano⁹⁹⁵ & Seishi Ogawa^{996,997}

Analysis team members

Ryuya Edahiro^{981,989}, Kyuto Sonehara⁹⁸¹, Yuya Shirai^{981,989} & Masahiro Kanai⁹⁷⁴

Data collection members

Makoto Ishii⁹⁸⁰, Hiroki Kabata⁹⁸⁰, Katsunori Masaki⁹⁸⁰, Hirofumi Kamata⁹⁸⁰, Shinnosuke Ikemura⁹⁸⁰, Shotaro Chubachi⁹⁸⁰, Satoshi Okamori⁹⁸⁰, Hideki Terai⁹⁸⁰, Hiromu Tanaka⁹⁸⁰, Atsuhō Morita⁹⁸⁰, Ho Lee⁹⁸⁰, Takanori Asakura⁹⁸⁰, Junichi Sasaki⁹⁸⁹, Hiroshi Morisaki¹⁰⁰⁰, Yoshifumi Uwamino¹⁰⁰¹, Kosaku Nanki⁹⁹⁴, Yohei Mikami⁹⁹⁴, Kazunori Tomono¹⁰⁰², Kazuto Kato¹⁰⁰³, Fumihiko Matsuda¹⁰⁰⁴, Meiko Takahashi¹⁰⁰⁴, Nobuyuki Hizawa¹⁰⁰⁵, Yoshito Takeda⁹⁸⁹, Haruhiko Hirata⁹⁸⁹, Takayuki Shiroyama⁹⁸⁹, Satoru Miyawaki¹⁰⁰⁶, Ken Suzuki⁹⁸¹, Yuichi Maeda^{988,1007}, Takuro Nii^{989,1007}, Yoshimi Noda⁹⁸⁹, Takayuki Niitsu⁹⁸⁹, Yuichi Adachi⁹⁸⁹, Takatoshi Enomoto⁹⁸⁹, Saori Amiya⁹⁸⁹, Reina Hara⁹⁸⁹, Kunihiko Takahashi⁹⁹⁵, Tatsuhiko Anzai⁹⁹⁵, Takanori Hasegawa⁹⁹⁵, Satoshi Ito⁹⁹⁵, Ryuji Koike¹⁰⁰⁹, Akifumi Endo¹⁰¹⁰, Yuji Uchimura¹⁰¹¹, Yasunari Miyazaki¹⁰¹², Takayuki Honda¹⁰¹², Tomoya Tateishi¹⁰¹², Shuji Tohda¹⁰¹³, Naoya Ichimura¹⁰¹³, Kazunari Sonobe¹⁰¹³, Chihiro Sassa¹⁰¹³, Jun Nakajima¹⁰¹³, Yasuhito Nannya¹⁰¹⁴, Yosuke Omae⁹⁹³, Kazuhisa Takahashi¹⁰¹⁵, Norihiro Harada¹⁰¹⁵, Makoto Hiki^{1016,1017}, Haruhi Takagi¹⁰¹⁵, Ai Nakamura¹⁰¹⁵, Etsuko Tagaya¹⁰¹⁸, Masatoshi Kawana¹⁰¹⁹, Ken Arimura¹⁰¹⁸, Takashi Ishiguro¹⁰²⁰, Noboru Takayanagi¹⁰²⁰, Taisuke Isono¹⁰²⁰, Yotaro Takaku¹⁰²⁰, Kenji Takano¹⁰²⁰, Ryusuke Anan¹⁰²¹, Yukiko Nakajima¹⁰²¹, Yasushi Nakano¹⁰²¹, Kazumi Nishio¹⁰²¹, Soichiro Ueda¹⁰²², Reina Hayashi¹⁰²², Hiroki Tateno¹⁰²³, Isano Hase¹⁰²³, Shuichi Yoshida¹⁰²³, Shoji Suzuki¹⁰²³, Keiko Mitamura¹⁰²⁴, Fumitake Saito¹⁰²⁵, Tetsuya Ueda¹⁰²⁶, Masanori Azuma¹⁰²⁶, Tadao Nagasaki¹⁰²⁶, Yoshinori Yasu¹⁰²⁸, Yoshinori Hasegawa¹⁰²⁶, Yoshikazu Mutoh¹⁰²⁹, Takashi Yoshiyama¹⁰³⁰, Tomohisa Shoko¹⁰³¹, Mitsuaki Kojima¹⁰³¹, Tomohiro Adachi¹⁰³¹, Motono Ishikawa¹⁰³², Kenichiro Takahashi¹⁰³³, Kazuyoshi Watanabe¹⁰³⁴, Tadashi Manabe¹⁰³⁵, Fumimaro Ito¹⁰³⁵, Takahiro Fukui¹⁰³⁵, Yohei Funatsu¹⁰³⁵, Hidefumi Koh¹⁰³⁵, Yoshihiro Hirai¹⁰³⁶, Hidetoshi Kawashima¹⁰³⁶, Atsuya Narita¹⁰³⁶, Kazuki Niwa¹⁰³⁷, Yoshiyuki Sekikawa¹⁰³⁷, Fukuki Saito¹⁰³⁸, Kazuhisa Yoshiya¹⁰³⁸, Tomoyuki Yoshihara¹⁰³⁸, Yusuke Suzuki¹⁰³⁹, Sohei Nakayama¹⁰³⁹, Keita Masuzawa¹⁰³⁹, Koichi Nishi¹⁰⁴⁰, Masaru Nishitsuji¹⁰⁴⁰, Maiko Tani¹⁰⁴⁰, Takashi Inoue¹⁰⁴¹, Toshiyuki Hirano¹⁰⁴¹, Keigo Kobayashi¹⁰⁴¹, Naoki Miyazawa¹⁰⁴², Yasuhiro Kimura¹⁰⁴², Reiko Sado¹⁰⁴², Takashi Ogura¹⁰⁴³, Hideya Kitamura¹⁰⁴³, Kota Murohashi¹⁰⁴³, Ichiro Nakachi¹⁰⁴⁴, Rie Baba¹⁰⁴⁴, Daisuke Arai¹⁰⁴⁴, Satoshi Fuke¹⁰⁴⁵, Hiroshi Saito¹⁰⁴⁵, Naota Kuwahara¹⁰⁴⁶, Akiko Fujiwara¹⁰⁴⁶, Takeroni Okada¹⁰⁴⁶, Tomoya Baba¹⁰⁴⁷, Junya Noda¹⁰⁴⁷, Shuko Mashimo¹⁰⁴⁷, Kazuma Yagi¹⁰⁴⁸, Tetsuya Shiomi¹⁰⁴⁸, Mizuha Hashiguchi¹⁰⁴⁸, Toshio Odani¹⁰⁴⁹, Takao Mochimar^{1050,1051}, Yoshitaka Oyamada^{1050,1051}, Nobuaki Mori¹⁰⁵², Namiki Izumi¹⁰⁵³, Kaoru Nagata¹⁰⁵³, Reiko Taki¹⁰⁵³, Koji Murakami¹⁰⁵⁴, Mitsuhiro Yamada¹⁰⁵⁴, Hisatoshi Sugiura¹⁰⁵⁴, Kentaro Hayashi¹⁰⁵⁵, Tetsuo Shimizu¹⁰⁵⁵, Yasuhiro Gon¹⁰⁵⁵, Shigeki Fujitani¹⁰⁵⁶, Tomoya Tsuchida¹⁰⁵⁷, Toru Yoshida¹⁰⁵⁶, Takashi Kagaya¹⁰⁵⁸, Toshiyuki Kita¹⁰⁵⁸, Satoru Sakagami¹⁰⁵⁸, Yoshifumi Kimizuka¹⁰⁵⁹, Akihiko Kawana¹⁰⁵⁹, Yoshihiko Nakamura¹⁰⁶⁰, Hiroyasu Ishikura¹⁰⁶⁰, Tohru Takata¹⁰⁶¹, Takahide Kikuchi¹⁰⁶², Daisuke Taniyama¹⁰⁶², Morio Nakamura¹⁰⁶², Nobuhiro Kodama¹⁰⁶³, Yasunari Kaneyama¹⁰⁶³, Shunsuke Maeda¹⁰⁶³, Yoji Nagasaki¹⁰⁶⁴, Masaki Okamoto^{1065,1027}, Sayoko Ishihara¹⁰⁶⁴, Akihiro Ito¹⁰⁶⁷, Yusuke Chihara¹⁰⁶⁸, Mayumi Takeuchi¹⁰⁶⁸, Keisuke Ono¹⁰⁶⁸, Naozumi Hashimoto¹⁰⁶⁹, Keiko Wakahara¹⁰⁶⁹, Akira Ando¹⁰⁶⁹, Makoto Masuda¹⁰⁷⁰, Aya Wakabayashi¹⁰⁷⁰, Hiroki Watanabe¹⁰⁷⁰, Hisako Sageshima¹⁰⁷¹, Taka-Aki Nakada¹⁰⁷², Ryuzo Abe¹⁰⁷², Tadanaga Shimada¹⁰⁷², Kodai Kawamura¹⁰⁷³, Kazuya Ichikado¹⁰⁷³, Kenta Nishiyama¹⁰⁷³, Masaki Yamasaki¹⁰⁷⁴, Satoru Hashimoto¹⁰⁷⁴, Yu Kusaka¹⁰⁷⁵, Takehiko Ohba¹⁰⁷⁵, Susumu Isogai¹⁰⁷⁵, Minoru Takada¹⁰⁷⁶, Hidenori Kanda¹⁰⁷⁶, Yoko Komase¹⁰⁷⁷, Fumiaki Sano¹⁰⁷⁸, Koichiro Asano¹⁰⁷⁹, Tsuyoshi Oguma¹⁰⁸⁰, Masahiro Harada¹⁰⁸¹, Takeshi Takahashi¹⁰⁸¹, Takayuki Shibusawa¹⁰⁸¹, Shinji Abe¹⁰⁸², Yuta Kono¹⁰⁸², Yuki Togashi¹⁰⁸², Takehiro Izumo¹⁰⁸³, Minoru Inomata¹⁰⁸³, Nobuyasu Awano¹⁰⁸³, Shinichi Ogawa¹⁰⁸⁴, Tomouki Ogata¹⁰⁸⁴, Shoichiro Ishihara¹⁰⁸⁴, Arihiko Kanehiro¹⁰⁸⁵, Shinji Ozaki¹⁰⁸⁵, Yasuko Fuchimoto¹⁰⁸⁵, Yuichiro Kitagawa¹⁰⁸⁶, Shozo Yoshida¹⁰⁸⁶, Shinji Ogura¹⁰⁸⁶, Kei Nishiyama¹⁰⁸⁷, Kousuke Yoshida¹⁰⁸⁸, Satoru Beppu¹⁰⁸⁸, Satoru Fukuyama¹⁰⁸⁹, Yoshihiro Eriguchi¹⁰⁹⁰, Akiko Yonekawa¹⁰⁹⁰, Yoshiaki Inoue¹⁰⁹¹, Kunihiro Yamagata¹⁰⁹², Shigeru Chiba¹⁰⁹³, Osamu Narumoto¹⁰⁹⁴, Hideaki Nagai¹⁰⁹⁴, Nobuharu Ooshima¹⁰⁹⁴, Mitsuru Motegi¹⁰⁹⁵, Hironori Sagara¹⁰⁹⁶, Akihiko Tanaka¹⁰⁹⁶, Shin Ohta¹⁰⁹⁶, Yoko Shibata¹⁰⁹⁷, Yoshinori Tanino¹⁰⁹⁷, Yuki Sato¹⁰⁹⁷, Yuichiro Yamada¹⁰⁹⁸, Takuya Hashino¹⁰⁹⁸, Masato Shinoki¹⁰⁹⁸, Hajime Iwagoe¹⁰⁹⁹, Tomonori Imamura¹¹⁰⁰, Akira Umeda¹¹⁰¹, Hisato Shimada¹¹⁰¹, Mayu Endo¹¹⁰², Shinichi Hayashi¹¹⁰³, Mai Takahashi¹¹⁰³, Shigefumi Nakano¹¹⁰³, Masakiyo Yatomai¹¹⁰⁴, Toshitaka Maeno¹¹⁰⁴, Tomoo Ishii¹¹⁰⁵, Mitsuyoshi Utsugi¹¹⁰⁶, Akihiro Ono¹¹⁰⁶, Kensuke Kanaoka¹¹⁰⁷, Shoichi Ihara¹¹⁰⁷ & Kiyoshi Komuta¹¹⁰⁷

Lifelines

Analysis team leader

Lude Franke⁵¹

Data collection leader

Marika Boezen¹¹⁰⁹

Analysis team members

Patrick Deelen^{51,52}, Annique Claringbould⁵¹, Esteban Lopera⁵¹, Robert Warmerdam⁵¹, Judith. M. Vonk¹¹⁰⁹ & Irene van Blokland⁵¹

Data collection members

Pauline Lanting⁵¹ & Anil P. S. Ori^{1112,1113}

Lung eQTL Consortium**Data collection members**

Ma'en Obeidat¹¹¹⁴, Ana I. Hernández Cordero¹¹¹⁴, Don D. Sin^{1114,1115}, Yohan Bossé¹¹¹⁶, Philippe Joubert¹¹¹⁶, Ke Hao¹¹¹⁷, David Nickle^{1118,1119}, Wim Timens^{1120,1121} & Maarten van den Berge^{1121,1122}

Mass General Brigham-Host Vulnerability to COVID-19**Analysis team leaders**

Yen-Chen Anne Feng¹¹²³ & Josep Mercader^{29,1123}

Data collection leaders

Scott T. Weiss¹¹²⁶, Elizabeth W. Karlson¹¹²⁷, Jordan W. Smoller¹¹²⁸, Shawn N. Murphy¹¹²⁹, James B. Meigs^{1130,1124,1125} & Ann E. Woolley¹¹²⁷

Admin team leader

Robert C. Green^{2,273}

Data collection member

Emma F. Perez²⁷³

Michigan Genomics Initiative (MGI)**Analysis team leader**

Brooke Wolford¹¹³²

Admin team leader

Sebastian Zöllner⁵⁰⁰

Analysis team members

Jiongming Wang⁵⁰⁰ & Andrew Beck⁵⁰⁰

Mount Sinai Health System COVID-19 Genomics Initiative**Analysis team leader**

Laura G. Sloofman²⁶

Data collection leaders

Steven Ascolillo¹¹³³, Robert P. Sebra^{1117,1135}, Brett L. Collins²⁶ & Tess Levy²⁶

Admin team leaders

Joseph D. Buxbaum²⁶ & Stuart C. Sealfon⁷

Analysis team members

Shea J. Andrews⁷, Daniel M. Jordan^{1117,1137}, Ryan C. Thompson^{1133,1140,1141}, Kyle Gettler¹¹¹⁷, Kumardeep Chaudhary^{1117,1143}, Gillian M. Belbin¹¹⁴⁴, Michael Preuss^{1143,1146}, Clive Hoggart^{1147,1148,1142}, Sam Choi^{1147,1148,1142,1149} & Slayton J. Underwood²⁶

Data collection members

Irene Salib¹¹¹⁷, Bari Britvan²⁶, Katherine Keller²⁶, Lara Tang²⁶, Michael Peruggia²⁶, Liam L. Hieste²⁶, Kristi Niblo²⁶, Alexandra Aksentijevich²⁶, Alexander Labkowsky²⁶, Avromie Karp²⁶, Menachem Zlatopolsky²⁶ & Marissa Zyndorf¹¹¹⁷

Admin team members

Alexander W. Charney^{1141,1150}, Noam D. Beckmann¹¹³³, Eric E. Schadt^{1117,1135}, Noura S. Abul-Husn¹¹⁴⁴, Judy H. Cho^{1117,1143}, Yuval Itan^{1117,1143}, Eimear E. Kenny¹¹⁴⁴, Ruth J. F. Loos^{1143,1146,1151}, Girish N. Nadkarni^{1133,1143,1153,1154,1155}, Ron Do^{1117,1143}, Paul O'Reilly^{1147,1148,1142,1149} & Laura M. Huckins^{1147,1148,1142}

MyCode Health Initiative**Analysis team leaders**

Manuel A. R. Ferreira¹¹⁵⁷ & Goncalo R. Abecasis¹¹⁵⁷

Data collection leaders

Joseph B. Leader¹¹⁵⁸ & Michael N. Cantor¹¹⁵⁷

Admin team leaders

Anne E. Justice¹¹⁵⁹ & Dave J. Carey¹¹⁶⁰

Analysis team members

Geetha Chittoor¹¹⁵⁹, Navya Shilpa Josyula¹¹⁵⁹, Jack A. Kosmicki¹¹⁵⁷, Julie E. Horowitz¹¹⁵⁷ & Aris Baras¹¹⁵⁷

Data collection members

Matthew C. Gass¹¹⁵⁸ & Ashish Yadav¹¹⁵⁷

Admin team member

Tooraj Mirshahi¹¹⁶⁰

Netherlands Twin Register**Analysis team leader**

Jouke Jan Hottenga¹²²

Data collection leader

Meike Bartels¹²²

Admin team leader

Eco J. C. de Geus¹²²

Analysis team member

Michel G. Nivard¹²²

Penn Medicine Biobank**Analysis team leaders**

Anurag Verma¹¹⁶² & Marylyn D. Ritchie¹¹⁶²

Admin team leader

Daniel Rader¹¹⁶²

Analysis team members

Binglan Li¹¹⁶³, Shefali S. Verma¹¹⁶², Anastasia Lucas¹¹⁶² & Yuki Bradford¹¹⁶²

Population controls**Analysis team leader**

Federico Zara¹²

Analysis team members

Vincenzo Salpietro¹², Marcello Scala¹¹⁷², Michele Iacomino¹², Paolo Scudieri¹² & Renata Boccardi¹²

Data collection members

Carlo Minetti¹², Antonella Riva¹¹⁷², Maria Stella Vari¹², Myriam Mni¹⁶³, Jean-François Rahier¹¹⁷³, Elisa Giorgio¹¹⁷⁴, Federico Zara¹² & Diana Carlì¹¹⁷⁵

Data collection leaders

Pasquale Striano^{12,13}, Edouard Louis¹⁷⁰, Michel Georges¹⁶³, Souad Rahmouni¹⁶³, Cynthia M. Bulik^{709,1166,1167}, Mikael Landén^{709,1168}, Alfredo Brusco¹¹⁶⁹ & Giovanni Battista Ferrero¹¹⁷⁰

Admin team leaders

Francesca Madia¹² & Bengt Fundin⁷⁰⁹

Qatar Genome Program**Analysis team leader**

Hamdi Mbarek⁸⁰

Data collection leader

Said I. Ismail⁸⁰

Analysis team members

Chadi Saad⁸⁰ & Yaser Al-Sarraj⁸⁰

Data collection members

Radja Messai Badji⁸⁰, Wadha Al-Muftah⁸⁰, Asma Al Thani⁸⁰ & Nahla Afifi¹¹⁷⁶

Study of the COVID-19 host genetics in the population of Latvia**Analysis team leader**

Janis Klovins¹¹⁷⁷

Data collection leader

Vita Rovite¹¹⁷⁷

Analysis team members

Raimonds Rescenko¹¹⁷⁷ & Raitis Peculis¹¹⁷⁷

Data collection member

Monta Ustinova¹¹⁷⁷

The genetic predisposition to severe COVID-19**Analysis team leader**

Mari E. K. Niemi¹¹²⁸⁰

Data collection leader

Hugo Zeberg^{1178,1179}

Article

Analysis team members

Mattia Cordioli¹, Sara Pigazzini¹ & Lindokuhle Nkambule^{3,29,167}

Data collection members

Robert Frithiof¹¹⁸⁰, Michael Hultström^{1180,1181} & Miklos Lipcsey^{1180,1182}

UCLA Precision Health COVID-19 Host Genomics Biobank

Analysis team leader

Ruth Johnson¹¹⁸³

Data collection leader

UCLA Health ATLAS & Data Mart Working Group*

UCLA Health ATLAS & Data Mart Working Group

Daniel H. Geschwind¹¹⁸⁴

Admin team leaders

Nelson Freimer¹¹⁸⁵, Manish J. Butte^{1186,1171,1184}, Daniel H. Geschwind^{1188,1187,1152} & Bogdan Pasaniuc^{1189,1190,1139}

Analysis team members

Yi Ding¹¹⁹¹, Alec Chiu¹¹⁹¹, Timothy S. Chang¹¹⁹² & Paul Boutros^{1193,1139}

UK 100,000 Genomes Project (Genomics England)

Analysis team leader

Loukas Moutsianas^{14,95}

Data collection leaders

Mark J. Caulfield^{95,695} & Richard H. Scott^{95,1195,1196}

Analysis team members

Athanasios Kousathanas⁹⁵, Dorota Pasko⁹⁵, Susan Walker⁹⁵, Alex Stuckey⁹⁵, Christopher A. Odhams⁹⁵ & Daniel Rhodes⁹⁵

Data collection members

Tom Fowler⁹⁵, Augusto Rendon^{95,1197}, Georgia Chan⁹⁵ & Prabhu Arumugam⁹⁵

UK Biobank

Analysis team leaders

Tomoko Nakanishi^{17,56,57}, Konrad J. Karczewski^{3,29}, Alicia R. Martin^{3,29}, Daniel J. Wilson¹¹⁹⁹ & Chris A. Spencer⁹¹

Data collection leaders

Derrick W. Crook¹²⁰¹, David H. Wyllie^{1201,1202} & Anne Marie O'Connell¹²⁰³

Admin team leader

J. Brent Richards^{17,53,55,56}

Analysis team members

Guillaume Butler-Laporte^{17,53}, Vincenzo Forgetta¹⁷, Elizabeth G. Atkinson^{3,29}, Masahiro Kana^{3,29,1204}, Kristin Tsuo^{3,29,1205}, Nikolas Baya^{3,29}, Patrick Turley^{3,29}, Rahul Gupta^{3,29}, Raymond K. Walters^{3,29}, Duncan S. Palmer^{3,29}, Gopal Sarma^{3,29}, Matthew Solomonson^{3,29}, Nathan Cheng^{3,29}, Wenhan Lu^{3,29}, Claire Churchhouse^{3,29}, Jacqueline I. Goldstein^{3,29}, Daniel King^{3,29}, Wei Zhou^{3,29}, Cotton Seed^{3,29}, Mark J. Daly^{1,2,3}, Benjamin M. Neale^{3,29}, Hilary Finucane^{3,29}, Sam Bryant², F. Kyle Satterstrom^{3,29}, Gavin Band⁷⁰⁰, Sarah G. Earle¹¹⁹⁹, Shang-Kuan Lin¹¹⁹⁹, Nicolas Arning¹¹⁹⁹ & Nils Koelling⁹¹

Data collection members

Jacob Armstrong¹¹⁹⁹ & Justine K. Rudkin¹¹⁹⁹

Admin team members

Shawneequa Callier²⁰⁷, Sam Bryant^{3,29} & Caroline Cusick²⁹

UK Blood Donors Cohort

Analysis team leaders

Nicole Soranzo^{1208,1209,1210} & Jing Hua Zhao¹²¹¹

Data collection leaders

John Danesh^{1211,1212,1213,1214,1215} & Emanuele Di Angelantonio^{1211,1212,1213,1214}

Analysis team member

Adam S. Butterworth^{1211,1212,1213,1214}

VA Million Veteran Program (MVP)

Analysis team leaders

Yan V. Sun^{1216,1217} & Jennifer E. Huffman¹²¹⁸

Data collection leader

Kelly Cho¹²¹⁹

Admin team leaders

Christopher J. O'Donnell¹²¹⁸, Phil Tsao^{1220,1221} & J. Michael Gaziano¹²¹⁹

Analysis team member

Gina Peloso^{1218,1222}

Data collection member

Yuk-Lam Ho¹²¹⁹

Val Gardena

Analysis team leader

Christian Fuchsberger²⁰⁹

Data collection leader

Michael Mian¹²²³

Data collection member

Federica Scaggianti¹²²⁴

Admin team members

Cristian Pattaro²⁰⁹ & Peter Pramstaller²⁰⁹

CHOP_CAG

Xiao Chang¹²²⁷, Joseph R. Glessner^{1227,1228} & Hakon Hakonarson^{1227,1228,1229}

GenOMICC/ISARIC4C

Data collection leaders

J. Kenneth Baillie^{60,61,62}, Peter J. McGuigan⁵²³, Luke Stephen Prockter Moore⁵²⁴, Marcela Paola Vizcaychipi⁵²⁴, Kathryn Hall⁵²⁵, Andy Campbell⁵²⁶, Ailstair Nichol⁵²⁷, Geraldine Ward⁵²⁸, Valerie Joan Page⁵²⁹, Malcolm G. Semple⁵³⁰, Kayode Adeniji⁵³¹, Daniel Agranoff⁵³², Ken Agwuh⁵³³, Dhiraj Ail⁵³⁴, Erin L. Aldera⁵³⁵, Ana Alegria^{536,506}, Brian Angus⁵³⁷, Abdul Ashish⁵³⁸, Dougal Atkinson⁵³⁹, Shahedal Bari⁵⁴⁰, Gavin Barlow⁵⁴¹, Stella Barnass⁵⁴², Nicholas Barrett⁵⁴³, Christopher Bassford⁵⁴⁴, Sneha Basude⁵⁴⁵, David Baxter⁵⁴⁶, Michael Beadsworth⁵⁴⁷, Jolanta Bernatoniene⁵⁴⁸, John Berridge⁵⁴⁹, Nicola Best⁵⁵⁰, Pieter Bothma⁵⁵¹, David Chadwick⁵⁵², Robin Brittain-Long⁵⁵³, Naomi Bulteel⁵⁵⁴, Tom Burden⁵⁵⁵, Andrew Burtenshaw⁵⁵⁶, Vikki Caruth⁵⁵⁷, David Chadwick⁵⁵², Duncan Chamber⁵⁵⁸, Nigel Chee⁵⁵⁹, Jenny Child⁵⁶⁰, Srikanth Chukkambotta⁵⁶¹, Tom Clark⁵⁶², Paul Collin⁵⁶³, Catherine Cosgrove⁵⁶⁴, Jason Cupitt⁵⁶⁵, Maria-Teresa Cutino-Mogueil⁵⁶⁶, Paul Dark⁵⁶⁷, Chris Dawson⁵⁶⁸, Samir Dervisevic⁵⁶⁹, Phil Donnison⁶³⁷, Sam Douthwaite⁵⁴³, Andrew Drummond^{572,773}, Ingrid DuRand⁵⁷³, Ahilanadan Dushianthan⁵⁷⁴, Tristan Dyer⁵⁷⁵, Cariad Evans⁵⁶³, Chi Eziefule⁵³², Christopher Fegan⁵⁷⁶, Adam Finn⁵⁷⁷, Duncan Fullerton⁵⁷⁸, Sanjeev Garg⁵⁷⁹, Atul Garg⁵⁸⁰, Effrossyni Gkrania-Klotsas⁵⁸¹, Jo Godden⁵⁸², Arthur Goldsmith⁵⁸³, Clive Graham⁵⁸⁴, Elaine Hardy⁵⁸⁵, Stuart Hartshorn⁵⁸⁶, Daniel Harvey⁵⁸⁷, Peter Havalda⁵⁸⁸, Daniel B. Hawcutt⁵⁸⁹, Maria Hobrok⁵⁹⁰, Luke Hodgson⁵⁹¹, Anil Hormis⁵⁹², Michael Jacobs⁵⁹³, Susan Jain⁵⁹⁴, Paul Jennings⁵⁹⁵, Agilan Kaliappan⁵⁹⁶, Vidya Kasipandian⁵⁹⁷, Stephen Kegg⁵⁹⁸, Michael Kelsey⁵⁹⁹, Jason Kendall¹²⁸¹, Caroline Kerrison⁶⁰⁰, Ian Kerstake⁶⁰¹, Oliver Koch⁶⁰², Gouri Koduri⁶⁰³, George Koshy⁶⁰⁴, Shondipon Laha⁶⁰⁵, Steven Laird⁶⁰⁶, Susan Larkin⁶⁰⁷, Tamas Leiner⁶⁰⁴, Patrick Lillie⁶⁰⁸, James Limb⁶⁰⁹, Vanessa Linnett⁶¹⁰, Jeff Little⁶¹¹, Mark Lyttle⁶¹², Michael MacMahon¹²⁸¹, Emily MacNaughton⁶¹³, Ravish Mankregod⁶¹⁴, Huw Masson⁶¹⁵, Elijah Matovu⁵⁷⁸, Katherine McCullough⁶¹⁶, Ruth McEwen⁶¹⁷, Manjula Meda⁶¹⁸, Gary H. Mills⁶⁶³, Jane Minton⁶²⁰, Karl Ward⁶²⁰, Mariyam Mirfenderesky⁶²¹, Kavya Mohandas⁶²², Quen Mok⁶²³, James Moon⁶²⁴, Elinor Moore⁵⁸¹, Patrick Morgan⁶²⁵, Craig Morris⁶²⁶, Katherine Mortimore⁶⁰⁴, Samuel Moses⁶²⁷, Mbiye Mpenge⁶²⁸, Rohinton Mulla⁶²⁹, Michael Murphy⁶³⁰, Megan Nagel⁶³¹, Thapas Nagarajan⁶³², Mark Nelson⁶³³, Matthew K. O'Shea⁶³⁴, Igor Otahal⁶³⁵, Marlies Ostermann⁶⁴³, Mark Pais⁶³⁶, Selva Panchatsaram⁶³⁷, Danaï Papakonstantinou⁶³⁸, Hassan Paraiso⁶³⁹, Brij Patel⁶⁴⁰, Natalie Pattison⁶⁴¹, Justin Pepperell⁶⁴², Mark Peters¹²⁸¹, Mandeep Phull⁶⁴³, Stefania Pintus⁶⁴⁴, Jagtur Singh Pooni⁶⁴⁵, Frank Post⁶⁴⁶, David Price⁶⁴⁷, Rachel Prout⁶⁴⁸, Nikolas Rae⁶⁴⁹, Henrik Reschreiter⁶⁵⁰, Tim Reynolds⁶⁵¹, Neil Richardson⁶⁵², Mark Roberts⁶⁵³, Devender Roberts⁶⁵⁴, Alistair Rose⁶⁵⁵, Guy Rousseau⁶⁵⁶, Brendan Ryan⁶⁵⁷, Taranpriti Saluja⁶⁵⁸, Aarti Shah⁶⁵⁹, Prad Shanmuga⁶⁶⁰, Anil Sharma⁶⁶¹, Anna Shawcross⁶⁶², Jeremy Sizer⁶⁶³, Manu Shankar-Har⁶⁴³, Richard Smith⁶⁶⁴, Catherine Snelson⁶⁶⁵, Nick Spittle⁶⁶⁶, Nikki Staines⁶⁶⁷, Tom Stambach⁶⁶⁸, Richard Stewart⁶⁶⁹, Pradeep Subudhi⁶⁷⁰, Tamas Szakmany⁶⁷¹, Kate Tatham⁶⁷², Jo Thomas⁶⁷³, Chris Thompson⁶⁷⁴, Robert Thompson¹²⁸¹, Ascanio Tridente⁶⁷⁵, Darell Tupper-Carey⁶⁵¹, Mary Twagira⁶⁷⁶, Andrew Ustianowski⁶⁷², Nick Vallotton⁶⁷⁷, Lisa Vincent-Smith⁶⁷⁸, Shico Visuvanathan⁶⁶⁷, Alan Vuylsteke⁶⁷⁹, Sam Waddy⁶⁸⁰, Rachel Wake⁶⁸¹, Andrew Walden⁶⁸², Ingeborg Welters⁵⁴⁷, Tony Whitehouse⁶⁶⁵, Paul Whittaker⁶⁸³, Ashley Whittington⁶⁸⁴, Padmasayee Papineni⁶⁸⁵, Meme Wijesinghe⁶⁸⁶, Martin Williams¹²⁸¹, Lawrence Wilson⁶¹⁷, Sarah Cole⁹⁶⁶, Stephen Winchester⁶⁸⁷, Martin Wiselka⁶⁸⁸, Adam Wolverson⁶⁸⁹, Daniel G. Wootton⁶⁹⁰, Andrew Workman⁶⁸⁸, Bryan Yates⁶⁹¹ & Peter Young⁶⁹²

Analysis team members

J. Kenneth Baillie^{60,61,62}, Rupert Beale⁶⁹³, Andrew D. Bretherick⁶², Mark J. Caulfield^{95,695}, Sara Clohisey⁹⁰, Max Head Fourman⁹⁰, James Furniss⁹⁰, Elvina Gountouna⁶⁹⁶, Graeme Grimes⁹², Chris Haley⁶⁰, David Harrison⁶⁹⁷, Caroline Hayward^{62,696}, Sean Keating⁶¹, Lucija Klaric⁶², Paul Klenerman⁷⁰⁰, Athanasios Kousathanas⁹⁵, Andy Law⁶⁰, Alison M. Meynert⁶², Jonathan Millar⁶⁰, Loukas Moutsianas^{14,95}, Erola Pairo-Castineira^{60,62}, Nicholas Parkinson⁶⁰, Dorota Pasko⁹⁵, Chris P. Ponting⁶², David J. Porteous⁹⁹⁶, Konrad Rawlik⁶⁰, Anne Richmond⁶², Kathy Rowan⁶⁹⁷, Clark D. Russell^{60,705}, Richard H. Scott^{95,706}, Xia Shen^{707,708,709}, Barbara Shih⁶⁰, Albert Tenesa^{60,62,708}, Veronique Vitart⁶², Susan Walker⁹⁵, Bo Wang⁶⁰, James F. Wilson^{62,708}, Yang Wu⁷¹⁰, Jian Yang^{711,712}, Zhijian Yang⁷⁰⁷, Marie Zechner⁶⁰, Ranran Zhai⁷⁰⁷, Chenqing Zheng⁷⁰⁷, Lisa Norman⁷¹⁴, Riinu Pius⁷¹⁴, Thomas M. Drake⁷¹⁴, Cameron J. Fairfield⁷¹⁴, Stephen R. Knight⁷¹⁴, Kenneth A. Mclean⁷¹⁴, Derek Murphy⁷¹⁴, Catherine A. Shaw⁷¹⁴, Jo Dalton⁷¹⁵, Michelle Girvan⁷¹⁵, Egle Saviciute⁷¹⁵, Stephanie Roberts⁷¹⁵, Janet Harrison⁷¹⁵, Laura Marsh⁷¹⁵, Marie Connor⁷¹⁵,

Sophie Halpin⁷¹⁵, Clare Jackson⁷¹⁵, Carrol Gamble⁷¹⁵, Gary Leeming⁷¹⁶, Andrew Law⁸⁰, Murray Wham⁷¹⁷, Sara Clohisey⁶⁰, Ross Hendry⁶⁰ & James Scott-Brown⁷¹⁸

Data collection members

Colin Begg⁷¹⁹, Sara Clohisey⁶⁰, Charles Hinds⁶⁹⁵, Antonia Ying Wai Ho⁷²¹, Peter W. Horby⁷²², Julian Knight⁷⁰⁰, Lowell Ling⁷²⁴, David Maslove⁷²⁵, Danny McAuley^{726,727}, Jonathan Miller⁶⁰, Hugh Montgomery⁷²⁸, Alistair Nichol⁷²⁹, Peter J. M. Openshaw^{730,731}, Chris P. Ponting⁶², Kathy Rowan⁶⁹⁷, Malcolm G. Semple^{732,733}, Manu Shankar-Hari⁷³⁴, Charlotte Summers⁷³⁵, Timothy Walsh⁶¹, Lisa Armstrong⁷³⁶, Hayley Bates⁷³⁶, Emma Dooks⁷³⁶, Fiona Farquhar⁷³⁶, Brigid Hairsine⁷³⁶, C. McParland⁷³⁶, Sophie Packham⁷³⁶, Zoe Alldis⁷³⁷, Raine Astin-Chamberlain⁷³⁷, Fatima Bibi⁷³⁷, Jack Biddle⁷³⁷, Sarah Blow⁷³⁷, Matthew Bolton⁷³⁷, Catherine Borra⁷³⁷, Ruth Bowles⁷³⁷, Maudrian Burton⁷³⁷, Yasmin Choudhury⁷³⁷, David Collier⁷³⁷, Amber Cox⁷³⁷, Amy Easthope⁷³⁷, Patrizia Ebanro⁷³⁷, Stavros Fotiadis⁷³⁷, Jana Gurasashvili⁷³⁷, Rosslyn Halls⁷³⁷, Pippa Hartridge⁷³⁷, Delordson Kallon⁷³⁷, Fotia Kassam⁷³⁷, Ivone Lancoma-Malcolm⁷³⁷, Maninderpal Matharu⁷³⁷, Peter May⁷³⁷, Oliver Mitchelmore⁷³⁷, Tabitha Newman⁷³⁷, Mital Patel⁷³⁷, Jane Pheby⁷³⁷, Irene Pinzuti⁷³⁷, Zoe Prime⁷³⁷, Oleksandra Pryszczyna⁷³⁷, Julian Shiel⁷³⁷, Melanie Taylor⁷³⁷, Carey Tierney⁷³⁷, Suzanne Wood⁷³⁷, Anne Zak⁷³⁷, Olivier Zongo⁷³⁷, Miranda Forsey⁷³⁸, Agilan Kaliappan⁷³⁸, Anne Nicholson⁷³⁸, Joanne Riches⁷³⁸, Mark Vertue⁷³⁸, Christopher Wasson⁵²³, Stephanie Finn⁵²³, Jackie Green⁵²³, Erin Collins⁵²³, Bernadette King⁵²³, Lina Grauslyte⁷³⁹, Musarat Hussain⁷³⁹, Mandeep Phull⁷³⁹, Tatiana Pogreban⁷³⁹, Lace Rosaroso⁷³⁹, Erika Salciute⁷³⁹, George Franke⁷³⁹, Joanna Wong⁷³⁹, Aparna George⁷³⁹, Louise Akeroyd⁷⁴⁰, Shereen Bano⁷⁴⁰, Matt Bromley⁷⁴⁰, Lucy Gurr⁷⁴⁰, Tom Lawton⁷⁴⁰, James Morgan⁷⁴⁰, Kirsten Sellick⁷⁴⁰, Deborah Warren⁷⁴⁰, Brian Wilkinson⁷⁴⁰, Janet McGowan⁷⁴⁰, Camilla Ledger⁷⁴⁰, Amelia Stacey⁷⁴⁰, Kate Pye⁷⁴⁰, Ruth Bellwood⁷⁴⁰, Michael Bentley⁷⁴⁰, Maria Hobrok⁷⁴¹, Ronda Loosley⁷⁴¹, Heather McGuinness⁷⁴¹, Helen Tench⁷⁴¹, Rebecca Wolf-Roberts⁷⁴¹, Sian Gibson⁷⁴², Amanda Lyle⁷⁴², Fiona McNeela⁷⁴², Jayachandran Radhakrishnan⁷⁴², Alistair Hughes⁷⁴², Asifa Ali⁷⁴³, Megan Brady⁷⁴³, Sam Dale⁷⁴³, Annalisa Dance⁷⁴³, Lisa Gledhill⁷⁴³, Jill Greig⁷⁴³, Kathryn Hanson⁷⁴³, Kelly Holdroyd⁷⁴³, Marie Home⁷⁴³, Diane Kelly⁷⁴³, Ross Kitch⁷⁴³, Lear Matapure⁷⁴³, Deborah Melia⁷⁴³, Samantha Mello⁷⁴³, Tonicha Nortcliffe⁷⁴³, Jez Pinnell⁷⁴³, Matthew Robinson⁷⁴³, Lisa Shaw⁷⁴³, Ryan Shaw⁷⁴³, Lesley Thomis⁷⁴³, Alison Wilson⁷⁴³, Tracy Wood⁷⁴³, Lee-Ann Bayo⁷⁴³, Ekta Merwaha⁷⁴³, Tahira Ishaq⁷⁴³, Sarah Hanley⁷⁴³, David Antcliffe⁷⁴⁴, Dorota Banach⁷⁴⁴, Stephen Brett⁷⁴⁴, Phoebe Coghlan⁷⁴⁴, Ziorzta Fernandez⁷⁴⁴, Anthony Gordon⁷⁴⁴, Roceld Rojo⁷⁴⁴, Sonia Sousa Arias⁷⁴⁴, Maie Templeton⁷⁴⁴, Rajeev Jha⁷⁴⁵, Vinodh Krishnamurthy⁷⁴⁵, Lai Lim⁷⁴⁵, Rehana Bi⁷⁴⁶, Barney Scholefield⁷⁴⁶, Lydia Ashton⁷⁴⁶, Alison Williams⁷⁴⁷, Claire Cheyne⁷⁴⁷, Anne Sanderson⁷⁴⁷, Angela Allan⁷⁴⁸, Felicity Anderson⁷⁴⁸, Callum Kaye⁷⁴⁸, Jade Liew⁷⁴⁸, Jasmine Medhora⁷⁴⁸, Teresa Scott⁷⁴⁸, Erin Trumper⁷⁴⁸, Adriana Botello⁷⁴⁸, Petra Polgarova⁷⁴⁹, Katerina Stroud⁷⁴⁹, Eoghan Meaney⁷⁴⁹, Megan Jones⁷⁴⁹, Anthony Ng⁷⁴⁹, Shruti Agrawal⁷⁴⁹, Nazima Pathan⁷⁴⁹, Deborah White⁷⁴⁹, Esther Daubney⁷⁴⁹, Kay Elston⁷⁴⁹, Robert Parker⁷⁵⁰, Amie Reddy⁷⁵⁰, Ian Turner-Bone⁷⁵⁰, Laura Wilding⁷⁵⁰, Peter Harding⁷⁵⁰, Reni Jacob⁷⁵², Cathy Jones⁷⁵², Craig Denmade⁷⁵², Maria Croft⁷⁵³, Ian White⁷⁵³, Rajeev Jha⁷⁴⁵, Vinodh Krishnamurthy⁷⁴⁵, Li Lim⁷⁴⁵, Denise Griffin⁷⁵⁴, Nycola Muchenje⁷⁵⁴, McDonald Mupuzi⁷⁵⁴, Richard Partridge⁷⁵⁴, Jo-Anna Conyngham⁷⁵⁴, Rachel Thomas⁷⁵⁴, Mary Wright⁷⁵⁴, Maria Alvarez Corral⁷⁵⁴, Victoria Bastion⁷⁵⁴, Daphne Clarke⁶⁶³, Beena David⁶⁶³, Harriet Kent⁶⁶³, Rachel Lorusso⁶⁶³, Gamar Lubimbi⁶⁶³, Sophie Murdoch⁶⁶³, Melchizedek Penacerrada⁶⁶³, Alastair Thomas⁶⁶³, Jennifer Valentine⁶⁶³, Ana Vochin⁶⁶³, Retno Wulandari⁶⁶³, Brice Djeugam⁶⁶³, Joy Dawson⁷⁵⁵, Sweyn Garricho⁷⁵⁵, Melanie Tolson⁷⁵⁵, Jonathan Aldridge⁷⁵⁵, Laura Gomes de Almeida Martins⁵²⁴, Jaime Carungcong⁵²⁴, Sarah Beavis⁷⁵⁶, Katie Dale⁷⁵⁶, Rachel Gascoyne⁷⁵⁶, Joanne Hawes⁷⁵⁶, Kelly Pritchard⁷⁵⁶, Lesley Stevenson⁷⁵⁶, Amanda Whiteman⁷⁵⁶, Anne Cowley⁷⁵⁷, Judith Highgate⁷⁵⁷, Rikki Crawley⁷⁵⁸, Abigail Crew⁷⁵⁸, Mishell Cunningham⁷⁵⁸, Allison Daniels⁷⁵⁸, Laura Harrison⁷⁵⁸, Susan Hope⁷⁵⁸, Ken Inweregbu⁷⁵⁸, Sian Jones⁷⁵⁸, Nicola Lancaster⁷⁵⁸, Jamie Matthews⁷⁵⁸, Alice Nicholson⁷⁵⁸, Gemma Wray⁷⁵⁸, Leonie Benham⁷⁵⁹, Zena Bradshaw⁷⁵⁹, Joanna Brown⁷⁵⁹, Melanie Caswell⁷⁵⁹, Jason Cupitt⁷⁵⁹, Sarah Melling⁷⁵⁹, Stephen Preston⁷⁵⁹, Nicola Lawson⁷⁵⁹, Emma Stoddard⁷⁵⁹, Scott Warden⁷⁵⁹, Edward Combes⁷⁶⁰, Teishel Joefield⁷⁶⁰, Sonja Monnery⁷⁶⁰, Valerie Beach⁷⁶⁰, Sallyanne Trotman⁷⁶⁰, Bridget Hopkins⁷⁶¹, James Scriven⁷⁶¹, Laura Theasvyvoulou⁷⁶¹, Heather Willis⁷⁶¹, Susan Anderson⁷⁶², Janine Birch⁷⁶², Emma Collins⁷⁶², Kate Hammerton⁷⁶², Ryan O'Leary⁷⁶², Caroline Abernathy⁷⁶³, Louise Foster⁷⁶³, Andrew Gratrix⁷⁶³, Vicky Martinson⁷⁶³, Priyai Parkinson⁷⁶³, Elizabeth Stones⁷⁶³, Lucia Carbal-Ortega⁷⁶³, Ritoo Kapoor⁷⁶⁵, David Loader⁷⁶⁵, Karen Castle⁷⁶⁵, Craig Brandwood⁷⁶⁶, Lara Smith⁷⁶⁶, Richard Clark⁷⁶⁶, Katie Birchall⁷⁶⁶, Laurel Kolakaluri⁷⁶⁶, Deborah Baines⁷⁶⁶, Anila Sukumaran⁷⁶⁶, Ishauneu Mapfunde⁵²⁵, Megan Meredith⁷⁶⁷, Lucy Morris⁷⁶⁷, Lucy Ryan⁷⁶⁷, Amy Clark⁷⁶⁷, Julia Sampson⁷⁶⁷, Cecilia Peters⁷⁶⁷, Martin Dent⁷⁶⁷, Margaret Langley⁷⁶⁷, Saima Ashraf⁷⁶⁷, Shuying Wei⁷⁶⁷, Angela Andrew⁷⁶⁷, Manish Chablani⁷⁶⁸, Amy Kirkby⁷⁶⁸, Kimberley Netherton⁷⁶⁸, Michelle Bates⁷⁶⁹, Jo Dasginn⁷⁶⁹, Jaspreet Gill⁷⁶⁹, Annette Nilsson⁷⁶⁹, James Scriven⁷⁶⁹, Elena Apetri⁷⁷⁰, Cathrine Basikolo⁷⁷⁰, Bethan Blackledge⁷⁷⁰, Laura Catlow⁷⁷⁰, Bethan Charles⁷⁷⁰, Paul Dark⁷⁷⁰, Reece Doonan⁷⁷⁰, Jade Harris⁷⁷⁰, Alice Harvey⁷⁷⁰, Daniel Horner⁷⁷⁰, Karen Knowles⁷⁷⁰, Stephanie Lee⁷⁷⁰, Diane Lomas⁷⁷⁰, Chloe Lyons⁷⁷⁰, Tracy Marsden⁷⁷⁰, Danielle McLaughlan⁷⁷⁰, Liam McMorrow⁷⁷⁰, Jessica Pendlebury⁷⁷⁰, Jane Perez⁷⁷⁰, Maria Poulaka⁷⁷⁰, Nicola Proudfoot⁷⁷⁰, Melanie Slaughter⁷⁷⁰, Kathryn Slevin⁷⁷⁰, Melanie Taylor⁷⁷⁰, Vicky Thomas⁷⁷⁰, Danielle Walker⁷⁷⁰, Angiy Michael⁷⁷⁰, Matthew Collins⁷⁷⁰, Martyn Clark⁷⁷¹, Martina Coulding⁷⁷¹, Edward Jude⁷⁷¹, Jacqueline McCormick⁷⁷¹, Oliver Mercer⁷⁷¹, Darsh Potla⁷⁷¹, Hafiz Rehman⁷⁷¹, Heather Savill⁷⁷¹, Victoria Turner⁷⁷¹, Miriam Davey⁷⁷², David Golden⁷⁷², Rebecca Seaman⁷⁷², Jodie Hunt⁷⁷², Joy Dearden⁷⁷², Emma Dobson⁷⁷², Andrew Drummond^{572,773}, Michelle Mulcahy⁷⁷³, Sheila Munt⁷⁷³, Grainne O'Connor⁷⁷³, Jennifer Philbin⁷⁷³, Chloe Rishton⁷⁷³, Redmond Tully⁷⁷³, Sarah Winnard⁷⁷³, Lenka Cagova⁷⁷⁴, Adama Fofano⁷⁷⁴, Lucie Garner⁷⁷⁴, Helen Holcombe⁷⁷⁴, Sue Mepham⁷⁷⁴, Alice Michael Mitchell⁷⁷⁴, Lucy Mwaura⁷⁷⁴, K. Praman⁷⁷⁴, Alan Vuylsteke⁷⁷⁴, Julie Zamikula⁷⁷⁴, Miriam Davey⁷⁷⁴, David Golden⁷⁷⁴, Rebecca Seaman⁷⁷⁴, Georgia Bercades⁷⁷⁵, David Brealey⁷⁷⁵, Ingrid Hass⁷⁷⁵, Niall MacCallum⁷⁷⁵, Gladys Martin⁷⁷⁵, Eamon Raith⁷⁷⁵, Anna Reyes⁷⁷⁵, Deborah Smyth⁷⁷⁵, Abigail Taylor⁷⁷⁶, Rachel Anne Hughes⁷⁷⁶, Helen Thomas⁷⁷⁶, Alun Rees⁷⁷⁶, Michaela Duskova⁷⁷⁶, Janet Phipps⁷⁷⁶, Suzanne Brooks⁷⁷⁶, Michelle Edwards⁷⁷⁶, Peter Alexander⁷⁷⁷, Schvearn Allen⁷⁷⁷, Joanne Bradley-Potts⁷⁷⁷, Craig Brantwood⁷⁷⁷, Jasmine Egan⁷⁷⁷, Timothy Felton⁷⁷⁷, Grace Padden⁷⁷⁷, Luke Ward⁷⁷⁷, Stuart Moss⁷⁷⁷, Susannah Glasgow⁷⁷⁷, Kate Beesley⁷⁷⁸, Sarah Board⁷⁷⁸, Agnieszka Kubisz-Pudelko⁷⁷⁸, Alison Lewis⁷⁷⁸, Jess Perry⁷⁷⁸, Lucy Pippard⁷⁷⁸, Di Wood⁷⁷⁸, Clare Buckley⁷⁷⁸, Alison Brown⁷⁷⁹, Jane Gregory⁷⁷⁹, Susan O'Connell⁷⁷⁹, Tim Smith⁷⁷⁹, Zakula Belagodu⁷⁸⁰, Bridget Fuller⁷⁸⁰, Anca Gherman⁷⁸⁰, Olumide Olufuwa⁷⁸⁰,

Remi Paramsothy⁷⁸⁰, Carmel Stuart⁷⁸⁰, Naomi Oakley⁷⁸⁰, Charlotte Kamundi⁷⁸⁰, David Tyl⁷⁸⁰, Katy Collins⁷⁸⁰, Pedro Silva⁷⁸⁰, June Taylor⁷⁸⁰, Laura King⁷⁸⁰, Charlotte Coates⁷⁸⁰, Maria Crowley⁷⁸⁰, Phillipa Wakefield⁷⁸⁰, Jane Beadle⁷⁸⁰, Laura Johnson⁷⁸⁰, Janet Sargeant⁷⁸⁰, Madeleine Anderson⁷⁸⁰, Catherine Jardine⁷⁸¹, Dewi Williams⁷⁸¹, Victoria Parris⁷⁸², Sheena Quaid⁷⁸², Ekaterina Watson⁷⁸², Julie Melville⁷⁸³, Jay Naisbitt⁷⁸³, Rosane Joseph⁷⁸³, Maria Lazo⁷⁸³, Olivia Walton⁷⁸³, Alan Neal⁷⁸³, Michaela Hill⁷⁸⁴, Thogulava Kannan⁷⁸⁴, Laura Wild⁷⁸⁴, Elizabeth Allan⁷⁸⁵, Kate Darlington⁷⁸⁵, Ffyon Davies⁷⁸⁵, Jack Easton⁷⁸⁵, Sumit Kumar⁷⁸⁵, Richard Lean⁷⁸⁵, Daniel Menzies⁷⁸⁵, Richard Pugh⁷⁸⁵, Xinyi Qiu⁷⁸⁵, Linos Davies⁷⁸⁵, Hannah Williams⁷⁸⁵, Jeremy Scanlon⁷⁸⁵, Gwyneth Davies⁷⁸⁵, Callum Mackay⁷⁸⁵, Joanne Lewis⁷⁸⁵, Stephanie Rees⁷⁸⁵, Samantha Coetzee⁷⁸⁶, Alistair Gales⁷⁸⁶, Igor Otahal⁷⁸⁶, Meena Raj⁷⁸⁶, Craig Sell⁷⁸⁶, Helen Langton⁷⁸⁷, Rachel Prout⁷⁸⁷, Malcolm Waters⁷⁸⁷, Catherine Novis⁷⁸⁷, Gill Arbane⁷⁸⁸, Aneta Bociek⁷⁸⁸, Sara Campos⁷⁸⁸, Neus Grau⁷⁸⁸, Tim Owen Jones⁷⁸⁸, Rosario Lim⁷⁸⁸, Martina Marotti⁷⁸⁸, Marlies Ostermann⁷⁸⁸, Manu Shankar-Hari⁷⁸⁸, Christopher Whitton⁷⁸⁸, Anthony Barron⁷⁸⁹, Ciara Collins⁷⁸⁹, Sundeep Kaul⁷⁸⁹, Heather Passmore⁷⁸⁹, Claire Prendergast⁷⁸⁹, Anna Reed⁷⁸⁹, Paula Rogers⁷⁸⁹, Rajvinder Shokkar⁷⁸⁹, Meriel Woodruff⁷⁸⁹, Hayley Middleton⁷⁸⁹, Oliver Polga⁷⁸⁹, Claire Nolan⁷⁸⁹, Vicky Thwaites⁷⁸⁹, Kanta Mahay⁷⁸⁹, Chunda Sri-Chandana⁷⁹⁰, Joslan Scherewode⁷⁹⁰, Lorraine Stephenson⁷⁹⁰, Sarah Marsh⁷⁹⁰, Hollie Bancroft⁶³⁸, Mary Bellamy⁶³⁸, Margaret Carmody⁶³⁸, Jacqueline Daghli⁶³⁸, Faye Moore⁶³⁸, Joanne Rhodes⁶³⁸, Mirriam Sangombe⁶³⁸, Salma Kadiri⁶³⁸, James Scriven⁶³⁸, Amanda Ayers⁷⁹², Wendy Harrison⁷⁹², Julie North⁷⁹², Anna Cavazza⁶⁴⁶, Maeve Cockrell⁶⁴⁶, Eleanor Corcoran⁶⁴⁶, Maria Depante⁶⁴⁶, Clare Finney⁶⁴⁶, Ellen Jerome⁶⁴⁶, Mark McPhail⁶⁴⁶, Monalisa Nayak⁶⁴⁶, Harriet Noble⁶⁴⁶, Kevin O'Reilly⁶⁴⁶, Evita Pappa⁶⁴⁶, Rohit Saha⁶⁴⁶, Sian Saha⁶⁴⁶, Inez Smyth⁶⁴⁶, Abigail Knighton⁶⁴⁶, Mandy Gill⁷⁹⁴, Paul Paul⁷⁹⁴, Valli Ratnam⁷⁹⁴, Sarah Shelton⁷⁹⁴, John Wyrther⁷⁹⁴, David Baptista⁷⁹⁵, Rebecca Crowe⁷⁹⁵, Rita Fernandes⁷⁹⁵, Rosaleen Herdman-Grant⁷⁹⁵, Anna Joseph⁷⁹⁵, Adam Loveridge⁷⁹⁵, India McKenzie⁷⁹⁵, Eriko Morino⁷⁹⁵, Andres Naranjo⁷⁹⁵, Richard Simms⁷⁹⁵, Kathryn Sollesta⁷⁹⁵, Andrew Swain⁷⁹⁵, Harish Venkatesh⁷⁹⁵, Jacyntha Khera⁷⁹⁵, Jonathan Fox⁷⁹⁵, Russell Barber⁷⁹⁶, Claire Hewitt⁷⁹⁶, Annette Hilldrith⁷⁹⁶, Karen Jackson-Lawrence⁷⁹⁶, Sarah Shepardson⁷⁹⁶, Maryanne Wills⁷⁹⁶, Susan Butler⁷⁹⁶, Silvia Tavares⁷⁹⁶, Amy Cunningham⁷⁹⁶, Julia Hindale⁷⁹⁶, Sarwat Arif⁷⁹⁶, Linsha George⁷⁹⁷, Sophie Tills⁷⁹⁷, David Wright⁷⁹⁷, Maureen Holland⁷⁹⁸, Natalie Keenan⁷⁹⁸, Marc Lyons⁷⁹⁸, Helen Wassall⁷⁹⁸, Chris Marsh⁷⁹⁸, Mervin Mahenthran⁷⁹⁸, Emma Carter⁷⁹⁸, Thomas Kong⁷⁹⁸, Oluronne Adaniri⁷⁹⁹, Nikhil Bhatia⁷⁹⁹, Maines Msiska⁷⁹⁹, Miranda Forsey⁷⁹⁸, Agilan Kaliappan⁷⁹⁸, Anne Nicholson⁷⁹⁸, Joanne Riches⁷⁹⁸, Mark Vertue⁷⁹⁸, Louise Mew⁸⁰⁰, Esther Mwaura⁸⁰⁰, Richard Stewart⁸⁰⁰, Felicity Williams⁸⁰⁰, Lynn Wren⁸⁰⁰, Sara-Beth Sutherland⁸⁰⁰, Ceri Battle⁸⁰¹, Elaine Brinkworth⁸⁰¹, Rachel Harford⁸⁰¹, Carl Murphy⁸⁰¹, Luke Newey⁸⁰¹, Tabitha Rees⁸⁰¹, Marie Williams⁸⁰¹, Sophie Arnold⁸⁰¹, David Brealey⁸⁰², John Hardy⁸⁰², Henry Houlden⁸⁰², Eleanor Moncur⁸⁰², Eamon Raith⁸⁰², Aamreen Tariq⁸⁰², Arianna Tucci⁸⁰², Karen Convery⁸⁰³, Deirdre Fottrell-Gould⁸⁰³, Lisa Hudig⁸⁰³, Jocelyn Keshet-Price⁸⁰³, Georgina Randel⁸⁰³, Katie Stammers⁸⁰³, Marwa Abdelrazek⁸⁰⁴, Dhanalakshmi Bakthavatsalam⁸⁰⁴, Munzir Elhassan⁸⁰⁴, Arunkumar Ganesan⁸⁰⁴, Anne Haldeos⁸⁰⁴, Jeronimo Moreno-Cuesta⁸⁰⁴, Dharam Purohit⁸⁰⁴, Rachel Vincent⁸⁰⁴, Kugan Xavier⁸⁰⁴, Kumar Rohit⁸⁰⁴, Frater Alasdair⁸⁰⁴, Malik Saleem⁸⁰⁴, Carter David⁸⁰⁴, Samuel Jenkins⁸⁰⁴, Zoe Lamond⁸⁰⁴, Alanna Wall⁸⁰⁴, Bryan Yates⁸⁰⁶, Jessica Reynolds⁸⁰⁶, Helen Campbell⁸⁰⁶, Maria Thompson⁸⁰⁶, Steve Dodds⁸⁰⁶, Deacon Duffy⁸⁰⁶, Deborah Butcher⁸⁰⁷, Susie O'Sullivan⁸⁰⁷, Nicola Butterworth-Cowin⁸⁰⁷, Bethan Stacey⁸⁰⁸, Meg Hibbert⁸⁰⁸, Carla Potheary⁸⁰⁸, Dariusz 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Aaysha Kaz⁸¹⁹, Janice Hartley⁸¹⁹, Joseph Dykes⁸¹⁹, Muhammad Hijazi⁸¹⁹, Sarah Keith⁸¹⁹, Meherunnisa Khan⁸¹⁹, Janet Ryan-Smith⁸¹⁹, Philippa Springe⁸¹⁹, Jacqueline Thomas⁸¹⁹, Nick Truman⁸¹⁹, Samuel Saad⁸¹⁹, Dabheec Coleman⁸¹⁹, Christopher Fine⁸¹⁹, Roseanna Matt⁸¹⁹, Bethan Gay⁸¹⁹, Jack Dalziel⁸¹⁹, Syamlan Ali⁸¹⁹, Drew Goodchild⁸¹⁹, Rhiannan Harling⁸¹⁹, Ravi Bhatteerje⁸¹⁹, Wendy Goddard⁸¹⁹, Chloe Davison⁸¹⁹, Stephen Duberly⁸¹⁹, Jeanette Hargreaves⁸¹⁹, Rachel Bolton⁸¹⁹, Shondipon Laha⁸²⁰, Mark Verlande⁸²⁰, Alexandra Williams⁸²⁰, Helen Blackman⁸²¹, Ben Creagh-Brown⁸²¹, Sinead Donlon⁸²¹, Natalia Michalak-Glinska⁸²¹, Sheila Mtuwa⁸²¹, Veronika Pripston⁸²¹, Armoree Salberg⁸²¹, Eleanor Smith⁸²¹, Sarah Stone⁸²¹, Charles Piercy⁸²¹, Jerik Verula⁸²¹, Dorota Burda⁸²¹, Rugia Montaser⁸²¹, Lesley Harden⁸²¹, Irving Mayangao⁸²¹, Cheryl Marriott⁸²¹, Paul Bradley⁸²¹, Celia Harris⁸²¹, Joshua Cooper⁸²², Cheryl Finch⁸²², Sarah Litherth⁸²², Alison Quinn⁸²², Natalia Waddington⁸²², Katy Fidler⁸²³, Emma Tagliavini⁸²³, Kevin Donnelly⁸²³, Lynn Abel⁸²⁴, Michael Brett⁸²⁴, Brian Digby⁸²⁴, Lisa Gemmel⁸²⁴, James Hornsby⁸²⁴, Patrick MacGoey⁸²⁴, Pauline O'Neil⁸²⁴, Richard Price⁸²⁴, Natalie Rodden⁸²⁴, Kevin Rooney⁸²⁴, Radha Sundaram⁸²⁴, Nicola Thomson⁸²⁴, Rebecca Flanagan⁸²⁵, Gareth Hughes⁸²⁵, Scott Latham⁸²⁵, Emma McKenna⁸²⁵, Jennifer Anderson⁸²⁵, Robert Hull⁸²⁵, Kat Rhead⁸²⁵, Debbie Branney⁸²⁶, Jordan Frankham⁸²⁶, Sally Pitts⁸²⁶, Nigel White⁸²⁶, Daniele Cristiano⁸²⁷, Natalie Dorman⁸²⁷, Zohreh Farza⁸²⁷, Mahitha Gummad⁸²⁷, Kamal Liyanage⁸²⁷, Brijesh V. Patel⁸²⁸, Sara Salmi⁸²⁸, Geraldine Sloane⁸²⁷, Vicky Thwaites⁸²⁷, Mathew Varghese⁸²⁷, Anelise C. Zborowski⁸²⁷, Sarah Bean⁸²⁹, Karen Burt⁸²⁹, Michael Spivey⁸²⁹, Christine Eastgate-Jackson⁸³⁰, Helder Filipe⁸³⁰, Daniel Martin⁸³⁰, Amita Mahajarj⁸³⁰, Sara Mingo Garcia⁸³⁰, Mark De Neef⁸³⁰, Bethan Deacon⁸³¹, Ceri Lynch⁸³¹, Carla Potheary⁸³¹, Lisa Roche⁸³¹, Gwenllian Sera Howe⁸³¹, Jayaprakash Singh⁸³¹, Kerri Turner⁸³¹, Hannah Ellis⁸³¹, Natalie Stroud⁸³¹, Shiney Cherian⁸³², Sean Cutler⁸³², Anna Emma Heron⁸³², Anna Roynon-Reed⁸³², Tamas Szakmany⁸³², Gemma Williams⁸³², Owen Richards⁸³², Yusuf Cheema⁸³², Norfaizan Ahmad^{563,833}, Joann Barker^{563,833}, Kris Baumuller^{563,833}, Sarah Bird^{563,833}, Kay Cawthron^{563,833}, Kate Harrington^{563,833}, Yvonne Jackson^{563,833}, Faith Kibbly^{563,833}, Becky Lenagh^{563,833}, Shamiso Masuku^{563,833}, Gary H. Mills^{563,833}, Ajay Raithatha^{563,833}, Matthew Wiles^{563,833}, Jayne Wilson^{563,833}, Helen Newell^{563,833}, Alison Lye^{563,833}, Lorenza Nwafor^{563,833}, Claire Jarman^{563,833}, Sarah Rowland-Jones^{563,833}, David Foote^{563,833}, Joby Cole^{563,833}, Roger Thompson^{563,833}, James Watson^{563,833},

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Lisa Hesselton^{563,833}, Irene Macharia^{563,833}, Luke Chetam^{563,833}, Jacqui Smith^{563,833}, Amber Ford^{563,833}, Samantha Anderson^{563,833}, Kathryn Birchall^{563,833}, Kay Housley^{563,833}, Sara Walker^{563,833}, Leanne Milner^{563,833}, Helena Hanratty^{563,833}, Helen Trower^{563,833}, Patrick Phillips^{563,833}, Simon Oxspring^{563,833}, Ben Donne^{563,833}, Emily Bevan⁸³⁴, Jane Martin⁸³⁴, Dawn Todd⁸³⁴, Geoff Watson⁸³⁴, Caroline Wrey Brown⁸³⁴, Lara Bunni⁸³⁵, Claire Jennings⁸³⁵, Monica Latif⁸³⁵, Rebecca Marshall⁸³⁵, Gayathri Subramanian⁸³⁵, Nageswar Bandla⁸³⁶, Minnie Gellamucho⁸³⁶, Michelle Davies⁸³⁶, Christopher Thompson⁸³⁶, Laura Ortiz-Ruiz de Gordoa⁸⁰⁹, Emily Peasgood⁸⁰⁹, Claire Phillips⁸⁰⁹, Denise Skinner⁸¹⁰, Jane Gaylard⁸¹⁰, Dee Mullan⁸¹⁰, Julie Newman⁸¹⁰, Phil Donnison⁸⁰⁷, Fiona Trim⁸³⁷, Beena Eapen⁸³⁷, Cecilia Ahmed⁸³⁸, Balvinder Baines⁸³⁸, Sarah Clamp⁸³⁸, Julie Colley⁸³⁸, Risna Haq⁸³⁸, Anne Hayes⁸³⁸, Jonathan Hulme⁸³⁸, Samia Hussain⁸³⁸, Sibet Joseph⁸³⁸, Rita Kumar⁸³⁸, Zahira Maqsood⁸³⁸, Manjit Purewal⁸³⁸, Ben Chandler⁸³⁹, Kerry Elliott⁸³⁹, Janine Mallinson⁸³⁹, Alison Turnbull⁸³⁹, Kathy Dent⁸⁴⁰, Elizabeth Horsley⁸⁴⁰, Muhammad Nauman Akhtar⁸⁴⁰, Sandra Pearson⁸⁴⁰, Dorota Potoczna⁸⁴⁰, Sue Spencer⁸⁴⁰, Hayley Blakemore⁸⁴¹, Borislava Borislavova⁸⁴¹, Beverley Faulkner⁸⁴¹, Emma Gendall⁸⁴¹, Elizabeth Goff⁸⁴¹, Kati Hayes⁸⁴¹, Matt Thomas⁸⁴¹, Ruth Worner⁸⁴¹, Kerry Smith⁸⁴¹, Deanna Stephens⁸⁴¹, Carlos Castro Delgado⁸⁴², Deborah Dawson⁸⁴², Lijun Ding⁸⁴², Georgia Durrant⁸⁴², Obiageri Ezeobu⁸⁴², Sarah Farnell-Ward⁸⁴², Abiola Harrison⁸⁴², Rebecca Kanu⁸⁴², Susannah Leaver⁸⁴², Elena Maccacari⁸⁴², Soumendu Manna⁸⁴², Romina Pepermans Saluzzio⁸⁴², Joana Queiroz⁸⁴², Tinashé Samakomva⁸⁴², Christine Sicat⁸⁴², Joana Teixeira⁸⁴², Edna Fernandes Da Gloria⁸⁴², Ana Lisboa⁸⁴², John Rawlins⁸⁴², Jisha Mathew⁸⁴², Ashley Kinch⁸⁴², William James Hurt⁸⁴², Nirav Shah⁸⁴², Victoria Clark⁸⁴², Maria Thanasi⁸⁴², Nikki Yun⁸⁴², Kamal Patel⁸⁴², Alison Brown⁸⁴³, Vikki Crickmore⁸⁴³, Gabor Debrecen⁸⁴³, Joy Wilkins⁸⁴³, Liz Nicol⁸⁴³, Iona Burn⁸⁴³, Geraldine Hambrook⁸⁴⁴, Katarina Manso⁸⁴⁴, Ruth Penn⁸⁴⁴, Pradeep Shanmugasundaram⁸⁴⁴, Julie Tebbutt⁸⁴⁴, Danielle Thornton⁸⁴⁴, Anthony Rostron⁸⁴⁵, Alistair Roy⁸⁴⁵, Lindsey Woods⁸⁴⁵, Sarah Cornell⁸⁴⁵, Fiona Wakinsaw⁸⁴⁵, Kimberley Rogerson⁸⁴⁵, Jordan Jarman⁸⁴⁵, Peter Anderson⁸⁴⁶, Katie Archer⁸⁴⁶, Karen Austin⁸⁴⁶, Caroline Davis⁸⁴⁶, Alison Durie⁸⁴⁶, Olivia Kelsal⁸⁴⁶, Jessica Thrush⁸⁴⁶, Charlie Vigurs⁸⁴⁶, Laura Wild⁸⁴⁶, Hannah-Louise Wood⁸⁴⁶, Helen Tranter⁸⁴⁶, Alison Harrison⁸⁴⁶, Nicholas Cowley⁸⁴⁶, Michael McAlindon⁸⁴⁶, Andrew Burtenshaw⁸⁴⁶, Stephen Digby⁸⁴⁶, Emma Low⁸⁴⁶, Aled Morgan⁸⁴⁶, Naiara Cother⁸⁴⁶, Tobias Rankin⁸⁴⁶, Sarah Clayton⁸⁴⁶, Alex McCurdy⁸⁴⁶, Suzanne Allibone⁸⁴⁷, Roman Mary-Genetu⁸⁴⁷, Vidya Kasipandian⁸⁴⁷, Amit Patel⁸⁴⁷, Ainhí Mac⁸⁴⁷, Anthony Murphy⁸⁴⁷, Parisa Mahjoub⁸⁴⁷, Roonak Nazari⁸⁴⁷, Lucy Worsley⁸⁴⁷, Andrew Fagan⁸⁴⁷, Intahak Ali Mohamed Ali⁸⁴⁸, Karen Beaumont⁸⁴⁸, Mark Blun⁸⁴⁸, Zoe Coton⁸⁴⁸, Hollie Curgenvin⁸⁴⁸, Mohamed Elsaadany⁸⁴⁸, Kay Fernandes⁸⁴⁸, Sameena Mohamed Ally⁸⁴⁸, Harini Rangarajan⁸⁴⁸, Varun Sarathy⁸⁴⁸, Sivarupan Selvanayagam⁸⁴⁸, Dave Vedage⁸⁴⁸, Matthew White⁸⁴⁸, Jaime Fernandez-Roman⁸⁴⁹, David O. Hamilton⁸⁴⁹, Emily Johnson⁸⁴⁹, Brian Johnston⁸⁴⁹, Maria Lopez Martinez⁸⁴⁹, Suleman Mulla⁸⁴⁹, David Shaw⁸⁴⁹, Alicia A. C. Waite⁸⁴⁹, Victoria Waugh⁸⁴⁹, Ingeborg D. Welters⁸⁴⁹, Karen Williams⁸⁴⁹, Thomas Bemand⁸⁵⁰, Ethel Black⁸⁵⁰, Arnold Dela Rosa⁸⁵⁰, Ryan Howle⁸⁵⁰, Shaman Jhanji⁸⁵⁰, Ravishankar Rao Baikady⁸⁵⁰, Kate Colette Tatham⁸⁵⁰, Benjamin Thomas⁸⁵⁰, Matthew Halkes⁸⁵¹, Pauline Mercer⁸⁵¹, Lorraine Thornton⁸⁵¹, Joe West⁸⁵², Tracy Baird⁸⁵², Jim Rudd⁸⁵², Rosie Reece-Anthony⁸⁵³, Mark Birt⁸⁵⁴, Amanda Cowton⁸⁵⁴, Andrea Kay⁸⁵⁴, Melanie Kent⁸⁵⁴, Kathryn Potts⁸⁵⁴, Ami Wilkinson⁸⁵⁴, Suzanne Taylor⁸⁵⁴, Ellen Brown⁸⁵⁴, Michele Clark⁸⁵⁵, Sarah Purvis⁸⁵⁵, Jade Cole⁸⁵⁶, Michelle Davies⁸⁵⁶, Rhys Davies⁸⁵⁶, Donna Duffin⁸⁵⁶, Helen Hill⁸⁵⁶, Ben Player⁸⁵⁶, Emma Thomas⁸⁵⁶, Angharad Williams⁸⁵⁶, Claire Marie Beith⁸⁵⁷, Karen Black⁸⁵⁷, Suzanne Clements⁸⁵⁷, Alan Morrison⁸⁵⁷, Dominic Strachan⁸⁵⁷, Margaret Taylor⁸⁵⁷, Michelle Clarkson⁸⁵⁷, Stuart D'Sylva⁸⁵⁷, Kathryn Norman⁸⁵⁷, Tina Coventry⁸⁵⁸, Susan Fowler⁸⁵⁸, Michael MacMahon⁸⁵⁸, Amanda McGregor⁸⁵⁸, Ailbhe Brady⁸⁵⁹, Rebekah Chan⁸⁵⁹, Jeff Little⁸⁵⁹, Shane McIvor⁸⁵⁹, Helena Prady⁸⁵⁹, Helen Whittle⁸⁵⁹, Bijoy Mathew⁸⁵⁹, Melanie Clapham⁸⁶⁰, Rosemary Harper⁸⁶⁰, Una Poutlney⁸⁶⁰, Polly Rice⁸⁶⁰, Tim Smith⁸⁶⁰, Rachel Mutch⁸⁶⁰, Yolanda Baird⁸⁶¹, Aaron Butler⁸⁶¹, Indra Chadbourne⁸⁶¹, Linda Folkes⁸⁶¹, Heather Fox⁸⁶¹, Amy Gardner⁸⁶¹, Raquel Gomez⁸⁶¹, Gillian Hobden⁸⁶¹, Luke Hodgson⁸⁶¹, Kirsten King⁸⁶¹, Michael Margaron⁸⁶¹, Tim Martindale⁸⁶¹, Emma Meadows⁸⁶¹, Dana Raynard⁸⁶¹, Yvette Thirlwall⁸⁶¹, David Helm⁸⁶¹, Jordi Margale⁸⁶¹, Sandra Greer⁸⁶², Karen Shuke⁸⁶², Ascanio Tridente⁸⁶², Sara Smuts⁸⁶², Joseph Duffield⁸⁶², Oliver Smith⁸⁶², Lewis Mallon⁸⁶², Watkins Claire⁸⁶², Isobel Birkinshaw⁸⁶³, Joseph Carter⁸⁶³, Kate Howard⁸⁶³, Joanne Ingham⁸⁶³, Rosie Joy⁸⁶³, Harriet Pearson⁸⁶³, Samantha Roche⁸⁶³, Zoe Scott⁸⁶³, Ellen Knights⁸⁶⁴, Alicia Price⁸⁶⁴, Alice Thomas⁸⁶⁴, Chris Thorpe⁸⁶⁴, Azmeralda Abraheem⁸⁶⁵, Peter Bamford⁸⁶⁵, Kathryn Cawley⁸⁶⁵, Charlie Dunmore⁸⁶⁵, Maria Faulkner⁸⁶⁵, Rumanah Girach⁸⁶⁵, Helen Jeffrey⁸⁶⁵, Rhianna Jones⁸⁶⁵, Emily London⁸⁶⁵, Imrun Nagra⁸⁶⁵, Farah Nasir⁸⁶⁵, Hannah Sainsbury⁸⁶⁵, Clare Smedley⁸⁶⁶, Reena Khade⁸⁶⁶, Ashok Sundar⁸⁶⁶, George Tsinaslanidis⁸⁶⁶, Teresa Behan⁸⁶⁷, Caroline Burnett⁸⁶⁷, Jonathan Hutton⁸⁶⁷, Elaine Heeney⁸⁶⁷, Atideb Mitra⁸⁶⁷, Maria Newton⁸⁶⁷, Rachel Pollard⁸⁶⁷, Rachael Stead⁸⁶⁷, Jenny Birch⁸⁶⁸, Laura Bough⁸⁶⁸, Josie Goodsell⁸⁶⁸, Rebecca Tutton⁸⁶⁸, Patricia Williams⁸⁶⁸, Sarah Williams⁸⁶⁸, Barbara Winter-Goodwin⁸⁶⁸, Anne Cowley⁸⁶⁹, Judith Highgate⁸⁶⁹, Fiona Auld⁸⁶⁹, Joanne Donnachie⁸⁶⁹, Ian Edmond⁸⁶⁹, Lynn Prentice⁸⁶⁹, Nikole Runciman⁸⁶⁹, Dario Salutous⁸⁶⁹, Lesley Symon⁸⁶⁹, Anne Todd⁸⁶⁹, Patricia Turner⁸⁶⁹, Abigail Short⁸⁶⁹, Laura Sweeney⁸⁶⁹, Euan Murdoch⁸⁶⁹, Dhaneesha Senaratne⁸⁶⁹, Karen Burns⁸⁷⁰, Andrew Higham^{870,905}, Taya Anderson⁸⁷¹, Dan Hawcutt⁸⁷¹, Laura O'Malley⁸⁷¹, Laura Rad⁸⁷¹, Naomi Rogers⁸⁷¹, Paula Saunderson⁸⁷¹, Kathryn Sian Allison⁸⁷¹, Deborah Afolabi⁸⁷¹, Jennifer Whitbread⁸⁷¹, Dawn Jones⁸⁷¹, Rachael Dore⁸⁷¹, Liana Lankester⁸⁷², Nikitas Nikitakis⁸⁷², Colin Wells⁸⁷², Bethan Stowe⁸⁷², Kayleigh Spencer⁸⁷², Susanne Cathcart⁸⁷³, Katharine Duffy⁸⁷³, Alex Puxty⁸⁷³, Kathryn Puxty⁸⁷³, Lynne Turner⁸⁷³, Jane Ireland⁸⁷³, Gary Semple⁸⁷³, Peter Barry⁸⁷⁴, Paula Hillout⁸⁷³, Jayne Evitts⁸⁷⁵, Amanda Tyler⁸⁷⁵, Joanne Waldron⁸⁷⁵, Val Irvine⁸⁷⁶, Benjamin Shelley⁸⁷⁶, Olugbenga Akinkugbe⁸⁷⁷, Alasdair Bamford⁸⁷⁷, Emily Beech⁸⁷⁷, Holly Belfield⁸⁷⁷, Michael Bell⁸⁷⁷, Charlene Davies⁸⁷⁷, Gareth A. L. Jones⁸⁷⁷, Tara McHugh⁸⁷⁷, Hamza Meghari⁸⁷⁷, Gauran O'Neill⁸⁷⁷, Mark J. Peters⁸⁷⁷, Samiran Ray⁸⁷⁷, Ana Luisa Tomas⁸⁷⁷, Amy Easthope⁸⁷⁸, Claire Lorman⁸⁷⁸, Abhinav Gupta⁸⁷⁸, Elizabeth Timlick⁸⁷⁸, Rebecca Brady⁸⁷⁸, Stephen Bonner⁸⁷⁹, Keith Hugill⁸⁷⁹, Jessica Jones⁸⁷⁹, Steven Liggett⁸⁷⁹, Archana Bhashya⁸⁸⁰, Neil Davidson⁸⁸⁰, Paula Hutton⁸⁸⁰, Stuart McKechnie⁸⁸⁰, Jean Wilson⁸⁸⁰, Neil Flint⁸⁸¹, Patel Rekha⁸⁸¹, Dawn Hales⁸⁸¹, Carina Cruz⁸⁸², Natalie Pattison⁸⁸², Shameer Gopal⁸⁸³, Nichola Harris⁸⁸³, Victoria Lake⁸⁸³, Stella Metherell⁸⁸³, Elizabeth Radford⁸⁸³, Ian Clement⁸⁸⁴, Bijal Patel⁸⁸⁴, A. Gulati⁸⁸⁴, Carole Hayes⁸⁸⁴, K. Webster⁸⁸⁴, Anne Hudson⁸⁸⁴, Andrea Webster⁸⁸⁴, Elaine Stephenson⁸⁸⁴, Louise McCormack⁸⁸⁴, Victoria Slater⁸⁸⁴, Rachel Nixon⁸⁸⁴, Helen Hanson⁸⁸⁴, Maggie Fearby⁸⁸⁴, Sinead Kelly⁸⁸⁴, Victoria Bridgett⁸⁸⁴, Philip Robinson⁸⁸⁴, Christine Almaden-Boyle⁸⁸⁵, Pauline Austin⁸⁸⁵, Louise Cabrelli⁸⁸⁵, Stephen Cole⁸⁸⁵, Matt Casey⁸⁸⁵, Susan Chapman⁸⁸⁵, Stephen Cole⁸⁸⁵,

Clare Whyte⁸⁸⁵, Adam Brayne⁸⁸⁶, Emma Fisher⁸⁸⁶, Jane Hunt⁸⁸⁶, Peter Jackson⁸⁸⁶, Duncan Kaye⁸⁸⁶, Nicholas Love⁸⁸⁶, Juliet Parkin⁸⁸⁶, Victoria Tuckey⁸⁸⁶, Lynne van Koutrik⁸⁸⁶, Sasha Carter⁸⁸⁶, Benedict Andrew⁸⁸⁶, Louise Findlay⁸⁸⁶, Katie Adams⁸⁸⁶, Michelle Bruce⁸⁸⁷, Karen Connolly⁸⁸⁷, Tracy Duncan⁸⁸⁷, Helen T.-Michael⁸⁸⁷, Gabriella Lindergard⁸⁸⁷, Samuel Hey⁸⁸⁷, Claire Fox⁸⁸⁷, Jordan Alfonso⁸⁸⁷, Laura Jayne Durran⁸⁸⁷, Jacinta Guerin⁸⁸⁷, Bethan Blackledge⁸⁸⁷, Jade Harris⁸⁸⁷, Martin Hruska⁸⁸⁷, Ayaa Eltayeb⁸⁸⁷, Thomas Lamb⁸⁸⁷, Tracey Hodgkiss⁸⁸⁷, Lisa Cooper⁸⁸⁷, Joanne Rothwell⁸⁸⁷, Catherine Dennis⁸⁸⁸, Alastair McGregor⁸⁸⁸, Victoria Parris⁸⁸⁸, Sinduya Srikanth⁸⁸⁸, Anisha Sukha⁸⁸⁸, Kim Davies⁸⁸⁹, Linda O'Brien⁸⁸⁹, Zohra Omar⁸⁸⁹, Igor Otaha⁸⁸⁹, Emma Perkins⁸⁸⁹, Tracy Lewis⁸⁸⁹, Isobel Sutherland⁸⁸⁹, Hollie Brooke⁸⁹⁰, Sarah Buckley⁸⁹⁰, Jose Cebrían Suarez⁸⁹⁰, Ruth Charlesworth⁸⁹⁰, Karen Hansson⁸⁹⁰, John Norris⁸⁹⁰, Alice Peel⁸⁹⁰, Alastair Rose⁸⁹⁰, Rajdeep Sandhu⁸⁹⁰, Brendan Sloan⁸⁹⁰, Elizabeth Smithson⁸⁹⁰, Muthu Thirumarani⁸⁹⁰, Veronica Wagstaff⁸⁹⁰, Alexandra Metcalfe⁸⁹⁰, Julie Camsooksai⁸⁹¹, Charlotte Humphrey⁸⁹¹, Sarah Jenkins⁸⁹¹, Henrik Reschreiter⁸⁹¹, Beverley Wadams⁸⁹¹, Yasmin DeAth⁸⁹¹, Colene Adams⁸⁹², Anita Agasol⁸⁹², Tracie Arden⁸⁹³, Amy Bowes⁸⁹², Pauline Boyle⁸⁹², Mandy Beekes⁸⁹³, Heather Button⁸⁹³, Nigel Capps^{893,893}, Mandy Carnahan⁸⁹², Anne Carter⁸⁹², Danielle Childs⁸⁹², Denise Donaldson⁸⁹², Kelly Hard⁸⁹², Fran Hurford⁸⁹³, Yasmin Hussain⁸⁹², Ayesha Javid⁸⁹³, James Jones⁸⁹³, Sanal Jose⁸⁹³, Michael Leigh⁸⁹², Terry Martin⁸⁹³, Helen Millward⁸⁹³, Nichola Motherwell⁸⁹³, Rachel Rikunen⁸⁹², Jo Stickley⁸⁹², Julie Summers⁸⁹³, Louise Ting⁸⁹³, Helen Tivenan⁸⁹², Louise Tonks⁸⁹³, Rebecca Wilcox⁸⁹², Maria Bokhari⁸⁹⁹, Vanessa Linnett⁸⁹², Rachael Lucas⁸⁹⁹, Wendy McCormick⁸⁹⁹, Jenny Ritzena⁸⁹⁹, Amanda Sanderson⁸⁹⁹, Helen Wilf⁸⁹⁹, Nicola Baxter⁹⁰⁰, Steven Henderson⁹⁰⁰, Sophie Kennedy-Hay⁹⁰⁰, Christopher McParland⁹⁰⁰, Laura Rooney⁹⁰⁰, Malcolm Sim⁹⁰⁰, Gordan McCreath⁹⁰⁰, Mark Brunton⁹⁰¹, Jess Catterson⁹⁰¹, Holly Coles⁹⁰¹, Matthew Frise⁹⁰¹, Sabi Gungurung⁹⁰¹, Nicola Jacques⁹⁰¹, Liza Keating⁹⁰¹, Emma Tilney⁹⁰¹, Shauna Bartley⁹⁰¹, Parminder Bhuie⁹⁰¹, Charlotte Downes⁹⁰², Kathleen Holding⁹⁰², Katie Riches⁹⁰², Mary Hilton⁹⁰², Mel Hayman⁹⁰², Deepak Subramanian⁹⁰², Priya Daniel⁹⁰², Letizia Zitter⁹⁰³, Sarah Benton⁹⁰³, Suzie Marriott⁹⁰³, Linda Park⁹⁰³, Samantha Keenan⁹⁰³, Elizabeth Gordon⁹⁰³, Helen Quinn⁹⁰³, Kizzy Baines⁹⁰³, Gillian Andrew⁹⁰⁴, J. Kenneth Baillie⁹⁰⁴, Lucy Barclay⁹⁰⁴, Marie Callaghan⁹⁰⁴, Rachael Campbell⁹⁰⁴, Sarah Clark⁹⁰⁴, Dave Hopy⁹⁰⁴, Lucy Marshall⁹⁰⁴, Corrienne McCulloch⁹⁰⁴, Kate Briton⁹⁰⁴, Jo Singleton⁹⁰⁴, Sophie Birch⁹⁰⁴, Andrew Higham⁹⁰⁵, Kerry Simpson⁹⁰⁵, Jayne Craig⁹⁰⁵, Carrie Demetriou⁹⁰⁶, Charlotte Eckbad⁹⁰⁶, Sarah Hierons⁹⁰⁶, Lucy Howie⁹⁰⁶, Sarah Mitchell⁹⁰⁶, Lidia Ramos⁹⁰⁶, Alfredo Serrano-Ruiz⁹⁰⁶, Katie White⁹⁰⁶, Fiona Kelly⁹⁰⁶, Vishal Amin⁹⁰⁷, Elena Anastasescu⁹⁰⁷, Vikram Anumakonda⁹⁰⁷, Komala Karthik⁹⁰⁷, Rizwana Kausar⁹⁰⁷, Karen Reid⁹⁰⁷, Jacqueline Smith⁹⁰⁷, Janet Imeson-Wood⁹⁰⁷, Arianna Bellini⁹⁰⁸, Jade Bryant⁹⁰⁸, Anton Mayer⁹⁰⁸, Amy Pickard⁹⁰⁸, Nicholas Roe⁹⁰⁸, Jason Sowter⁹⁰⁸, Alex Howlett⁹⁰⁸, Kristine Criste⁹⁰⁹, Rebecca Cusack⁹⁰⁹, Kim Golder⁹⁰⁹, Hannah Golding⁹⁰⁹, Oliver Jones⁹⁰⁹, Samantha Leggett⁹⁰⁹, Michelle Male⁹⁰⁹, Martyna Marani⁹⁰⁹, Kirsty Prager⁹⁰⁹, Toran Williams⁹⁰⁹, Belinda Roberts⁹⁰⁹, Karen Salmon⁹⁰⁹, Prisca Gondro⁹¹⁰, B. Hadebe⁹¹⁰, Abdul Kayan⁹¹⁰, Bridgett Masunda⁹¹⁰, Ashar Ahmed⁹¹¹, Anna Morris⁹¹¹, Srinivas Jakkula⁹¹¹, Kate Long⁹¹², Simon Whiteley⁹¹², Elizabeth Wilby⁹¹², Bethan Ogg⁹¹², Sam Moulter⁹¹², M. Odam⁹¹², Jeremy Bewley⁹¹², Zoe Garland⁹¹³, Lisa Grimm⁹¹³, Bethany Gumbrell⁹¹³, Rebekah Johnson⁹¹³, Katie Sweet⁹¹³, Denise Webster⁹¹³, Georgia Efford⁹¹³, Sara Bennett⁹¹⁴, Emma Goodwin⁹¹⁴, Matthew Jackson⁹¹⁴, Alissa Kent⁹¹⁴, Clare Tibke⁹¹⁴, Wiesia Woodyatt⁹¹⁴, Ahmed Zaki⁹¹⁴, Amelia Daniel⁹¹⁵, Joanne Finn⁹¹⁵, Rajnish Saha⁹¹⁵, Nikki Staines⁹¹⁵, Amy Easthope⁹¹⁵, Pamela Bremmer⁵²⁸, J. Allan⁹¹⁶, T. Geary⁹¹⁶, Gordon Houston⁹¹⁶, A. Meikl⁹¹⁶, P. O'Brien⁹¹⁶, Dina Bell⁹¹⁷, Rosalind Boyle⁹¹⁷, Katie Douglas⁹¹⁷, Lynn Glass⁹¹⁷, Emma Lee⁹¹⁷, Liz Lennon⁹¹⁷, Austin Rattray⁹¹⁷, Rob Charnock⁹¹⁸, Denise McFarland⁹¹⁸, Denise Cosgrove⁹¹⁸, Ben Attwood⁹¹⁹, Penny Parsons⁹¹⁹, Siobhain Carmody⁹¹⁹, Metod Oblak⁹²⁰, Monica Popescu⁹²⁰, Mini Thankachen⁹²⁰, Rosie Baruah⁹²⁰, Sheila Morris⁹²⁰, Susie Ferguson⁹²⁰, Amy Shepherd⁹²⁰, Abdelhakim Altabaibeh⁹²², Ana Alvaro⁹²², Kayleigh Gilbert⁹²², Louise Ma⁹²², Loreta Mostoles⁹²², Chetan Parmar⁹²², Kathryn Simpson⁹²², Champa Jetha⁹²², Lauren Booker⁹²², Anezka Pratley⁹²², Tracey Cosier⁹²³, Gemma Millen⁹²³, Neil Richardson⁹²³, Natasha Schumacher⁹²³, Heather Weston⁹²³, James Rand⁹²³, Beatrice Ewe⁹²⁴, Benjamin Bach⁹²⁴, Wendy S. Barclay⁹³², Debby Bogaert⁷⁰⁵, Meera Chand⁹³³, Graham S. Cooke⁹³⁴, Annemarie B. Docherty⁷¹⁴, Jake Dunning⁹³⁵, Ana da Silva Filipe⁹³⁶, Tom Fletcher⁹³⁷, Christopher A. Green⁶³⁴, Ewen M. Harrison⁷¹⁴, Julian A. Hiscox⁹³⁸, Samreen Ijaz⁹⁴⁰, Saye Khoo⁹⁴¹, Paul Klenerman⁹⁴², Andrew Law⁶⁰, Wei Shen Lim⁹⁴⁴, Alexander J. Mentzer⁹⁴⁵, Laura Merson⁹⁴⁶, Alison M. Meynert⁶², Mahdad Noursadeghi⁹⁴⁷, Shona C. Moore⁹⁴⁸, Massimo Palmirani⁹³⁶, William A. Paxton⁹⁴⁸, Georgios Poulakis⁹⁴⁸, Nicholas Price⁹⁴⁹, Andrew Rambaut⁹⁵⁰, David L. Robertson⁹³⁶, Clark D. Russell⁷⁰⁵, Vanessa Sancho-Shimizu⁹⁵¹, Janet T. Scott⁹³⁶, Thushan de Silva⁹⁵², Louise Sigfrid⁹⁵⁶, Tom Solomon⁹⁵⁶, Shiranee Sriksandan⁹³⁴, David Stuart⁸⁵³, Richard S. Tedder⁹⁵⁵, Emma C. Thomson⁹⁵⁶, A. A. Roger Thompson⁹⁵⁶, Ryan S. Thwaites³⁰, Lance C. W. Turtle^{530,732}, Rishi K. Gupta⁹⁵⁷, Carlo Palmieri⁹⁵⁸, Olivia V. Swann⁹⁵⁹, Maria Zambon⁹³⁵, Marc-Emmanuel Dumas⁹⁶⁰, Julian L. Griffin⁹⁶⁰, Zoltan Takats⁹⁶⁰, Kanta Chechi⁹⁶¹, Petros Andrikopoulos⁹⁶⁰, Anthonia Osagie⁹⁶⁰, Michael Olanipekun⁹⁶⁰, Sonia Ligg⁹⁶⁰, Matthew R. Lewis⁹⁶², Gonçalo dos Santos Correia⁹⁶², Caroline J. Sands⁹⁶², Panteleimon Takis⁹⁶², Lynn Maslen⁹⁶², William Greenhalf⁹⁶³, Victoria Shaw⁹⁶⁴, Sarah E. McDonald⁹³⁶, Sean Keating⁹⁶⁵, Katie A. Ahmed⁹⁶⁶, Jane A. Armstrong⁹⁶⁶, Milton Asworth⁹⁶⁶, Innocent G. Asimwe⁹⁶⁶, Siddharth Bakshi⁹⁶⁶, Samantha L. Barlow⁹⁶⁶, Laura Booth⁹⁶⁶, Benjamin Brennan⁹⁶⁷, Katie Bullock⁹⁶⁶, Benjamin W. A. Catterall⁹⁶⁶, Jordan J. Clark⁹⁶⁶, Emily A. Clarke⁹⁶⁶, Louise Cooper⁹⁶⁶, Helen Cox⁹⁶⁶, Christopher Davis⁹⁶⁶, Oslem Dincarslan⁹⁶⁶, Chris Dunn⁹⁶⁶, Philip Dyer⁹⁶⁶, Angela Elliott⁹⁶⁶, Anthony Evans⁹⁶⁶, Lorna Finch⁹⁶⁶, Lewis W. S. Fisher⁹⁶⁶, Terry Foster⁹⁶⁶, Isabel Garcia-Dorival⁹⁶⁶, William Greenhalf⁹⁶⁶, Philip Gunnings⁹⁶⁶, Catherine Hartley⁹⁶⁶, Rebecca B. Jensen⁹⁶⁶, Christopher B. Jones⁹⁶⁶, Trevor R. Jones⁹⁶⁶, Shadia Khandaker⁹⁶⁶, Katharine King⁹⁶⁶, Robyn T. Kiy⁹⁶⁶, Chrysa Koukorava⁹⁶⁶, Annette Lake⁹⁶⁷, Suzanne Lant⁹⁶⁶, Diane Latwiec⁹⁶⁶, Lara Lavelle-Langham⁹⁶⁶, Daniela Letter⁹⁶⁷, Lauren Lett⁹⁶⁶, Lucia A. Livoti⁹⁶⁶, Maria Mancini⁹⁶⁶, Sarah McDonald⁹⁶⁶, Laurence McEvoy⁹⁶⁶, John McLauchlan⁹⁶⁷, Soeren Metelmann⁹⁶⁶, Nahida S. Miah⁹⁶⁶, Joanna Middleton⁹⁶⁶, Joyce Mitchell⁹⁶⁶, Shona C. Moore⁹⁶⁶, Ellen G. Murphy⁹⁶⁶, Rebekah Penrice-Randal⁹⁶⁶, Jack Pilgrim⁹⁶⁶, Tessa Prince⁹⁶⁶, Will Reynolds⁹⁶⁶, P. Matthew Ridley⁹⁶⁶, Debby Sales⁹⁶⁶, Victoria E. Shaw⁹⁶⁶, Rebecca K. Shears⁹⁶⁶, Benjamin Small⁹⁶⁶, Krishanthi S. Subramaniam⁹⁶⁶, Agnieska Szemie⁹⁶⁶, Aislynn Taggart⁹⁶⁷, Jolanta Taniais-Hughes⁹⁶⁶, Jordan Thomas⁹⁶⁶, Erwan Trochu⁹⁶⁶, Libby van Tonder⁹⁶⁶, Eve Wilcock⁹⁶⁶, J. Eunice Zhang⁹⁶⁶, Lisa Flaherty⁹⁶⁶, Nicole Maziere⁹⁶⁶, Emily Cass⁹⁶⁶, Alejandra Doce Carracedo⁹⁶⁶, Nicola Carlucci⁹⁶⁶, Anthony Holmes⁹⁶⁶, Hannah Massey⁹⁶⁶, Lee Murphy⁹⁵⁴, Nicola Wrobel⁹⁵⁴, Sarah McCafferty⁹⁵⁴, Kirstie Morrice⁹⁵⁴ & Alan MacLean⁹⁵⁴

Admin team members

Ruth Armstrong⁶⁰, J. Kenneth Baillie^{60,61,62}, Ceilia Boz⁶⁰, Adam Brown⁶⁰, Richard Clark^{96B}, Sara Clohisey⁶⁰, Audrey Coutts^{96B}, Louise Cullum⁶⁰, Nicky Day⁶⁰, Lorna Donnelly^{96B}, Esther Duncan⁶⁰, Angie Fawkes^{96B}, Paul Finerman⁶⁰, Max Head Fourman⁶⁰, James Furniss⁶⁰, Tammy Gilchrist^{96B}, Ailsa Golightly⁶⁰, Katarzyna Hafezi^{96B}, Ross Hendry⁶⁰, Andy Law⁶⁰, Dawn Law⁶⁰, Rachel Law⁶⁰, Sarah Law⁶⁰, Louise Macgillivray^{96B}, Alan Maclean^{96B}, Hanning Ma⁶⁰, Sarah McCafferty^{96B}, Ellie McMaster⁶⁰, Jen Meikle⁶⁰, Shona C. Moore⁷³², Kirstie Morrice^{96B}, Lee Murphy^{96B}, Wilna Oosthuizen⁶⁰, Nicholas Parkinson⁶⁰, Trevor Paterson⁶⁰, Andrew Stenhouse⁶⁰, Maaikie Swets^{60,970}, Helen Szoor-McElhinney⁶⁰, Filip Taneski⁶⁰, Lance C. W. Turtle^{530,732}, Tony Wackett⁶⁰, Mairi Ward⁶⁰, Jane Weaver⁶⁰, Nicola Wrobel^{96B}, Marie Zechner⁶⁰, Judy Coyle⁶⁰, Bernadette Gallagher⁶⁰, Rebecca Lidstone-Scott⁶⁰, Debbie Hamilton⁶⁰, Katherine Schon⁹⁷¹, Anita Furlong⁹⁷¹, Heather Biggs⁹⁷¹, Fiona Griffiths⁶⁰, Eleanor Andrews⁷⁶², Kathy Brickell⁵²⁷, Michelle Smyth⁵²⁷, Lorna Murphy⁵²⁷, Gail Carson⁹⁴⁶, Hayley Hardwick⁵³⁰ & Chloe Donohue⁷¹⁵

COVID-19 HGI corresponding authors

Benjamin M. Neale^{4,1280,625}, Mark Daly^{1,2,3,1280,625} & Andrea Ganna^{1,2,3,1280,625}

¹Institute for Molecular Medicine Finland (FIMM), University of Helsinki, Helsinki, Finland.

²Broad Institute of MIT and Harvard, Cambridge, MA, USA. ³Analytic and Translational Genetics Unit, Massachusetts General Hospital, Boston, MA, USA. ⁴Massachusetts General Hospital, Broad Institute of MIT and Harvard, Cambridge, MA, USA. ⁵Yale University, New Haven, CT, USA. ⁷Icahn School of Medicine at Mount Sinai, New York, NY, USA. ⁸Stroke Pharmacogenomics and Genetics, Biomedical Research Institute Sant Pau (IIB Sant Pau), Sant Pau Hospital, Immungen-CoV2, Barcelona, Spain. ⁹Institute of Virology, Technical University Munich and Helmholtz Zentrum München, Munich, Germany. ¹⁰Institute of Psychiatric Phenomics and Genomics, Medical Center of the University of Munich, Munich, Germany.

¹¹Department of Psychiatry, Medical Center of the University of Munich, Munich, Germany.

¹²IRCCS, Istituto Giannina Gaslini, Genova, Italy. ¹³Department of Neurosciences, Rehabilitation, Ophthalmology, Genetics, Maternal and Child Health, University of Genova, Genova, Italy. ¹⁴Queen Mary University of London, London, UK. ¹⁵Open Targets, Wellcome Genome Campus, Hinxton, UK. ¹⁶Department of Complex Trait Genetics, Center for Neurogenetics and Cognitive Research, Amsterdam Neuroscience, Vrije Universiteit Amsterdam, Amsterdam, The Netherlands. ¹⁷Lady Davis Institute, Jewish General Hospital, McGill University, Montreal, Quebec, Canada. ¹⁸Medical Research Institute, Kangbuk Samsung Hospital, Sungkyunkwan University School of Medicine, Suwon, Republic of Korea.

¹⁹Osaka University Graduate School of Medicine, Osaka, Japan. ²⁰Baylor College of Medicine, Houston, TX, USA. ²¹Mohammed Bin Rashid University of Medicine and Health Sciences, Dubai, United Arab Emirates. ²²MRC Integrative Epidemiology Unit (IEU), University of Bristol, Bristol, UK. ²³Department of Internal Medicine, Division of Cardiovascular Medicine, Michigan Medicine, Ann Arbor, MI, USA. ²⁴Department of Human Genetics, University of Michigan Medical School, Ann Arbor, MI, USA. ²⁵Department of Computational Medicine and Bioinformatics, University of Michigan Medical School, Ann Arbor, MI, USA. ²⁶Seaver Autism Center for Research and Treatment, Department of Psychiatry, Icahn School of Medicine at Mount Sinai, New York, NY, USA. ²⁹Program in Medical and Population Genetics, Broad Institute of MIT and Harvard, Cambridge, MA, USA. ³²David Geffen School of Medicine at UCLA, Los Angeles, CA, USA. ³³Institut Pasteur, Paris, France. ³⁴Harvard School of Public Health, Boston, MA, USA. ³⁵Institute for Molecular Bioscience, The University of Queensland, Brisbane, Queensland, Australia. ³⁸Wellcome Sanger Institute, Wellcome Genome Campus, Hinxton, UK. ⁴⁰European Molecular Biology Laboratory, European Bioinformatics Institute (EMBL-EBI), Wellcome Genome Campus, Hinxton, UK. ⁴²Centre for Bioinformatics and Data Analysis, Medical University of Białystok, Białystok, Poland. ⁴³Trieste University, Trieste, Italy.

⁴⁴Vanderbilt University Medical Center, Nashville, TN, USA. ⁴⁵University of California San Francisco, San Francisco, CA, USA. ⁴⁶Stanford University, Stanford, CA, USA. ⁴⁷University of Siena, Siena, Italy. ⁴⁹Boston Children's Hospital, Broad Institute of MIT and Harvard, Cambridge, MA, USA. ⁵⁰Blizard Institute, Queen Mary University of London, London, UK.

⁵¹Department of Genetics, University Medical Centre Groningen, Groningen, The Netherlands. ⁵²Department of Genetics, University Medical Centre Utrecht, Utrecht, The Netherlands.

⁵³Department of Epidemiology, Biostatistics and Occupational Health, McGill University, Montreal, Quebec, Canada. ⁵⁵Department of Twin Research, King's College London, London, UK. ⁵⁶Department of Human Genetics, McGill University, Montreal, Quebec, Canada.

⁵⁷Kyoto-McGill International Collaborative School in Genomic Medicine, Graduate School of Medicine, Kyoto University, Kyoto, Japan. ⁵⁹National Institutes of Health, Bethesda, MD, USA. ⁶⁰The Roslin Institute, University of Edinburgh, Edinburgh, UK. ⁶¹Intensive Care Unit, Royal Infirmary of Edinburgh, Edinburgh, UK. ⁶²MRC Human Genetics Unit, Institute of Genetics and Molecular Medicine, University of Edinburgh, Western General Hospital, Edinburgh, UK.

⁶³Molecular Genetics, University of Siena, Siena, Italy. ⁶⁴Genetica Medica, Azienda Ospedaliero-Universitaria Senese, Siena, Italy. ⁶⁵Med Biotech Hub and Competence Center, Department of Medical Biotechnologies, University of Siena, Siena, Italy. ⁶⁶Department of Electronics, Information and Bioengineering (DEIB), Politecnico di Milano, Milano, Italy.

⁶⁷Politecnico di Milano, Milan, Italy. ⁶⁸University of Michigan, Ann Arbor, MI, USA. ⁶⁹Vanderbilt School of Medicine, Nashville, TN, USA. ⁷⁰All India Institute of Medical Sciences Kalyani, Kalyani, India. ⁷¹Hasso Plattner Institute, New York, NY, USA. ⁷²Naina Tech, Hyderabad, India. ⁷³EMBL-European Bioinformatics Institute, Hinxton, UK. ⁷⁴University of Northampton, Northampton, UK. ⁷⁵University of Helsinki, Helsinki, Finland. ⁷⁶University of Miami, Miami, FL, USA. ⁷⁸Ecole Centrale de Nantes, Inserm, Centre de Recherche en Transplantation et Immunologie, Nantes University, UMR1064, ITUN, Nantes, France. ⁷⁹University of Liège, Liège, Belgium. ⁸⁰Qatar Genome Program, Qatar Foundation Research, Development and Innovation, Qatar Foundation, Doha, Qatar. ⁸²Medical and Population Genetics and Cardiovascular Disease Initiative, Broad Institute of Harvard and MIT, Cambridge, Cambridge, MA, USA. ⁸³Cardiovascular Research Center, Massachusetts General Hospital, Boston, MA, USA. ⁸⁴Intensive Care Unit, Vall d'Hebron Hospital, Barcelona, Spain. ⁸⁵Institut de Biomedicina de València - CSIC, València, Spain. ⁸⁶Centro de Investigación Biomédica en Red en Enfermedades Neurodegenerativas (CIBERNED), València, Spain. ⁸⁷Unidad Mixta de Neurología y Genética, Instituto de Investigación Sanitaria La Fe, València, Spain. ⁸⁸Erasmus Medical Center, Rotterdam, The Netherlands. ⁸⁹National Genome Center, Copenhagen,

Denmark. ⁹⁰University of Copenhagen, Copenhagen, Denmark. ⁹¹Genomics PLC, Oxford, UK.

⁹²Institute for Community Medicine, University Medicine Greifswald, Greifswald, Germany.

⁹⁴Department of Population Medicine and Lifestyle Diseases Prevention, Medical University of Białystok, Białystok, Poland. ⁹⁵Genomics England, London, UK. ⁹⁶Junta de Andalucía, Seville, Spain. ⁹⁷Human Genetics Program of ICBM and Department of Basic-Clinical Oncology, University of Chile, Santiago, Chile. ⁹⁸Center for the Development of Scientific Research (CEDIC), Asunción, Paraguay. ¹⁰⁰Translational Bioinformatics Unit, Navarrabiomed, Complejo Hospitalario de Navarra (CHN), Universidad Pública de Navarra (UPNA), IIdISA, Pamplona, Spain. ¹⁰¹Mucosal & Salivary Biology Division, King's College London Dental Institute, London, UK. ¹⁰²GENYO, Center for Genomics and Oncological Research Pfizer, University of Granada, Andalusian Regional Government, Granada, Spain. ¹⁰³University of Puerto Rico, San Juan, Puerto Rico. ¹⁰⁴National Laboratory of Genomics for Biodiversity (LANGEBIO), Advanced Genomics Unit, CINVESTAV, Irapuato, Mexico. ¹⁰⁵Queensland University of Technology, Brisbane, Queensland, Australia. ¹⁰⁶Clinical Research Unit of Nanoro, Institut de Recherche en Sciences de la Santé, CNRST, Ouagadougou, Burkina Faso. ¹⁰⁷McGill University, Montreal, Quebec, Canada. ¹⁰⁸Université de Montréal, Montreal, Quebec, Canada. ¹⁰⁹Fonds de la Recherche Scientifique (FNRS) & Centre de Génétique Humaine, Hôpital Erasme, Université Libre de Bruxelles, Brussels, Belgium. ¹¹²University of Pecs Medical School, Pécs, Hungary. ¹¹³Institute of Biomedicine and Cancer Research Laboratories, Western Cancer Centre FICAN West, University of Turku, Turku, Finland. ¹¹⁴Institute of Biomedical Technologies, National Research Council, Segrate, Italy. ¹¹⁵Immediata, Milan, Italy. ¹¹⁶University of Cambridge, Cambridge, UK. ¹¹⁷Genome Opinion, Seoul, Republic of Korea. ¹¹⁹University of Groningen, Groningen, The Netherlands. ¹²⁰Universiti Malaysia Pahang, Gambang, Malaysia. ¹²²Vrije Universiteit Amsterdam, Amsterdam, The Netherlands. ¹²³University Medical Centre Groningen, University of Groningen, Groningen, The Netherlands. ¹²⁴MNM DIAGNOSTICS, Poznań, Poland. ¹²⁵Institute for Systems Biology, Seattle, WA, USA. ¹²⁶Sultan Idris Education University, Tanjung Malim, Malaysia. ¹²⁷Hospital Kulim, Kedah, Malaysia. ¹²⁸AbbVie, Lake Buff, IL, USA. ¹²⁹Root Deep Insight, Boston MA, USA. ¹³⁰23andMe, Sunnyvale, CA, USA. ¹³¹GSK, Stevenage, UK. ¹³²Department of Pharmacology, Feinberg School of Medicine, Northwestern University, Chicago, IL, USA. ¹³³Department of Medicine, Northwestern University, Chicago, IL, USA. ¹³⁴Washington DC Veterans Affairs Medical Center, Hospital Medicine, Washington, DC, USA. ¹³⁵Department of Medicine, George Washington University, Washington, DC, USA.

¹³⁶Section of Hospital Medicine, Department of Medicine, University of Chicago, Chicago, IL, USA. ¹³⁷Section of Hematology and Oncology, Department of Medicine, University of Chicago, Chicago, IL, USA. ¹³⁸College of Pharmacy, University of Illinois at Chicago, Chicago, IL, USA.

¹⁴²Department of Pharmacology, George Washington University, Washington, DC, USA. ¹⁴⁸Department of Neurology, Amsterdam UMC, Amsterdam Neuroscience, Amsterdam, The Netherlands. ¹⁴⁹Department of Intensive Care, Amsterdam UMC, Amsterdam, The Netherlands. ¹⁵⁰Department of Infectious Diseases, Amsterdam UMC, Amsterdam, The Netherlands. ¹⁵¹Department of Clinical Epidemiology, Biostatistics and Bioinformatics, Amsterdam UMC, Amsterdam, The Netherlands. ¹⁵²Experimental Immunology, Amsterdam UMC, Amsterdam, The Netherlands. ¹⁵³Department of Pulmonology, Amsterdam UMC, Amsterdam, The Netherlands. ¹⁵⁴Department of Pathology, Amsterdam UMC, Amsterdam, The Netherlands. ¹⁵⁵Department of Anesthesiology, Amsterdam UMC, Amsterdam, The Netherlands. ¹⁵⁶Amsterdam UMC Biobank Core Facility, Amsterdam UMC, Amsterdam, The Netherlands. ¹⁵⁷Department of Radiology, Amsterdam UMC, Amsterdam, The Netherlands. ¹⁵⁸Department of Medical Microbiology, Amsterdam UMC, Amsterdam, The Netherlands. ¹⁵⁹Department of Clinical Chemistry, Amsterdam UMC, Amsterdam, The Netherlands.

¹⁶⁰Amsterdam UMC Biobank, Amsterdam UMC, Amsterdam, The Netherlands. ¹⁶¹Core Facility Genomics, Amsterdam UMC, Amsterdam, The Netherlands. ¹⁶²Ancestry, Lehi, UT, USA. ¹⁶³GIGA-Institute, University of Liège, Liège, Belgium. ¹⁶⁴CHC Mont-Légia, Liège, Belgium. ¹⁶⁵BHUL (Liège Biobank), CHU of Liège, Liège, Belgium. ¹⁶⁷Stanley Center for Psychiatric Research, Broad Institute of MIT and Harvard, Cambridge, MA, USA. ¹⁶⁸Centre de Génétique Humaine, Hôpital Erasme, Université Libre de Bruxelles, Brussels, Belgium. ¹⁶⁹Service de Médecine Interne, Hôpital Erasme, Université Libre de Bruxelles, Brussels, Belgium. ¹⁷⁰CHU of Liège, University of Liège, Liège, Belgium. ¹⁷⁴McGill Genome Centre, McGill University, Montréal, Québec, Canada. ¹⁷⁷Department of Emergency Medicine, McGill University, Montreal, Quebec, Canada. ¹⁷⁸Emergency Department, Jewish General Hospital, McGill University, Montreal, Quebec, Canada. ¹⁷⁹McGill AIDS Centre, Department of Microbiology and Immunology, Lady Davis Institute for Medical Research, Jewish General Hospital, McGill University, Montreal, Quebec, Canada. ¹⁸⁰McGill Centre for Viral Diseases, Department of Infectious Disease, Lady Davis Institute, Jewish General Hospital, Montreal, Quebec, Canada. ¹⁸¹Research Centre of the Centre Hospitalier de l'Université de Montréal, Montreal, Quebec, Canada. ¹⁸²Department of Medicine, Research Centre of the Centre Hospitalier de l'Université de Montréal, Montreal, Quebec, Canada. ¹⁸³Department of Medicine, Université de Montréal, Montreal, Quebec, Canada. ¹⁸⁴Department of Medicine and Human Genetics, McGill University, Montreal, Quebec, Canada. ¹⁸⁵Department of Intensive Care, Research Centre of the Centre Hospitalier de l'Université de Montréal, Montreal, Quebec, Canada. ¹⁸⁶Division of Infectious Diseases, Research Centre of the Centre Hospitalier de l'Université de Montréal, Montréal, Quebec, Canada. ¹⁸⁷Division of Genetic Medicine, Department of Medicine, Vanderbilt University Medical Center, Nashville, TN, USA. ¹⁸⁸Vanderbilt Genetics Institute, Vanderbilt University Medical Center, Nashville, TN, USA. ¹⁸⁹Institute of Human Genetics, University Hospital Bonn, Medical Faculty University of Bonn, Bonn, Germany. ¹⁹⁰Institute of Genomic Statistics and Bioinformatics, University Hospital Bonn, Medical Faculty University of Bonn, Bonn, Germany. ¹⁹¹Department of Gastroenterology, Hepatology and Infectious Diseases, University Hospital Düsseldorf, Medical Faculty Heinrich Heine University, Düsseldorf, Germany. ¹⁹²Institute of Human Genetics, Medical Faculty, RWTH Aachen University, Aachen, Germany. ¹⁹³Clinic for Cardiology, Angiology and Internal Intensive Medicine, Medical Clinic I, RWTH Aachen University, Aachen, Germany. ¹⁹⁴Department of Pneumology and Intensive Care Medicine, Faculty of Medicine, RWTH Aachen University, Aachen, Germany. ¹⁹⁵Department of Pneumology, Hannover Medical School, Hannover, Germany. ¹⁹⁶Department of Gastroenterology, Hepatology and Endocrinology, Hannover Medical School, Hannover, Germany. ¹⁹⁷Hannover Unified Biobank, Hannover Medical School, Hannover, Germany. ¹⁹⁸Department I of Internal Medicine, Faculty of Medicine and University Hospital of Cologne, University of Cologne, Cologne, Germany. ¹⁹⁹Center for Molecular Medicine Cologne (CMCC), University of Cologne, Cologne, Germany. ²⁰⁰German Center for Infection Research (DZIF), Partner Site Bonn-Cologne, Cologne, Germany. ²⁰²Cologne Center

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for Genomics (CCG), University of Cologne, Cologne, Germany.²⁰³Department of Anesthesiology and Intensive Care Medicine, University Hospital Essen, University Duisburg-Essen, Essen, Germany.²⁰⁴Department of Child and Adolescent Psychiatry, University Hospital Essen, University of Duisburg-Essen, Essen, Germany.²⁰⁵Department of Infectious Diseases, University Hospital Essen, University Duisburg-Essen, Essen, Germany.²⁰⁶Department of Pneumology, Allergology and Respiratory Medicine, University Hospital Saarland, Homburg/Saar, Germany.²⁰⁷Center of Human and Molecular Biology, Department of Human Genetics, University Hospital Saarland, Homburg/Saar, Germany.²⁰⁸Department of Genetics & Epigenetics, Saarland University, Saarbrücken, Germany.²⁰⁹Eurac Research, Institute for Biomedicine (affiliated to the University of Lübeck), Bolzano, Italy.²¹⁰University of Colorado Anschutz Medical Campus, Aurora, CO, USA.²¹¹Department of Genetics and Development, Institute for Genomic Medicine, Columbia University, New York, NY, USA.²¹²Department of Medicine, Institute for Genomic Medicine, Columbia University, New York, NY, USA.²¹³Department of Biomedical Informatics, Columbia University, New York, NY, USA.²¹⁴Department of Pediatrics, Columbia University, New York, NY, USA.²¹⁵Department of Medicine, Columbia University, New York, NY, USA.²¹⁶Institute for Genomic Medicine, Columbia University, New York, NY, USA.²¹⁷Department of Biostatistics, Mailman School of Public Health, Columbia University, New York, NY, USA.²¹⁸Department of Pathology and Cell Biology, Columbia University, New York, NY, USA.²¹⁹Medical Research Institute, Kangbuk Samsung Hospital, Sungkyunkwan University School of Medicine, Seoul, Republic of Korea.²²⁰Department of Clinical Research Design and Evaluation, SAHST, Sungkyunkwan University, Seoul, Republic of Korea.²²¹Division of Gastroenterology, Department of Medicine, Kangbuk Samsung Hospital, Sungkyunkwan University, School of Medicine, Seoul, Republic of Korea.²²²Department of Biochemistry, College of Medicine, Ewha Womans University, Seoul, Republic of Korea.²²³Department of Internal Medicine, Seoul National University Hospital, Seoul National University College of Medicine, Seoul, Republic of Korea.²²⁴Department of Periodontology, Section of Dentistry, Seoul National University Bundang Hospital, Seongnam, Republic of Korea.²²⁵Department of Internal Medicine, Seoul National University Bundang Hospital, Seoul National University College of Medicine, Seongnam, Republic of Korea.²²⁶Department of Physical & Rehabilitation Medicine, Kangbuk Samsung Hospital, Sungkyunkwan University School of Medicine, Seoul, Republic of Korea.²²⁷Department of Clinical Research Design & Evaluation, SAHST, Sungkyunkwan University, Seoul, Republic of Korea.²²⁸Biomedical Institute for Convergence at SKKU, Sungkyunkwan University School of Medicine, Suwon, Republic of Korea.²²⁹Department of Public Health Service, Seoul National University Bundang Hospital, Seongnam, Republic of Korea.²³⁰Department of Rehabilitation Medicine, Seoul National University College of Medicine, Seoul, Republic of Korea.²³¹Korea Research Environment Open NETwork, Korea Institute of Science and Technology Information, Daejeon, Republic of Korea.²³²Global Science Experimental Data Hub Center, Korea Institute of Science and Technology Information, Daejeon, Republic of Korea.²³³Division of Infectious Diseases, Department of Medicine, Kangbuk Samsung Hospital, Sungkyunkwan University School of Medicine, Seoul, Republic of Korea.²³⁴Center for Cohort Studies, Kangbuk Samsung Hospital, Sungkyunkwan University School of Medicine, Seoul, Republic of Korea.²³⁵Department of Occupational and Environmental Medicine, Sungkyunkwan University School of Medicine, Seoul, Republic of Korea.²³⁶Department of Laboratory Medicine, Seoul National University Bundang Hospital, Seoul National University College of Medicine, Seongnam, Republic of Korea.²³⁷Institute of Clinical Molecular Biology, Christian-Albrechts-University, Kiel, Germany.²³⁸Novo Nordisk Foundation Center for Protein Research, Disease Systems Biology, Faculty of Health and Medical Sciences, University of Copenhagen, Copenhagen, Denmark.²³⁹Institut de Biociències i de Biomedicina, Universitat Autònoma de Barcelona, Barcelona, Spain.²⁴⁰ICREA, Barcelona, Spain.²⁴¹Research Group for Evolutionary Immunogenomics, Max Planck Institute for Evolutionary Biology, Plön, Germany.²⁴²Research Unit for Evolutionary Immunogenomics, Department of Biology, University of Hamburg, Hamburg, Germany.²⁴³Department of Gastroenterology, Hospital Universitario Ramón y Cajal, University of Alcalá, Instituto Ramón y Cajal de Investigación Sanitaria (IRYCIS), Madrid, Spain.²⁴⁴Centro de Investigación Biomédica en Red en Enfermedades Hepáticas y Digestivas (CIBEREHD), Instituto de Salud Carlos III (ISCIII), Madrid, Spain.²⁴⁵Vall d'Hebron Institut de Recerca (VHIR), Vall d'Hebron Hospital Universitari, Barcelona, Spain.²⁴⁶Charité Universitätsmedizin Berlin, Berlin, Germany.²⁴⁷Hospital Universitario Clínico San Cecilio, Granada, Spain.²⁴⁸Instituto de Investigación Ibs.Granada, Granada, Spain.²⁴⁹Emergency Department, University Hospital Regensburg, Regensburg, Germany.²⁵⁰Department for Infectious Diseases and Infection Control, University Hospital Regensburg, Regensburg, Germany.²⁵¹Medical University of Innsbruck, Department of Medicine and Christian Doppler Laboratory on Iron and Phosphate Biology, Innsbruck, Austria.²⁵²Institute of Clinical Medicine, University of Oslo, Oslo, Norway.²⁵³Department of Microbiology, Oslo University Hospital, Oslo, Norway.²⁵⁴Hospital Clinic, University of Barcelona and IDIBAPS, Barcelona, Spain.²⁵⁵European Foundation for the Study of Chronic Liver Failure (EF-CLIF), Barcelona, Spain.²⁵⁶Cologne Excellence Cluster on Cellular Stress Responses in Aging-Associated Diseases (CECAD), University of Cologne, Cologne, Germany.²⁵⁷Center for Molecular Medicine Cologne (CMCC), University of Cologne, Cologne, Germany.²⁵⁸Genomes for Life-GCAT lab Germans Trias i Pujol Research Institute (IGTP), Badalona, Spain.²⁵⁹IRCCS Humanitas Research Hospital, Milan, Italy.²⁶⁰Department of Biomedical Sciences, Humanitas University, Pieve Emanuele, Milan, Italy.²⁶¹Institute of Transfusionsmedicine, University Hospital Schleswig-Holstein (UKSH), Kiel, Germany.²⁶²Klinik für Innere Medizin I, Universitätsklinikum Schleswig-Holstein, Kiel Campus, Kiel, Germany.²⁶³Zentrum für Humangenetik Regensburg, Regensburg, Germany.²⁶⁴University Hospital Schleswig-Holstein (UKSH), Kiel Campus, Kiel, Germany.²⁶⁵Section for Gastroenterology, Department of Transplantation Medicine, Division for Cancer Medicine, Surgery and Transplantation, Oslo University Hospital Rikshospitalet, Oslo, Norway.²⁶⁶Research Institute for Internal Medicine, Division of Surgery, Inflammatory Diseases and Transplantation, Oslo University Hospital Rikshospitalet and University of Oslo, Oslo, Norway.²⁶⁷Norwegian PSC Research Center, Department of Transplantation Medicine, Division of Surgery, Inflammatory Diseases and Transplantation, Oslo University Hospital Rikshospitalet, Oslo, Norway.²⁶⁸Division of Rheumatology, Inflammation and Immunity, Brigham and Women's Hospital and Harvard Medical School, Boston, MA, USA.²⁶⁹Division of Genetics, Department of Medicine, Brigham and Women's Hospital, Boston, MA, USA.²⁷⁰Department of Biomedical Informatics, Harvard Medical School, Boston, MA, USA.²⁷¹Center for Data Sciences, Brigham and Women's Hospital, Boston, MA, USA.²⁷²Randaberg Municipality, Randaberg, Norway.²⁷³Department of

Quality and Health Technology, Faculty of Health Sciences, University of Stavanger, Stavanger, Norway.²⁷⁴Department of Genetics and Bioinformatics (HDGB), Division of Health Data and Digitalization, Norwegian Institute of Public Health, Oslo, Norway.²⁷⁵Centre for Genetics and Genomics Versus Arthritis, Centre for Musculoskeletal Research, Manchester Academic Health Science Centre, The University of Manchester, Manchester, UK.²⁷⁶Department of Intensive Care, Hospital Universitario Ramón y Cajal, Instituto Ramón y Cajal de Investigación Sanitaria (IRYCIS), University of Alcalá, Madrid, Spain.²⁷⁷Osakidetza Basque Health Service, Donostialdea Integrated Health Organisation, Clinical Biochemistry Department, San Sebastian, Spain.²⁷⁸Research Center and Memory Clinic, Fundació ACE, Institut Català de Neurociències Aplicades, Universitat Internacional de Catalunya, Barcelona, Spain.²⁷⁹Networking Research Center on Neurodegenerative Diseases (CIBERNED), Instituto de Salud Carlos III, Madrid, Spain.²⁸⁰Department of Acute Medicine, Oslo University Hospital, Oslo, Norway.²⁸¹Fondazione IRCCS Ca' Granda Ospedale Maggiore Policlinico, Milan, Italy.²⁸²European Reference Network on Hepatological Diseases (ERN RARE LIVER), San Gerardo Hospital, Monza, Italy.²⁸³Division of Gastroenterology, Center for Autoimmune Liver Diseases, Department of Medicine and Surgery, University of Milan Bicocca, Milan, Italy.²⁸⁴German Center for Neurodegenerative Diseases (DZNE Bonn), Bonn, Germany.²⁸⁵Division of Neurogenetics and Molecular Psychiatry, Department of Psychiatry and Psychotherapy, Medical Faculty, University of Cologne, Cologne, Germany.²⁸⁶Department of Psychiatry, Glenn Biggs Institute for Alzheimer's and Neurodegenerative Diseases, San Antonio, TX, USA.²⁸⁷Department of Neurodegenerative Diseases and Geriatric Psychiatry, University Hospital Bonn, Bonn, Germany.²⁸⁸Liver Unit, Department of Internal Medicine, Hospital Universitari Vall d'Hebron, Vall d'Hebron Barcelona Hospital Campus, Barcelona, Spain.²⁸⁹Department of Anesthesiology and Intensive Care, University Hospital of North Norway, Tromsø, Norway.²⁹⁰Klinik für Innere Medizin I, Universitätsklinikum Schleswig-Holstein, Kiel Campus, Kiel, Germany.²⁹¹Gastroenterology Unit, Fondazione IRCCS Casa Sollievo della Sofferenza, San Giovanni Rotondo, Italy.²⁹²Department of Infectious Diseases, Oslo University Hospital, Oslo, Norway.²⁹³Microbiology Department, Hospital Universitari Vall d'Hebron, Barcelona, Spain.²⁹⁴Universitat Autònoma de Barcelona, Bellaterra, Spain.²⁹⁵Department of Respiratory Diseases, Hospital Universitario Ramón y Cajal, Instituto Ramón y Cajal de Investigación Sanitaria (IRYCIS), Madrid, Spain.²⁹⁶Department of Respiratory Medicine and Allergology, University Hospital, Goethe University, Frankfurt am Main, Germany.²⁹⁷Department of Infectious Diseases, Hospital Universitario Ramón y Cajal, Instituto Ramón y Cajal de Investigación Sanitaria (IRYCIS), University of Alcalá, Madrid, Spain.²⁹⁸Department of Internal Medicine II, Technical University of Munich, School of Medicine, University Hospital rechts der Isar, Munich, Germany.²⁹⁹Division of Clinical Infectious Diseases, Research Center Borstel, Borstel, Germany.³⁰⁰German Center for Infection Research (DZIF) Clinical Tuberculosis Unit, Borstel, Germany.³⁰¹Respiratory Medicine & International Health, University of Lübeck, Lübeck, Germany.³⁰²Osakidetza Basque Health Service, Basurto University Hospital, Respiratory Service, Bilbao, Spain.³⁰³Department of Clinical and Molecular Medicine, Faculty of Medicine and Health Science, Norwegian University of Science and Technology, Trondheim, Norway.³⁰⁴Clinic Ålesund Hospital, Department of Medicine, Møre & Romsdal Hospital Trust, Ålesund, Norway.³⁰⁵Department of Anesthesiology, Hospital Universitario Ramón y Cajal, Instituto Ramón y Cajal de Investigación Sanitaria (IRYCIS), University of Alcalá, Madrid, Spain.³⁰⁶Spain Hospital Clinic, University of Barcelona and IDIBAPS, Barcelona, Spain.³⁰⁷Osakidetza Basque Health Service, Galdakao Hospital, Respiratory Service, Galdakao, Spain.³⁰⁸BMDR - E.Ospedale Galliera, Genova, Italy.³⁰⁹Liver ICU, Hospital Clinic Barcelona, Barcelona, Spain.³¹⁰Biocruces Bizkaia Health Research Institute, Barakaldo, Spain.³¹¹Histocompatibilidad y Biología Molecular, Centro de Transfusión de Madrid, Madrid, Spain.³¹²University of Milan, Milan, Italy.³¹³Fondazione Grigioni per il Morbo di Parkinson, Milan, Italy.³¹⁴Department of Anesthesiology, Intensive Care Medicine and Pain Therapy, University Hospital Frankfurt, Frankfurt am Main, Germany.³¹⁵German Center for Infection Research (DZIF), Medical Faculty and University Hospital Cologne, University of Cologne, Partner Site Bonn-Cologne, Cologne, Germany.³¹⁶Ikerbasque, Basque Foundation for Science, Bilbao, Spain.³¹⁷Department of Liver and Gastrointestinal Diseases, Biodonostia Health Research Institute, Donostia University Hospital, University of the Basque Country (UPV/EHU), San Sebastian, Spain.³¹⁸Infectious Diseases Service, Osakidetza, Biocruces Bizkaia Health Research Institute, Barakaldo, Spain.³¹⁹Medical Department, Drammen Hospital, Vestre Viken Hospital Trust, Drammen, Norway.³²⁰Research Center Borstel, BioMaterialBank Nord, Borstel, Germany.³²¹German Center for Lung Research (DZL), Airway Research Center North (ARCN), Giessen, Germany.³²²Popgen 2.0 Network (P2N), Kiel, Germany.³²³Department of Liver and Gastrointestinal Diseases, Biodonostia Health Research Institute, Donostia University Hospital, University of the Basque Country (UPV/EHU), CIBERehd, San Sebastian, Spain.³²⁴Department of Infectious Diseases, Oslo University Hospital, Oslo, Norway.³²⁵Department of Clinical Science, University of Bergen, Bergen, Norway.³²⁶Biodonostia Health Research Institute, Donostia University Hospital, San Sebastian, Spain.³²⁷Germans Trias i Pujol Research Institute (IGTP), Badalona, Spain.³²⁸ISGlobal, Barcelona, Spain.³²⁹CIBER Epidemiología y Salud Pública (CIBERESP), Madrid, Spain.³³⁰Universitat Pompeu Fabra (UPF), Barcelona, Spain.³³¹Hospital del Mar Medical Research Institute (IMIM), Barcelona, Spain.³³²Osakidetza Basque Health Service, Donostialdea Integrated Health Organization, San Sebastian, Spain.³³³Department of Internal Medicine, Infectious Diseases, University Hospital Frankfurt and Goethe University Frankfurt, Frankfurt am Main, Germany.³³⁴Humanitas Gavazzeni-Castelli, Bergamo, Italy.³³⁵School of Biological Sciences, Monash University, Clayton, Victoria, Australia.³³⁶Munich Clinic Schwabing, Academic Teaching Hospital, Ludwig-Maximilians-University (LMU), Munich, Germany.³³⁷Department of Anesthesiology, Hospital Universitario Ramón y Cajal, Instituto Ramón y Cajal de Investigación Sanitaria (IRYCIS), Madrid, Spain.³³⁸Clinical Trials Centre Cologne, ZKS Köln, Cologne, Germany.³³⁹Institute of Human Genetics, University of Bonn School of Medicine, University Hospital Bonn, Bonn, Germany.³⁴⁰Institute of Clinical Molecular Biology, Christian-Albrechts-University of Kiel, Kiel, Germany.³⁴¹UKSH Schleswig-Holstein, Kiel, Germany.³⁴²Institute of Immunology, Christian-Albrechts-University of Kiel, Kiel, Germany.³⁴³Institute of Medical Virology, University Hospital Frankfurt, Goethe University, Frankfurt am Main, Germany.³⁴⁴German Centre for Infection Research (DZIF), External Partner Site Frankfurt, Frankfurt am Main, Germany.³⁴⁵Department of Neurology, Bezirksklinikum Regensburg, University of Regensburg, Regensburg, Germany.³⁴⁶Charité Universitätsmedizin Berlin, Berlin Institute of Health, Berlin, Germany.³⁴⁷German Center for Infection Research (DZIF), Partner Site Munich, Munich, Germany.³⁴⁸Department of Infectious Diseases,

University Hospital of North Norway, Tromsø, Norway.³⁶²Faculty of Health Sciences, UiT The Arctic University of Norway, Tromsø, Norway.³⁶³Catalan Institute of Oncology (ICO), Barcelona, Spain.³⁶⁴Bellvitge Biomedical Research Institute (IDIBELL), Barcelona, Spain.³⁶⁵Universitat de Barcelona (UB), Barcelona, Spain.³⁶⁶deCODE genetics, Reykjavik, Iceland.³⁶⁸Mucosal Immunology Lab, Unidad de Excelencia Instituto de Biomedicina y Genética Molecular de Valladolid (IBGM), Universidad de Valladolid-CSIC, Valladolid, Spain.³⁶⁹Centro de Investigaciones Biomédicas en Red de Enfermedades Hepáticas y Digestivas (CIBERehd), Madrid, Spain.³⁷⁰Valladolid University Hospital, Valladolid, Spain.³⁷¹Estonian Genome Centre, Institute of Genomics, University of Tartu, Tartu, Estonia.³⁷²SYNLAB Estonia, University of Tartu, Tartu, Estonia.³⁷³University of Tartu, Tartu, Estonia.³⁷⁴Kuressaare Hospital, Kuressaare, Estonia.³⁷⁵Institute of Biomedicine and Translational Medicine, University of Tartu, Tartu, Estonia.³⁷⁷West Tallinn Central Hospital, Tallinn, Estonia.³⁷⁸University of Tartu, Tartu University Hospital, Tartu, Estonia.³⁷⁹Estonian Health Insurance Fund, Tallinn, Estonia.³⁸⁰Tartu University Hospital, Tartu, Estonia.³⁸¹FinnGen, Helsinki, Finland.³⁸²Finnish Institute for Health and Welfare (THL), Helsinki, Finland.³⁸³University of Helsinki, Faculty of Medicine, Clinical and Molecular Metabolism Research Program, Helsinki, Finland.³⁸⁴Institute of Molecular and Clinical Ophthalmology Basel (IOB), Basel, Switzerland.³⁸⁵Department of Ophthalmology, University of Basel, Basel, Switzerland.³⁸⁶Infectious Diseases Service, Department of Medicine, University Hospital and University of Lausanne, Lausanne, Switzerland.³⁸⁸Centre for Primary Care and Public Health, University of Lausanne, Lausanne, Switzerland.³⁸⁹Division of Infectious Diseases and Hospital Epidemiology, Cantonal Hospital St Gallen, St Gallen, Switzerland.³⁹⁰Division of Intensive Care, Geneva University Hospitals and the University of Geneva Faculty of Medicine, Geneva, Switzerland.³⁹¹Infectious Disease Service, Department of Internal Medicine, Geneva University Hospital, Geneva, Switzerland.³⁹²Clinique de Médecine et spécialités, Infectiologie, HFR-Fribourg, Fribourg, Switzerland.³⁹³Infectious Diseases Division, University Hospital Centre of the Canton of Vaud, Hospital of Valais, Sion, Switzerland.³⁹⁴Functional Host Genomics of Infectious Diseases, University Hospital and University of Lausanne, Lausanne, Switzerland.³⁹⁵Registry COVID, University Hospital and University of Lausanne, Lausanne, Switzerland.³⁹⁶Pneumonia Prediction using Lung Ultrasound, University Hospital and University of Lausanne, Lausanne, Switzerland.³⁹⁷Center for Primary Care and Public Health (Unisanté), University of Lausanne, Lausanne, Switzerland.³⁹⁸COVID-19 Risk Prediction in Swiss ICUs-Trial, Division of Infectious Diseases and Hospital Epidemiology, Cantonal Hospital St Gallen, St Gallen, Switzerland.³⁹⁹GCAT-Genomes for Life, Germans Trias i Pujol Health Sciences Research Institute (IGTP), Badalona, Spain.⁴⁰⁰Catalan Institute of Oncology, Bellvitge Biomedical Research Institute, Consortium for Biomedical Research in Epidemiology and Public Health, University of Barcelona, Barcelona, Spain.⁴⁰¹Barcelona Supercomputing Center, Centro Nacional de Supercomputación (BSC-CNS), Life & Medical Sciences, Barcelona, Spain.⁴⁰⁴University of Siena, DIISM-SAILAB, Siena, Italy.⁴⁰⁵Université Côte d'Azur, Inria, CNRS, I3S, Maasai, Nice, France.⁴⁰⁶Division of Infectious Diseases and Immunology, Department of Medical Sciences and Infectious Diseases, Fondazione IRCCS Policlinico San Matteo, Pavia, Italy.⁴⁰⁹Department of Internal Medicine and Therapeutics, University of Pavia, Pavia, Italy.⁴¹⁰Department of Infectious and Tropical Diseases, University of Brescia and ASST Spedali Civili Hospital, Brescia, Italy.⁴¹¹Chirurgia Vascolare, Ospedale Maggiore di Crema, Crema, Italy.⁴¹²III Infectious Diseases Unit, ASST-FBF-Sacco, Milan, Italy.⁴¹³Department of Biomedical and Clinical Sciences Luigi Sacco, University of Milan, Milan, Italy.⁴¹⁴Department of Specialized and Internal Medicine, Tropical and Infectious Diseases Unit, Azienda Ospedaliera Universitaria Senese, Siena, Italy.⁴¹⁵Unit of Respiratory Diseases and Lung Transplantation, Department of Internal and Specialist Medicine, University of Siena, Siena, Italy.⁴¹⁶Department of Emergency and Urgency, Medicine, Surgery and Neurosciences, Unit of Intensive Care Medicine, Siena University Hospital, Siena, Italy.⁴¹⁷Department of Medical, Surgical and Neurosciences and Radiological Sciences, Unit of Diagnostic Imaging, University of Siena, Siena, Italy.⁴¹⁸Rheumatology Unit, Department of Medicine, Surgery and Neurosciences, University of Siena, Policlinico Le Scotte, Siena, Italy.⁴¹⁹Department of Specialized and Internal Medicine, Infectious Diseases Unit, San Donato Hospital Arezzo, Arezzo, Italy.⁴²⁰Department of Emergency, Anesthesia Unit, San Donato Hospital, Arezzo, Italy.⁴²¹Department of Specialized and Internal Medicine, Pneumology Unit and UTIP, San Donato Hospital, Arezzo, Italy.⁴²²Department of Emergency, Anesthesia Unit, Misericordia Hospital, Grosseto, Italy.⁴²³Department of Specialized and Internal Medicine, Infectious Diseases Unit, Misericordia Hospital, Grosseto, Italy.⁴²⁴Department of Preventive Medicine, Azienda USL Toscana Sud Est, Arezzo, Italy.⁴²⁵Clinical Chemical Analysis Laboratory, Misericordia Hospital, Grosseto, Italy.⁴²⁶Territorial Scientific Technician Department, Azienda USL Toscana Sud Est, Arezzo, Italy.⁴²⁷Clinical Chemical Analysis Laboratory, San Donato Hospital, Arezzo, Italy.⁴²⁸Department of Health Sciences, Clinic of Infectious Diseases, ASST Santi Paolo e Carlo, University of Milan, Milan, Italy.⁴²⁹Department of Anesthesia and Intensive Care, University of Modena and Reggio Emilia, Modena, Italy.⁴³⁰HIV/AIDS Department, National Institute for Infectious Diseases, IRCCS, Lazzaro Spallanzani, Rome, Italy.⁴³¹Infectious Diseases Clinic, Department of Medicine, Azienda Ospedaliera di Perugia, Perugia, Italy.⁴³²Infectious Diseases Clinic, Santa Maria Hospital, University of Perugia, Perugia, Italy.⁴³³Department of Infectious Diseases, Treviso Hospital, Treviso, Italy.⁴³⁴Clinical Infectious Diseases, Mestre Hospital, Venezia, Italy.⁴³⁵Infectious Diseases Clinic, ULSS1, Belluno, Italy.⁴³⁶Medical Genetics and Laboratory of Medical Genetics Unit, A.O.R.N. "Antonio Cardarelli", Naples, Italy.⁴³⁷Department of Molecular Medicine and Medical Biotechnology, University of Naples Federico II, Naples, Italy.⁴³⁸CEINGE Biotechnology Avanzate, Naples, Italy.⁴³⁹IRCCS SDN, Naples, Italy.⁴⁴⁰Unit of Respiratory Physiopathology, AORN dei Colli, Monaldi Hospital, Naples, Italy.⁴⁴¹Division of Medical Genetics, Fondazione IRCCS Casa Sollievo della Sofferenza Hospital, San Giovanni Rotondo, Italy.⁴⁴²Department of Medical Sciences, Fondazione IRCCS Casa Sollievo della Sofferenza Hospital, San Giovanni Rotondo, Italy.⁴⁴³Infectious Diseases Clinic, Policlinico San Martino Hospital, IRCCS for Cancer Research, Genova, Italy.⁴⁴⁴Microbiology, Fondazione Policlinico Universitario Agostino Gemelli IRCCS, Catholic University of Medicine, Rome, Italy.⁴⁴⁵Department of Laboratory Sciences and Infectious Diseases, Fondazione Policlinico Universitario A Gemelli IRCCS, Rome, Italy.⁴⁴⁶Department of Cardiovascular Diseases, University of Siena, Siena, Italy.⁴⁴⁷Otolaryngology Unit, University of Siena, Siena, Italy.⁴⁴⁸Department of Internal Medicine, ASST Valtellina e Alto Lario, Sondrio, Italy.⁴⁴⁹First Aid Department, Luigi Curto Hospital, Polla, Italy.⁴⁵⁰U.O.C. Laboratorio di Genetica Umana, Genova, Italy.⁴⁵¹Infectious Diseases Clinics, University of Modena and Reggio Emilia, Modena, Italy.⁴⁵²Department of Respiratory Diseases, Azienda Ospedaliera di Cremona, Cremona, Italy.⁴⁵³U.O.C. Medicina, ASST Nord Milano, Ospedale Bassini, Milan, Italy.⁴⁵⁴Department of Cardiovascular, Neural and Metabolic Sciences, Istituto Auxologico Italiano, IRCCS, San Luca Hospital, Milan, Italy.⁴⁵⁵Department of Medicine and Surgery, University of Milano-Bicocca, Milan, Italy.⁴⁵⁶Center for Cardiac Arrhythmias of Genetic Origin, Istituto Auxologico Italiano, IRCCS, Milan, Italy.⁴⁵⁷Laboratory of Cardiovascular Genetics, Istituto Auxologico Italiano, IRCCS, Milan, Italy.⁴⁵⁸Unit of Infectious Diseases, ASST Papa Giovanni XXIII Hospital, Bergamo, Italy.⁴⁵⁹Department of Cardiology, Institute of Montescano, Istituti Clinici Scientifici Maugeri, IRCCS, Pavia, Italy.⁴⁶⁰Department of Cardiac Rehabilitation, Institute of Tradate (VA), Istituti Clinici Scientifici Maugeri, IRCCS, Pavia, Italy.⁴⁶¹Cardiac Rehabilitation Unit, Fondazione Salvatore Maugeri, IRCCS, Scientific Institute of Milan, Milan, Italy.⁴⁶²IRCCS C Mondino Foundation, Pavia, Italy.⁴⁶³Medical Genetics Unit, Meyer Children's University Hospital, Florence, Italy.⁴⁶⁴Department of Medicine, Pneumology Unit, Misericordia Hospital, Grosseto, Italy.⁴⁶⁵Department of Preventive Medicine, Azienda USL Toscana Sud Est, Arezzo, Italy.⁴⁶⁶Department of Anesthesia and Intensive Care Unit, ASST Fatebenefratelli Sacco, Luigi Sacco Hospital, Polo Universitario, University of Milan, Milan, Italy.⁴⁶⁷Health Management, Azienda USL Toscana Sud Est, Arezzo, Italy.⁴⁶⁸Department of Mathematics, University of Pavia, Pavia, Italy.⁴⁶⁹Independent researcher, Milan, Italy.⁴⁷⁰Scuola Normale Superiore, Pisa, Italy.⁴⁷¹CNR-Consiglio Nazionale delle Ricerche, Istituto di Biologia e Biotecnologia Agraria (IBBA), Milano, Italy.⁴⁷³Veos Digital, Milan, Italy.⁴⁷⁵Core Research Laboratory, ISPRO, Florence, Italy.⁴⁷⁸Division of Infectious Diseases and Immunology, Fondazione IRCCS Policlinico San Matteo, Pavia, Italy.⁴⁷⁹Department of Molecular and Translational Medicine, University of Brescia, Brescia, Italy.⁴⁸⁰Clinical Chemistry Laboratory, Cytogenetics and Molecular Genetics Section, Diagnostic Department, ASST Spedali Civili di Brescia, Brescia, Italy.⁴⁸¹Department of Medical and Surgical Sciences for Children and Adults, University of Modena and Reggio Emilia, Modena, Italy.⁴⁸²Department of Molecular Medicine, University of Padova, Padua, Italy.⁴⁸³Laboratory of Regulatory and Functional Genomics, Fondazione IRCCS Casa Sollievo della Sofferenza, San Giovanni Rotondo, Italy.⁴⁸⁴Clinical Trial Office, Fondazione IRCCS Casa Sollievo della Sofferenza Hospital, San Giovanni Rotondo, Italy.⁴⁸⁵Department of Health Sciences, University of Genova, Genova, Italy.⁴⁸⁶Oncologia Medica e Ufficio Flussi Sondrio, Sondrio, Italy.⁴⁸⁷Local Health Unit, Pharmaceutical Department of Grosseto, Toscana Sud Est Local Health Unit, Grosseto, Italy.⁴⁸⁸Independent researcher, Milan, Italy.⁴⁸⁹Direzione Scientifica, Istituti Clinici Scientifici Maugeri IRCCS, Pavia, Italy.⁴⁹⁰Fondazione per la ricerca Ospedale di Bergamo, Bergamo, Italy.⁴⁹¹Allelica, New York, NY, USA.⁴⁹³School of Basic and Medical Biosciences, Faculty of Life Sciences and Medicine, King's College London, London, UK.⁴⁹⁴Medical and Population Genomics, Wellcome Sanger Institute, Hinxton, UK.⁴⁹⁵Bradford Institute for Health Research, Bradford Teaching Hospitals National Health Service (NHS) Foundation Trust, Bradford, UK.⁴⁹⁷Institute of Population Health Sciences, Queen Mary University of London, London, UK.⁴⁹⁸Genes & Health, Blizard Institute, Queen Mary University of London, London, UK.⁴⁹⁹Institute of Population Health Sciences, Queen Mary University of London, London, UK.⁵⁰⁰Department of Biostatistics, University of Michigan, Ann Arbor, MI, USA.⁵⁰¹Heart Institute (InCor), University of Sao Paulo Med School, São Paulo, Brazil.⁵⁰²Genentech, San Francisco, CA, USA.⁵⁰³DNA Link Inc., Seoul, Republic of Korea.⁵⁰⁴Seoul National University Hospital Gangnam Center, Seoul, Republic of Korea.⁵⁰⁵Division of Infectious Diseases, Department of Internal Medicine, Chungnam National University School of Medicine, Daejeon, Republic of Korea.⁵⁰⁶East Kent Hospitals NHS Foundation Trust, Canterbury, UK.⁵⁰⁷Department of Internal Medicine, School of Medicine, Kyungpook National University, Daegu, Republic of Korea.⁵⁰⁸Division of Infectious Diseases, Department of Internal Medicine, Incheon Medical Center, Incheon, Republic of Korea.⁵⁰⁹Department of Infectious Diseases, Keimyung University Dongsan Hospital, Keimyung University School of Medicine, Daegu, Republic of Korea.⁵¹⁰Department of Internal Medicine, Pusan National University School of Medicine and Medical Research Institute, Pusan National University Hospital, Busan, Republic of Korea.⁵¹¹Division of Infectious Diseases, Department of Internal Medicine, Myongji Hospital, Goyang, Republic of Korea.⁵¹²Institute for Health Promotion, Graduate School of Public Health, Yonsei University, Seoul, Republic of Korea.⁵¹³Division of Cardiovascular Medicine, Stanford University, Stanford, CA, USA.⁵¹⁴Department of Medicine, Stanford University, Stanford, CA, USA.⁵¹⁵Department of Genetics, Stanford University, Stanford, CA, USA.⁵¹⁶Department of Biomedical Data Science, Stanford University, Stanford, CA, USA.⁵¹⁸Department of Pathology, Stanford University, Stanford, CA, USA.⁵¹⁹illumina, San Diego, CA, USA.⁵²⁰Computational Biology, Drug Discovery Sciences, Takeda Pharmaceuticals, Boston, MA, USA.⁵²¹Department of Computational Biology, Swiss Institute of Bioinformatics (SIB), University of Lausanne, Lausanne, Switzerland.⁵²³Royal Victoria Hospital, Belfast, UK.⁵²⁴Chelsea & Westminster NHS Foundation Trust, London, UK.⁵²⁵Northampton General Hospital NHS Trust, Northampton, UK.⁵²⁶Wrexham Maelor Hospital, Wrexham, UK.⁵²⁷University College Dublin, St Vincent's University Hospital, Dublin, Ireland.⁵²⁸University Hospitals Coventry & Warwickshire NHS Trust, Coventry, UK.⁵²⁹Watford General Hospital, Watford, UK.⁵³⁰NiHR Health Protection Research Unit, Institute of Infection, Veterinary and Ecological Sciences, Faculty of Health and Life Sciences, University of Liverpool, Liverpool, UK.⁵³¹Queen Alexandra Hospital (Hampshire), Portsmouth Hospital Trust, Portsmouth, UK.⁵³²Princess Royal Hospital, Brighton & Sussex Universities Hospitals NHS Trust, Brighton, UK.⁵³³Bassetlaw Hospital, Doncaster and Bassetlaw, Worksop, UK.⁵³⁴Darent Valley Hospital, Dartford and Gravesham NHS Trust, Dartford, UK.⁵³⁵High Containment Laboratories, University of Birmingham, Birmingham, UK.⁵³⁶Queen Elizabeth the Queen Mother Hospital, Margate, UK.⁵³⁷John Radcliffe Hospital, Oxford University Hospitals NHS Foundation Trust, Oxford, UK.⁵³⁸Royal Albert Edward Infirmary (Wigan), Warrington, Wigan and Leigh, Wigan, UK.⁵³⁹Manchester Royal Infirmary, Manchester University Hospitals NHS Foundation Trust, Manchester, UK.⁵⁴⁰Furness General Hospital, Morecambe Bay NHS Foundation Trust, Barrow-in-Furness, UK.⁵⁴¹Castle Hill Hospital, Hull University Teaching Hospital Trust, Hull, UK.⁵⁴²Hillingdon Hospital, Hillingdon Hospital, London, UK.⁵⁴³St Thomas Hospital, Guys and St Thomas Foundation Trust, London, UK.⁵⁴⁴University Hospitals Coventry and Warwickshire, Coventry, UK.⁵⁴⁵St Michaels Hospital (Bristol), University Hospitals Bristol and Weston NHS Foundation Trust, Bristol, UK.⁵⁴⁶Stepping Hill Hospital, Stockport NHS Foundation Trust, Manchester, UK.⁵⁴⁷Royal Liverpool Hospital, Liverpool University Hospitals NHS Foundation Trust, Liverpool, UK.⁵⁴⁸Bristol Royal Hospital (Children's), University Hospitals Bristol and Weston NHS Foundation Trust, Bristol, UK.⁵⁴⁹Scarborough Hospital, York Teaching Hospitals NHS Foundation Trust, York, UK.⁵⁵⁰Liverpool Heart & Chest Hospital, Liverpool Heart & Chest NHS Foundation Trust, Liverpool, UK.⁵⁵¹James Paget University Hospital, James Paget University Hospitals NHS Foundation Trust, Great Yarmouth, UK.⁵⁵²The

Article

James Cook University Hospital, South Tees NHS Foundation Trust, Middlesbrough, UK.
⁵⁵³Aberdeen Royal Infirmary, Grampian, Aberdeen, UK. ⁵⁵⁴University of Edinburgh, Edinburgh, UK. ⁵⁵⁵Royal Devon and Exeter Hospital, Royal Devon and Exeter NHS Foundation Trust, Exeter, UK. ⁵⁵⁶Worcestershire Royal Hospital, Worcestershire Acute Hospitals NHS Trust, Worcester, UK. ⁵⁵⁷Conquest Hospital, Hastings, East Sussex Healthcare NHS Trust, Seaford, UK. ⁵⁵⁸Dorset County Hospital, Dorset County Hospital NHS Foundation Trust, Dorchester, UK. ⁵⁵⁹Royal Bournemouth General Hospital, University Hospitals Dorset NHS Foundation Trust, Bournemouth, UK. ⁵⁶⁰Harrogate Hospital, Harrogate and District NHS Foundation Trust, Harrogate, UK. ⁵⁶¹Burnley General Teaching Hospital, East Lancashire Hospitals NHS Hospitals, Burnley, UK. ⁵⁶²Torbay Hospital, Torbay & South Devon NHS Foundation Trust, Torquay, UK. ⁵⁶³Royal Hallamshire Hospital, Sheffield Teaching Hospitals NHS Foundation Trust, Sheffield, UK. ⁵⁶⁴St Georges Hospital (Tooting), St Georges University Hospitals NHS Foundation Trust, London, UK. ⁵⁶⁵Blackpool Victoria Hospital, Blackpool Teaching Hospitals NHS Foundation Trust, Blackpool, UK. ⁵⁶⁶The Royal London Hospital, Barts Health NHS Trust, London, UK. ⁵⁶⁷Salford Royal NHS Foundation Trust, Salford Royal NHS Foundation Trust, Manchester, UK. ⁵⁶⁸University Hospital of North Durham, County Durham and Darlington Foundation Trust, Durham, UK. ⁵⁶⁹Norfolk and Norwich University Hospital, Norfolk and Norwich University Hospital NHS Foundation Trust, Norwich, UK. ⁵⁷⁰Fairfield General Hospital, Pennine Acute Hospitals NHS Trust, Manchester, UK. ⁵⁷¹Hereford County Hospital, Wye Valley NHS Trust, Hereford, UK. ⁵⁷²Southampton General Hospital, University Hospital Southampton NHS Foundation Trust, Southampton, UK. ⁵⁷³Northampton General Hospital, Northampton General Hospital NHS Trust, Northampton, UK. ⁵⁷⁴University Hospital of Wales, Cardiff and Vale University Health Board, Cardiff, UK. ⁵⁷⁵University of Bristol, Bristol, UK. ⁵⁷⁶Leighton Hospital, Mid Cheshire Hospitals NHS Foundation Trust, Crewe, UK. ⁵⁷⁷Diana Princess of Wales Hospital (Grimsby), North Lincolnshire & Goole, Grimsby, UK. ⁵⁷⁸Manor Hospital, Walsall Healthcare NHS Trust, Walsall, UK. ⁵⁷⁹Addenbrookes Hospital, Cambridge University Hospital NHS Foundation Trust, Cambridge, UK. ⁵⁸⁰West Suffolk Hospital, West Suffolk Hospital NHS Foundation Trust, Bury St Edmunds, UK. ⁵⁸¹Basingstoke and North Hampshire Hospital, Hampshire Hospitals NHS Foundation Trust, Basingstoke, UK. ⁵⁸²North Cumbria Integrated Care NHS Foundation Trust, Carlisle, UK. ⁵⁸³Warwick Hospital, South Warwickshire NHS Foundation Trust, Warwick, UK. ⁵⁸⁴Birmingham Women's and Children's Hospital, Birmingham Women's and Children's Hospital NHS Foundation Trust, Birmingham, UK. ⁵⁸⁵Nottingham City Hospital, Nottingham University Hospitals NHS Trust, Nottingham, UK. ⁵⁸⁶Glangwili Hospital Child Health Section, Hywel Dda University Health Board, Carmarthen, UK. ⁵⁸⁷Alder Hey Children's Hospital, Alder Hey Children's NHS Foundation Trust, Liverpool, UK. ⁵⁸⁸Bronglais General Hospital, Hywel Dda University Health Board, Aberystwyth, UK. ⁵⁸⁹Worthing Hospital, Western Sussex Hospitals NHS Foundation Trust, Worthing, UK. ⁵⁹⁰Rotheram District General Hospital, The Rotheram NHS Foundation Trust, Rotherham, UK. ⁵⁹¹Royal Free Hospital, Royal Free London NHS Foundation Trust, London, UK. ⁵⁹²Homerton Hospital, Homerton University Hospital NHS Foundation Trust, London, UK. ⁵⁹³Airedale Hospital, Airedale NHS Foundation Trust, Keighley, UK. ⁵⁹⁴Basildon Hospital, Basildon and Thurrock University Hospitals NHS Foundation Trust, Basildon, UK. ⁵⁹⁵The Christie NHS Foundation Trust, Manchester, UK. ⁵⁹⁶Queen Elizabeth Hospital (Greenwich), Lewisham and Greenwich NHS Trust, London, UK. ⁵⁹⁷The Whittington Hospital, Whittington Health NHS Trust, London, UK. ⁵⁹⁸Sheffield Children's Hospital, Sheffield Children's NHS Foundation Trust, Sheffield, UK. ⁵⁹⁹Royal United Hospital, Bath, Royal United Hospitals Bath NHS Foundation Trust, Bath, UK. ⁶⁰⁰Western General Hospital, Edinburgh, UK. ⁶⁰¹Mid and South Essex NHS Foundation Trust, Basildon, UK. ⁶⁰²Hinchingbrooke Hospital, North West Anglia NHS Foundation Trust, Peterborough, UK. ⁶⁰³Royal Preston Hospital, Lancashire Teaching Hospitals NHS Foundation Trust, Preston, UK. ⁶⁰⁴University Hospital (Coventry), University Hospitals Coventry and Warwickshire, Coventry, UK. ⁶⁰⁵The Walton Centre, The Walton Centre, Liverpool, UK. ⁶⁰⁶Hull Royal Infirmary, Hull University Teaching Hospital Trust, Hull, UK. ⁶⁰⁷Darlington Memorial Hospital, County Durham and Darlington Foundation Trust, Darlington, UK. ⁶⁰⁸Queen Elizabeth Hospital (Gateshead), Gateshead NHS Foundation Trust, Newcastle, UK. ⁶⁰⁹Warrington Hospital, Warrington & Halton Hospitals NHS Foundation Trust, Warrington, UK. ⁶¹⁰University Hospitals Bristol and Weston NHS Foundation Trust, Bristol, UK. ⁶¹¹St Mary's Hospital (Isle of Wight), Isle of Wight NHS Trust, Isle of Wight, UK. ⁶¹²The Maidstone Hospital, Maidstone & Tunbridge Wells NHS Trust, Maidstone, UK. ⁶¹³Huddersfield Royal, Calderdale and Huddersfield NHS Foundation Trust, Huddersfield, UK. ⁶¹⁴Royal Surrey County Hospital, Guildford, UK. ⁶¹⁵Countess of Chester Hospital, Countess of Chester Hospital NHS Foundation Trust, Chester, UK. ⁶¹⁶Frimley Park Hospital, Frimley Health Foundation Trust, Frimley, UK. ⁶¹⁷Leeds General Infirmary, Leeds Teaching Hospitals, Leeds, UK. ⁶¹⁸North Middlesex Hospital, North Middlesex University Hospital NHS Trust, London, UK. ⁶¹⁹Arrow Park Hospital, Wirral University Teaching Hospital NHS Foundation Trust, Wirral, UK. ⁶²⁰Great Ormond Street Hospital, Great Ormond Street Hospital for Children NHS Foundation Trust, London, UK. ⁶²¹Royal Shrewsbury Hospital, Shrewsbury and Telford Hospital NHS Trust, Shrewsbury, UK. ⁶²²East Surrey Hospital (Redhill), Surrey & Sussex Healthcare, Redhill, UK. ⁶²³Burton Hospital, University Hospitals of Derby & Burton NHS Foundation Trust, Burton-on-Trent, UK. ⁶²⁴Kent and Canterbury Hospital, East Kent Hospitals NHS Foundation Trust, Canterbury, UK. ⁶²⁵Weston Area General Trust, University Hospitals Bristol and Weston NHS Foundation Trust, Bristol, UK. ⁶²⁶Luton and Dunstable University Hospital, Luton, UK. ⁶²⁷Glasgow Royal Infirmary, Greater Glasgow and Clyde, Glasgow, UK. ⁶²⁸Derbyshire Healthcare, Derbyshire Healthcare NHS Foundation Trust, Derby, UK. ⁶²⁹Macclesfield General Hospital, East Cheshire NHS Foundation Trust, Macclesfield, UK. ⁶³⁰Chelsea and Westminster Hospital, Chelsea and Westminster NHS Trust, London, UK. ⁶³¹Institute of Microbiology and Infection, University of Birmingham, Birmingham, UK. ⁶³²Prince Philip Hospital, Hywel Dda University Health Board, Llanelli, UK. ⁶³³George Eliot Hospital - Acute Services, George Eliot Hospital, Nuneaton, UK. ⁶³⁴Kettering General Hospital, Kettering General Hospital NHS Foundation Trust, Kettering, UK. ⁶³⁵Birmingham Heartlands Hospital, Birmingham, UK. ⁶³⁶Russells Hall Hospital, The Dudley Group NHS Foundation Trust, Dudley, UK. ⁶³⁷Harefield Hospital, Royal Brompton & Harefield Trust, London, UK. ⁶³⁸Lister Hospital, East and North Hertfordshire NHS Trust, Stevenage, UK. ⁶³⁹Musgrove Park Hospital (Taunton & Somerset), Somerset NHS Foundation Trust, Taunton, UK. ⁶⁴⁰Queen's Hospital, Havering (Romford), Barking, Havering and Redbridge University Hospitals NHS Trust, London, UK. ⁶⁴¹Southport & Formby District General Hospital, Southport and Ormskirk Hospital NHS Trust, Southport, UK. ⁶⁴²New Cross Hospital, The Royal Wolverhampton NHS Trust, Wolverhampton, UK. ⁶⁴³King's College Hospital, London, UK. ⁶⁴⁴The Royal Victoria Infirmary, Newcastle Hospitals NHS Trust, Newcastle, UK. ⁶⁴⁵The Great Western Hospital,

Great Western Hospitals NHS Foundation Trust, Swindon, UK. ⁶⁴⁶Ninewells Hospital, Tayside, Dundee, UK. ⁶⁴⁷Poole Hospital NHS Trust, Poole, UK. ⁶⁴⁸Burton Hospital, University Hospitals of Derby & Burton NHS Foundation Trust, Derby, UK. ⁶⁴⁹William Harvey Hospital, Ashford, East Kent Hospitals NHS Foundation Trust, Willesborough, UK. ⁶⁵⁰King's Mill Hospital, Sherwood Forest Hospitals NHS Foundation Trust, Sutton-in-Ashfield, UK. ⁶⁵¹Liverpool Women's NHS Foundation Trust, Liverpool, UK. ⁶⁵²Dewsbury Hospital, Mid Yorkshire Hospitals NHS Trust, Dewsbury, UK. ⁶⁵³Northern Devon District Hospital, Northern Devon Healthcare NHS Trust, Barnstaple, UK. ⁶⁵⁴Tameside General Hospital, Tameside and Glossop Integrated Care NHS Foundation Trust, Manchester, UK. ⁶⁵⁵Sandwell General Hospital, Sandwell and West Birmingham Hospitals NHS Trust, Birmingham, UK. ⁶⁵⁶Broomfield Hospital, Mid and South Essex University Hospitals Group, Broomfield, UK. ⁶⁵⁷Wycombe Hospital, Buckingham Healthcare NHS Trust, Wycombe, UK. ⁶⁵⁸University Hospital of North Tees, North Tees and Hartlepool NHS Trust, Stockton-on-Tees, UK. ⁶⁵⁹Royal Manchester Children's Hospital, Manchester University Hospitals NHS Foundation Trust, Manchester, UK. ⁶⁶⁰Bedford Hospital, Bedford, UK. ⁶⁶¹Colchester General Hospital, East Suffolk and North Essex Foundation Trust, Colchester, UK. ⁶⁶²Queen Elizabeth Hospital (Birmingham) and Heartlands, University Hospital Birmingham NHS Foundation Trust, Birmingham, UK. ⁶⁶³Chesterfield Royal Hospital, Chesterfield Royal Hospital NHS Foundation Trust, Chesterfield, UK. ⁶⁶⁴Princess Alexandra Hospital, The Princess Alexandra Hospital NHS Trust, Harlow, UK. ⁶⁶⁵Watford General Hospital, West Hertfordshire Hospitals NHS Trust, Watford, UK. ⁶⁶⁶Milton Keynes Hospital, Milton Keynes University Hospital NHS Foundation Trust, Milton Keynes, UK. ⁶⁶⁷Royal Bolton General Hospital, Bolton Foundation Trust, Bolton, UK. ⁶⁶⁸Royal Gwent (Newport), Aneurin Bevan University Health Board, Newport, UK. ⁶⁶⁹The Royal Marsden Hospital (London), The Royal Marsden NHS Foundation Trust, London, UK. ⁶⁷⁰Queen Victoria Hospital (East Grinstead), Queen Victoria Hospital NHS Foundation Trust, East Grinstead, UK. ⁶⁷¹County Hospital (Stafford), University Hospitals of North Midlands NHS Trust, Stafford, UK. ⁶⁷²Whiston Hospital, St Helen's & Knowsley Hospitals NHS Trust, Prescot, UK. ⁶⁷³Croydon University Hospital, London, UK. ⁶⁷⁴Gloucester Royal, Gloucestershire Hospitals NHS Foundation Trust, Gloucester, UK. ⁶⁷⁵Medway Maritime Hospital, Medway Maritime NHS Trust, Gillingham, UK. ⁶⁷⁶Royal Papworth Hospital Everard, Royal Papworth Hospital NHS Foundation Trust, Cambridge, UK. ⁶⁷⁷Derriford (Plymouth), University Hospital Plymouth NHS Trust, Plymouth, UK. ⁶⁷⁸St Helier Hospital, Epsom and St Helier University Hospital NHS Trust, London, UK. ⁶⁷⁹Royal Berkshire Hospital, Royal Berkshire Foundation Trust, London, UK. ⁶⁸⁰Bradford Royal Infirmary, Bradford Teaching Hospitals NHS Foundation Trust, Bradford, UK. ⁶⁸¹Northwick Park, London North West University Hospital Trust, London, UK. ⁶⁸²Ealing Hospital, London North West University Hospital Trust, London, UK. ⁶⁸³Royal Cornwall Hospital (Tresliske), Royal Cornwall NHS Trust, Truro, UK. ⁶⁸⁴Ashford Hospital, Ashford & St Peter's Hospital, Stanwell, UK. ⁶⁸⁵Leicester Royal Infirmary (includes Glenfield Site), University Hospitals of Leicester, Leicester, UK. ⁶⁸⁶Grantham and District Hospital, United Lincolnshire Hospitals NHS Trust, Grantham, UK. ⁶⁸⁷University Hospital Aintree, Liverpool University Hospitals NHS Foundation Trust, Liverpool, UK. ⁶⁸⁸North Tyneside General Hospital, Northumbria Healthcare NHS Trust, North Shields, UK. ⁶⁸⁹Queen Elizabeth Hospital (King's Lynn), Queen Elizabeth Hospital King's Lynn NHS Foundation Trust, King's Lynn, UK. ⁶⁹⁰The Crick Institute, London, UK. ⁶⁹¹William Harvey Research Institute, Barts and the London School of Medicine and Dentistry, Queen Mary University of London, London, UK. ⁶⁹²Centre for Genomic and Experimental Medicine, Institute of Genetics and Molecular Medicine, University of Edinburgh, Western General Hospital, Edinburgh, UK. ⁶⁹³Intensive Care National Audit & Research Centre, London, UK. ⁶⁹⁴Wellcome Centre for Human Genetics, University of Oxford, Oxford, UK. ⁶⁹⁵Centre for Inflammation Research, The Queen's Medical Research Institute, University of Edinburgh, Edinburgh, UK. ⁶⁹⁶Great Ormond Street Hospital for Children NHS Foundation Trust, London, UK. ⁶⁹⁷Biostatistics Group, School of Life Sciences, Sun Yat-sen University, Guangzhou, China. ⁶⁹⁸Centre for Global Health Research, Usher Institute of Population Health Sciences and Informatics, Edinburgh, UK. ⁶⁹⁹Department of Medical Epidemiology and Biostatistics, Karolinska Institutet, Stockholm, Sweden. ⁷⁰⁰Institute for Molecular Bioscience, The University of Queensland, Brisbane, Queensland, Australia. ⁷⁰¹School of Life Sciences, Westlake University, Hangzhou, China. ⁷⁰²Westlake Laboratory of Life Sciences and Biomedicine, Westlake University, Hangzhou, China. ⁷⁰³Centre for Medical Informatics, The Usher Institute, University of Edinburgh, Edinburgh, UK. ⁷⁰⁴Liverpool Clinical Trials Centre, University of Liverpool, Liverpool, UK. ⁷⁰⁵Centre for Health Informatics, Division of Informatics, Imaging and Data Science, School of Health Sciences, Faculty of Biology, Medicine and Health, University of Manchester, Manchester Academic Health Science Centre, Manchester, UK. ⁷⁰⁶MRC Human Genetics Unit, MRC Institute of Genetics and Molecular Medicine, University of Edinburgh, Edinburgh, UK. ⁷⁰⁷School of Informatics, University of Edinburgh, Edinburgh, UK. ⁷⁰⁸Royal Hospital for Children, Glasgow, UK. ⁷⁰⁹MRC-University of Glasgow Centre for Virus Research, Institute of Infection, Immunity and Inflammation, College of Medical, Veterinary and Life Sciences, University of Glasgow, Glasgow, UK. ⁷¹⁰Centre for Tropical Medicine and Global Health, Nuffield Department of Medicine, University of Oxford, Oxford, UK. ⁷¹¹Department of Anaesthesia and Intensive Care, The Chinese University of Hong Kong, Prince of Wales Hospital, Hong Kong, China. ⁷¹²Department of Critical Care Medicine, Queen's University and Kingston Health Sciences Centre, Kingston, Ontario, Canada. ⁷¹³Wellcome-Wolfson Institute for Experimental Medicine, Queen's University Belfast, Belfast, UK. ⁷¹⁴Department of Intensive Care Medicine, Royal Victoria Hospital, Belfast, UK. ⁷¹⁵UCL Centre for Human Health and Performance, London, UK. ⁷¹⁶Clinical Research Centre at St Vincent's University Hospital, University College Dublin, Dublin, Ireland. ⁷¹⁷National Heart and Lung Institute, Imperial College London, London, UK. ⁷¹⁸Imperial College Healthcare NHS Trust London, London, UK. ⁷¹⁹NIHR Health Protection Research Unit for Emerging and Zoonotic Infections, Institute of Infection, Veterinary and Ecological Sciences University of Liverpool, Liverpool, UK. ⁷²⁰Respiratory Medicine, Alder Hey Children's Hospital, Institute in the Park, University of Liverpool, Alder Hey Children's Hospital, Liverpool, UK. ⁷²¹Department of Intensive Care Medicine, Guy's and St Thomas NHS Foundation Trust, London, UK. ⁷²²Department of Medicine, University of Cambridge, Cambridge, UK. ⁷²³Airedale General Hospital, Keighley, UK. ⁷²⁴Barts Health NHS Trust, London, UK. ⁷²⁵Basildon Hospital, Basildon, UK. ⁷²⁶BHRUT (Barking Havering) - Queens Hospital and King George Hospital, Romford, UK. ⁷²⁷Bradford Royal Infirmary, Bradford, UK. ⁷²⁸Bronglais General Hospital, Aberystwyth, UK. ⁷²⁹Broomfield Hospital, Chelmsford, UK. ⁷³⁰Calderdale Royal Hospital, Halifax, UK. ⁷³¹Charing Cross Hospital, St Mary's Hospital and Hammersmith Hospital, London, UK. ⁷³²Barnet Hospital, London, UK. ⁷³³Birmingham Children's Hospital, Birmingham, UK. ⁷³⁴St John's Hospital Livingston,

Livingston, UK. ⁷⁴⁸Aberdeen Royal Infirmary, Aberdeen, UK. ⁷⁴⁹Addenbrooke's Hospital, Cambridge, UK. ⁷⁵⁰Aintree University Hospital, Liverpool, UK. ⁷⁵²Arrow Park Hospital, Warral, UK. ⁷⁵³Ashford and St Peter's Hospital, Lyne, UK. ⁷⁵⁴Basingstoke and North Hampshire Hospital, Basingstoke, UK. ⁷⁵⁵Borders General Hospital, Melrose, UK. ⁷⁵⁶Chesterfield Royal Hospital Foundation Trust, Chesterfield, UK. ⁷⁵⁷Eastbourne District General Hospital, East Sussex, UK and Conquest Hospital, Eastbourne, UK. ⁷⁵⁸Barnsley Hospital, Barnsley, UK. ⁷⁵⁹Blackpool Victoria Hospital, Blackpool, UK. ⁷⁶⁰East Surrey Hospital, Redhill, UK. ⁷⁶¹Good Hope Hospital, Birmingham, UK. ⁷⁶²Hereford County Hospital, Hereford, UK. ⁷⁶³Hull Royal Infirmary, Hull, UK. ⁷⁶⁵Kent & Canterbury Hospital, Canterbury, UK. ⁷⁶⁶Manchester Royal Infirmary, Manchester, UK. ⁷⁶⁷Nottingham University Hospital, Nottingham, UK. ⁷⁶⁸Pilgrim Hospital, Lincoln, UK. ⁷⁶⁹Queen Elizabeth Hospital, Birmingham, UK. ⁷⁷⁰Salford Royal Hospital, Manchester, UK. ⁷⁷¹Tameside General Hospital, Ashton-under-Lyne, UK. ⁷⁷²The Tunbridge Wells Hospital and Maidstone Hospital, Maidstone, UK. ⁷⁷³The Royal Oldham Hospital, Manchester, UK. ⁷⁷⁴The Royal Papworth Hospital, Cambridge, UK. ⁷⁷⁵University College Hospital, London, UK. ⁷⁷⁶Withybush General Hospital, Haverfordwest, UK. ⁷⁷⁷Wythenshawe Hospital, Manchester, UK. ⁷⁷⁸Yeovil Hospital, Yeovil, UK. ⁷⁷⁹Cumberland Infirmary, Carlisle, UK. ⁷⁸⁰Darent Valley Hospital, Dartford, UK. ⁷⁸¹Dumfries and Galloway Royal Infirmary, Dumfries, UK. ⁷⁸²Ealing Hospital, London, UK. ⁷⁸³Fairfield General Hospital, Bury, UK. ⁷⁸⁴George Eliot Hospital NHS Trust, Nuneaton, UK. ⁷⁸⁵Glau Clwyd Hospital, Bodelwyddan, UK. ⁷⁸⁶Glangwili General Hospital, Camarthen, UK. ⁷⁸⁷The Great Western Hospital, Swindon, UK. ⁷⁸⁸Guys and St Thomas' Hospital, London, UK. ⁷⁸⁹Harefield Hospital, London, UK. ⁷⁹⁰Harrogate and District NHS Foundation Trust, Harrogate, UK. ⁷⁹²James Paget University Hospital NHS Trust, Great Yarmouth, UK. ⁷⁹⁴King's Mill Hospital, Nottingham, UK. ⁷⁹⁵Kingston Hospital, Kingston, UK. ⁷⁹⁶Lincoln County Hospital, Lincoln, UK. ⁷⁹⁷Liverpool Heart and Chest Hospital, Liverpool, UK. ⁷⁹⁸Macclesfield District General Hospital, Macclesfield, UK. ⁷⁹⁹Medway Maritime Hospital, Gillingham, UK. ⁸⁰⁰Milton Keynes University Hospital, Milton Keynes, UK. ⁸⁰¹Morrison Hospital, Swansea, UK. ⁸⁰²National Hospital for Neurology and Neurosurgery, London, UK. ⁸⁰³Norfolk and Norwich University Hospital (NNUH), Norwich, UK. ⁸⁰⁴North Middlesex University Hospital NHS Trust, London, UK. ⁸⁰⁶Northumbria Healthcare NHS Foundation Trust, North Shields, UK. ⁸⁰⁷Peterborough City Hospital, Peterborough, UK. ⁸⁰⁸Prince Charles Hospital, Merthyr Tydfil, UK. ⁸⁰⁹Royal Sussex County Hospital, Brighton, UK. ⁸¹⁰Princess Royal Hospital, Haywards Heath, UK. ⁸¹¹Princess of Wales Hospital, Llantrisant, UK. ⁸¹²Queen Alexandra Hospital, Portsmouth, UK. ⁸¹³Queen Elizabeth Hospital, London, UK. ⁸¹⁵Queen Victoria Hospital, East Grinstead, UK. ⁸¹⁶Queen's Hospital Burton, Burton-On-Trent, UK. ⁸¹⁷Raigmore Hospital, Inverness, UK. ⁸¹⁸Rotherham General Hospital, Rotherham, UK. ⁸¹⁹Royal Blackburn Teaching Hospital, Blackburn, UK. ⁸²⁰Royal Preston Hospital, Preston, UK. ⁸²¹Royal Surrey County Hospital, Guildford, UK. ⁸²²Royal Albert Edward Infirmary, Wigan, UK. ⁸²³The Royal Alexandra Children's Hospital, Brighton, UK. ⁸²⁴Royal Alexandra Hospital, Paisley, UK. ⁸²⁵Royal Bolton Hospital, Bolton, UK. ⁸²⁶University Hospitals Dorset NHS Foundation Trust, Dorchester, UK. ⁸²⁷Royal Brompton Hospital, London, UK. ⁸²⁸Imperial College London, London, UK. ⁸²⁹Royal Cornwall Hospital, Truro, UK. ⁸³⁰Royal Free Hospital, London, UK. ⁸³¹Royal Glamorgan Hospital, Pontyclun, UK. ⁸³²Royal Gwent Hospital, Newport, UK. ⁸³³Northern General Hospital, Sheffield, UK. ⁸³⁴Royal Hampshire County Hospital, Winchester, UK. ⁸³⁵Royal Manchester Children's Hospital, Manchester, UK. ⁸³⁶Royal Stoke University Hospital, Stoke-on-Trent, UK. ⁸³⁷Salisbury District Hospital, Salisbury, UK. ⁸³⁸Sandwell General Hospital, Birmingham, UK. ⁸³⁹Scarborough General Hospital, Scarborough, UK. ⁸⁴⁰Scunthorpe General Hospital, Scunthorpe, UK. ⁸⁴¹Southmead Hospital, Bristol, UK. ⁸⁴²St George's Hospital, London, UK. ⁸⁴³St Mary's Hospital, Newport, UK. ⁸⁴⁴Stoke Mandeville Hospital, Aylesbury, UK. ⁸⁴⁵Sunderland Royal Hospital, Sunderland, UK. ⁸⁴⁶Alexandra Hospital, Redditch and Worcester Royal Hospital, Worcester, UK. ⁸⁴⁷The Christie NHS Foundation Trust, Manchester, UK. ⁸⁴⁸The Queen Elizabeth Hospital, King's Lynn, UK. ⁸⁴⁹The Royal Liverpool University Hospital, Liverpool, UK. ⁸⁵⁰The Royal Marsden NHS Foundation Trust, London, UK. ⁸⁵¹Torbay Hospital, Torquay, UK. ⁸⁵²University Hospital Monklands, Airdrie, UK. ⁸⁵³University Hospital Lewisham, London, UK. ⁸⁵⁴University Hospital North Durham, Darlington, UK. ⁸⁵⁵University Hospital of North Tees, Stockton-on-Tees, UK. ⁸⁵⁶University Hospital of Wales, Cardiff, UK. ⁸⁵⁷University Hospital Wishaw, Wishaw, UK. ⁸⁵⁸Victoria Hospital, Kirkcaldy, UK. ⁸⁵⁹Warrington General Hospital, Warrington, UK. ⁸⁶⁰West Cumberland Hospital, Whitehaven, UK. ⁸⁶¹Western Sussex Hospitals, Chichester, UK. ⁸⁶²Whiston Hospital, Prescot, UK. ⁸⁶³York Hospital, York, UK. ⁸⁶⁴Ysbyty Gwynedd, Bangor, UK. ⁸⁶⁵Countess of Chester Hospital, Chester, UK. ⁸⁶⁶Croydon University Hospital, Croydon, UK. ⁸⁶⁷Diana Princess of Wales Hospital, Grimsby, UK. ⁸⁶⁸Dorset County Hospital, Dorchester, UK. ⁸⁶⁹Forth Valley Royal Hospital, Falkirk, UK. ⁸⁷⁰Furness General Hospital, Barrow-in-Furness, UK. ⁸⁷¹Alder Hey Children's Hospital, Liverpool, UK. ⁸⁷²Derriford Hospital, Plymouth, UK. ⁸⁷³Glasgow Royal Infirmary, Glasgow, UK. ⁸⁷⁴Glenfield Hospital, Leicester, UK. ⁸⁷⁵Gloucestershire Royal Hospital, Gloucester, UK. ⁸⁷⁶Golden Jubilee National Hospital, Clydebank, UK. ⁸⁷⁷Great Ormond St Hospital and UCL Great Ormond St Institute of Child Health NIHR Biomedical Research Centre, London, UK. ⁸⁷⁸Homerton University Hospital Foundation NHS Trust, London, UK. ⁸⁷⁹James Cook University Hospital, Middlesbrough, UK. ⁸⁸⁰John Radcliffe Hospital, Oxford, UK. ⁸⁸¹Leicester Royal Infirmary, Leicester, UK. ⁸⁸²Lister Hospital, Stevenage, UK. ⁸⁸³New Cross Hospital, Wolverhampton, UK. ⁸⁸⁴Royal Victoria Infirmary, Newcastle Upon Tyne, UK. ⁸⁸⁵Ninewells Hospital, Dundee, UK. ⁸⁸⁶North Devon District Hospital, Barnstaple, UK. ⁸⁸⁷North Manchester General Hospital, Manchester, UK. ⁸⁸⁸Northwick Park Hospital, London, UK. ⁸⁸⁹Prince Philip Hospital, Lianelli, UK. ⁸⁹⁰Pinderfields General Hospital, Wakefield, UK. ⁸⁹¹Poole Hospital, Poole, UK. ⁸⁹²Royal Shrewsbury Hospital, Shrewsbury, UK. ⁸⁹³Princess Royal Hospital, Telford, UK. ⁸⁹⁹Queen Elizabeth Hospital Gateshead, Gateshead, UK. ⁹⁰⁰Queen Elizabeth University Hospital, Glasgow, UK. ⁹⁰¹Royal Berkshire NHS Foundation Trust, Reading, UK. ⁹⁰²Royal Derby Hospital, Derby, UK. ⁹⁰³Royal Devon and Exeter Hospital, Exeter, UK. ⁹⁰⁴Royal Infirmary of Edinburgh, Edinburgh, UK. ⁹⁰⁵Royal Lancaster Infirmary, Lancaster, UK. ⁹⁰⁶Royal United Hospital, Bath, UK. ⁹⁰⁷Russells Hall Hospital, Dudley, UK. ⁹⁰⁸Sheffield Children's Hospital, Sheffield, UK. ⁹⁰⁹Southampton General Hospital, Southampton, UK. ⁹¹⁰Southend University Hospital, Westcliff-on-Sea, UK. ⁹¹¹Southport and Formby District General Hospital, Ormskirk, UK. ⁹¹²St James's University Hospital and Leeds General Infirmary, Leeds, UK. ⁹¹³Bristol Royal Infirmary, Bristol, UK. ⁹¹⁴Stepping Hill Hospital, Stockport, UK. ⁹¹⁵The Princess Alexandra Hospital, Harlow, UK. ⁹¹⁶University Hospital Crosshouse, Kilmarnock, UK. ⁹¹⁷University Hospital Hairmyres, East Kilbride, UK. ⁹¹⁸Craigavon Area Hospital, Craigavon, UK. ⁹¹⁹Warwick Hospital, Warwick, UK. ⁹²⁰West Middlesex Hospital, Isleworth, UK. ⁹²²Whittington Hospital, London, UK. ⁹²³William Harvey Hospital, Ashford, UK. ⁹³²Section of Molecular Virology, Imperial College London,

London, UK. ⁹³³Antimicrobial Resistance and Hospital Acquired Infection Department, Public Health England, London, UK. ⁹³⁴Department of Infectious Disease, Imperial College London, London, UK. ⁹³⁵National Infection Service, Public Health England, London, UK. ⁹³⁶MRC-University of Glasgow Centre for Virus Research, Glasgow, UK. ⁹³⁷Liverpool School of Tropical Medicine, Liverpool, UK. ⁹³⁸Institute of Infection and Global Health, University of Liverpool, Liverpool, UK. ⁹⁴⁰Virology Reference Department, National Infection Service, Public Health England, London, UK. ⁹⁴¹Department of Pharmacology, University of Liverpool, Liverpool, UK. ⁹⁴²Nuffield Department of Medicine, University of Oxford, Oxford, UK. ⁹⁴⁴Nottingham University Hospitals NHS Trust, Nottingham, UK. ⁹⁴⁵Nuffield Department of Medicine, John Radcliffe Hospital, Oxford, UK. ⁹⁴⁶SARIC Global Support Centre, Centre for Tropical Medicine and Global Health, Nuffield Department of Medicine, University of Oxford, Oxford, UK. ⁹⁴⁷Division of Infection and Immunity, University College London, London, UK. ⁹⁴⁸Institute of Infection, Veterinary and Ecological Sciences, University of Liverpool, Liverpool, UK. ⁹⁴⁹Centre for Clinical Infection and Diagnostics Research, Department of Infectious Diseases, School of Immunology and Microbial Sciences, King's College London, London, UK. ⁹⁵⁰Institute of Evolutionary Biology, University of Edinburgh, Edinburgh, UK. ⁹⁵¹Department of Pediatrics and Virology, Imperial College London, London, UK. ⁹⁵²The Florey Institute for Host-Pathogen Interactions, Department of Infection, Immunity and Cardiovascular Disease, University of Sheffield, Sheffield, UK. ⁹⁵³Division of Structural Biology, The Wellcome Centre for Human Genetics, University of Oxford, Oxford, UK. ⁹⁵⁵Blood Borne Virus Unit, Virus Reference Department, National Infection Service, Public Health England, London, UK. ⁹⁵⁶Department of Infection, Immunity and Cardiovascular Disease, University of Sheffield, Sheffield, UK. ⁹⁵⁷Institute for Global Health, University College London, London, UK. ⁹⁵⁸Molecular and Clinical Cancer Medicine, Institute of Systems, Molecular and Integrative Biology, University of Liverpool, Liverpool, UK. ⁹⁵⁹Department of Child Life and Health, University of Edinburgh, Edinburgh, UK. ⁹⁶⁰Section of Biomolecular Medicine, Division of Systems Medicine, Department of Metabolism, Digestion and Reproduction, Imperial College London, London, UK. ⁹⁶¹Department of Epidemiology and Biostatistics, School of Public Health, Faculty of Medicine, Imperial College London, London, UK. ⁹⁶²National Phenome Centre, Department of Metabolism, Digestion and Reproduction, Imperial College London, London, UK. ⁹⁶³Department of Molecular and Clinical Cancer Medicine, University of Liverpool, Liverpool, UK. ⁹⁶⁴Institute of Translational Medicine, University of Liverpool, Liverpool, UK. ⁹⁶⁵Intensive Care Unit, Royal Infirmary Edinburgh, Edinburgh, UK. ⁹⁶⁶University of Liverpool, Liverpool, UK. ⁹⁶⁷University of Glasgow, Glasgow, UK. ⁹⁶⁸Edinburgh Clinical Research Facility, Western General Hospital, University of Edinburgh, Edinburgh, UK. ⁹⁷²Department of Infectious Diseases, Leiden University Medical Center, Leiden, The Netherlands. ⁹⁷³Cambridge University Hospitals NHS Foundation Trust, Cambridge, UK. ⁹⁷⁴Genotek, Moscow, Russia. ⁹⁷⁵Helix, San Mateo, CA, USA. ⁹⁷⁶Center for Genomic Medicine, Desert Research Institute, Reno, NV, USA. ⁹⁷⁷Renown Health, Reno, NV, USA. ⁹⁷⁸24Genetics, Boston, MA, USA. ⁹⁷⁹Hospital La Paz Institute for Health Research, Madrid, Spain. ⁹⁸⁰Division of Pulmonary Medicine, Department of Medicine, Keio University School of Medicine, Tokyo, Japan. ⁹⁸¹Department of Statistical Genetics, Osaka University Graduate School of Medicine, Suita, Japan. ⁹⁸²Laboratory of Statistical Immunology, Immunology Frontier Research Center (WPI-IFReC), Osaka University, Suita, Japan. ⁹⁸³Integrated Frontier Research for Medical Science Division, Institute for Open and Transdisciplinary Research Initiatives, Osaka University, Suita, Japan. ⁹⁸⁴Division of Health Medical Intelligence, Human Genome Center, the Institute of Medical Science, The University of Tokyo, Tokyo, Japan. ⁹⁸⁵Laboratory of Viral Infection I, Department of Infection Control and Immunology, Omura Satoshi Memorial Institute & Graduate School of Infection Control Sciences, Kitasato University, Tokyo, Japan. ⁹⁸⁶Department of Surgery, Keio University School of Medicine, Tokyo, Japan. ⁹⁸⁷Department of Organoid Medicine, Keio University School of Medicine, Tokyo, Japan. ⁹⁸⁸Department of Infectious Diseases, Keio University School of Medicine, Tokyo, Japan. ⁹⁸⁹Department of Respiratory Medicine and Clinical Immunology, Osaka University Graduate School of Medicine, Suita, Japan. ⁹⁹⁰Department of Immunopathology, Immunology Frontier Research Center (WPI-IFReC), Osaka University, Suita, Japan. ⁹⁹¹Institute of Research, Tokyo Medical and Dental University, Tokyo, Japan. ⁹⁹²Department of Insured Medical Care Management, Tokyo Medical and Dental University Hospital of Medicine, Tokyo, Japan. ⁹⁹³Genome Medical Science Project (Toyama), National Center for Global Health and Medicine, Chiba, Japan. ⁹⁹⁴Division of Gastroenterology and Hepatology, Department of Medicine, Keio University School of Medicine, Tokyo, Japan. ⁹⁹⁵M&D Data Science Center, Tokyo Medical and Dental University, Tokyo, Japan. ⁹⁹⁶Department of Pathology and Tumor Biology Institute for the Advanced Study of Human Biology (WPI-ASHBi), Kyoto University, Kyoto, Japan. ⁹⁹⁷Department of Medicine, Center for Hematology and Regenerative Medicine, Karolinska Institute, Stockholm, Sweden. ⁹⁹⁹Department of Emergency and Critical Care Medicine, Keio University School of Medicine, Tokyo, Japan. ¹⁰⁰⁰Department of Anesthesiology, Keio University School of Medicine, Tokyo, Japan. ¹⁰⁰¹Department of Laboratory Medicine, Keio University School of Medicine, Tokyo, Japan. ¹⁰⁰²Division of Infection Control and Prevention, Osaka University Hospital, Suita, Japan. ¹⁰⁰³Department of Biomedical Ethics and Public Policy, Osaka University Graduate School of Medicine, Suita, Japan. ¹⁰⁰⁴Center for Genomic Medicine, Kyoto University Graduate School of Medicine, Kyoto, Japan. ¹⁰⁰⁵Department of Pulmonary Medicine, Faculty of Medicine, University of Tsukuba, Tsukuba, Japan. ¹⁰⁰⁶Department of Neurosurgery, Faculty of Medicine, The University of Tokyo, Tokyo, Japan. ¹⁰⁰⁷Laboratory of Immune Regulation, Department of Microbiology and Immunology, Osaka University Graduate School of Medicine, Suita, Japan. ¹⁰⁰⁸Medical Innovation Promotion Center, Tokyo Medical and Dental University, Tokyo, Japan. ¹⁰¹⁰Clinical Research Center, Tokyo Medical and Dental University Hospital of Medicine, Tokyo, Japan. ¹⁰¹¹Department of Medical Informatics, Tokyo Medical and Dental University Hospital of Medicine, Tokyo, Japan. ¹⁰¹²Respiratory Medicine, Tokyo Medical and Dental University, Tokyo, Japan. ¹⁰¹³Clinical Laboratory, Tokyo Medical and Dental University Hospital of Medicine, Tokyo, Japan. ¹⁰¹⁴Department of Pathology and Tumor Biology, Kyoto University, Kyoto, Japan. ¹⁰¹⁵Department of Respiratory Medicine, Graduate School of Medicine, Faculty of Medicine, Juntendo University, Tokyo, Japan. ¹⁰¹⁶Department of Emergency and Disaster Medicine, Graduate School of Medicine, Faculty of Medicine, Juntendo University, Tokyo, Japan. ¹⁰¹⁷Department of Cardiovascular Biology and Medicine, Graduate School of Medicine, Faculty of Medicine, Juntendo University, Tokyo, Japan. ¹⁰¹⁸Department of Respiratory Medicine, Tokyo Women's Medical University, Tokyo, Japan. ¹⁰¹⁹Department of General Medicine, Tokyo Women's Medical University, Tokyo, Japan. ¹⁰²⁰Department of Respiratory

Article

Medicine, Saitama Cardiovascular and Respiratory Center, Saitama, Japan.¹⁰²⁷Kawasaki Municipal Ida Hospital, Kanagawa, Japan.¹⁰²²Saitama Medical Center, Internal Medicine, Japan Community Healthcare Organization (JCHO), Saitama, Japan.¹⁰²³Saitama City Hospital, Saitama, Japan.¹⁰²⁴Division of Infection Control, Eiju General Hospital, Tokyo, Japan.¹⁰²⁵Department of Pulmonary Medicine, Eiju General Hospital, Tokyo, Japan.¹⁰²⁶Department of Respiratory Medicine, Osaka Saiseikai Nakatsu Hospital, Osaka, Japan.¹⁰²⁷Division of Respiriology, Rheumatology, and Neurology, Department of Internal Medicine Kurume University School of Medicine, Fukuoka, Japan.¹⁰²⁸Department of Infection Control, Osaka Saiseikai Nakatsu Hospital, Osaka, Japan.¹⁰²⁹Department of Infectious Diseases, Tosei General Hospital, Aichi, Japan.¹⁰³⁰Fukujuji Hospital, Kiyose, Japan.¹⁰³¹Department of Emergency and Critical Care Medicine, Tokyo Women's Medical University Medical Center East, Tokyo, Japan.¹⁰³²Department of Medicine, Tokyo Women's Medical University Medical Center East, Tokyo, Japan.¹⁰³³Department of Pediatrics, Tokyo Women's Medical University Medical Center East, Tokyo, Japan.¹⁰³⁴Japan Community Healthcare Organization Kanazawa Hospital, Kanazawa, Japan.¹⁰³⁵Division of Pulmonary Medicine, Department of Internal Medicine, Federation of National Public Service Personnel Mutual Aid Associations, Tachikawa Hospital, Tachikawa, Japan.¹⁰³⁶Department of Respiratory Medicine, Japan Organization of Occupational Health and Safety, Kanto Rosai Hospital, Kawasaki, Japan.¹⁰³⁷Department of General Internal Medicine, Japan Organization of Occupational Health and Safety, Kanto Rosai Hospital, Kawasaki, Japan.¹⁰³⁸Department of Emergency and Critical Care Medicine, Kansai Medical University General Medical Center, Kirakata, Japan.¹⁰³⁹Department of Respiratory Medicine, Kitasato University, Kitasato Institute Hospital, Tokyo, Japan.¹⁰⁴⁰Ishikawa Prefectural Central Hospital, Kanazawa, Japan.¹⁰⁴¹Internal Medicine, Sano Kosei General Hospital, Sano, Japan.¹⁰⁴²Saiseikai Yokohamashi Nanbu Hospital, Yokohama, Japan.¹⁰⁴³Kanagawa Cardiovascular and Respiratory Center, Yokohama, Japan.¹⁰⁴⁴Saiseikai Utsunomiya Hospital, Utsunomiya, Japan.¹⁰⁴⁵Department of Respiratory Medicine, KKR Sapporo Medical Center, Sapporo, Japan.¹⁰⁴⁶Internal Medicine, Internal Medicine Center, Showa University Koto Toyosu Hospital, Tokyo, Japan.¹⁰⁴⁷Department of Respiratory Medicine, Toyohashi Municipal Hospital, Toyohashi, Japan.¹⁰⁴⁸Keiyu Hospital, Yokohama, Japan.¹⁰⁴⁹Department of Rheumatology, National Hospital Organization Hokkaido Medical Center, Sapporo, Japan.¹⁰⁵⁰Department of Respiratory Medicine, National Hospital Organization Tokyo Medical Center, Tokyo, Japan.¹⁰⁵¹Department of Allergy, National Hospital Organization Tokyo Medical Center, Tokyo, Japan.¹⁰⁵²Department of General Internal Medicine and Infectious Diseases, National Hospital Organization Tokyo Medical Center, Tokyo, Japan.¹⁰⁵³Japanese Red Cross Musashino Hospital, Musashino, Japan.¹⁰⁵⁴Department of Respiratory Medicine, Tohoku University Graduate School of Medicine, Sendai, Japan.¹⁰⁵⁵Division of Respiratory Medicine, Department of Internal Medicine, Nihon University School of Medicine, Tokyo, Japan.¹⁰⁵⁶Department of Emergency and Critical Care Medicine, St Marianna University School of Medicine, Kawasaki, Japan.¹⁰⁵⁷Division of General Internal Medicine, Department of Internal Medicine, St Marianna University School of Medicine, Kawasaki, Japan.¹⁰⁵⁸National Hospital Organization Kanazawa Medical Center, Kanazawa, Japan.¹⁰⁵⁹Division of Infectious Diseases and Respiratory Medicine, Department of Internal Medicine, National Defense Medical College, Tokorozawa, Japan.¹⁰⁶⁰Department of Emergency and Critical Care Medicine, Faculty of Medicine, Fukuoka University, Fukuoka, Japan.¹⁰⁶¹Department of Infection Control, Fukuoka University Hospital, Fukuoka, Japan.¹⁰⁶²Tokyo Saiseikai Central Hospital, Tokyo, Japan.¹⁰⁶³Department of Internal Medicine, Fukuoka Tokushukai Hospital, Kasuga, Japan.¹⁰⁶⁴Department of Infectious Disease and Clinical Research Institute, National Hospital Organization Kyushu Medical Center, Fukuoka, Japan.¹⁰⁶⁵Department of Respiriology, National Hospital Organization Kyushu Medical Center, Fukuoka, Japan.¹⁰⁶⁷Matsumoto City Hospital, Matsumoto, Japan.¹⁰⁶⁸Uji-Tokushukai Medical Center, Uji, Japan.¹⁰⁶⁹Department of Respiratory Medicine, Nagoya University Graduate School of Medicine, Nagoya, Japan.¹⁰⁷⁰Department of Respiratory Medicine, Fujisawa City Hospital, Fujisawa, Japan.¹⁰⁷¹Sapporo City General Hospital, Sapporo, Japan.¹⁰⁷²Department of Emergency and Critical Care Medicine, Chiba University Graduate School of Medicine, Chiba, Japan.¹⁰⁷³Division of Respiratory Medicine, Social Welfare Organization Saiseikai Imperial Gift Foundation, Saiseikai Kumamoto Hospital, Kumamoto, Japan.¹⁰⁷⁴Department of Anesthesiology and Intensive Care Medicine, Kyoto Prefectural University of Medicine, Kyoto, Japan.¹⁰⁷⁵Ome Municipal General Hospital, Ome, Japan.¹⁰⁷⁶Hanwa Daini Hospital, Osaka, Japan.¹⁰⁷⁷Department of Respiratory Internal Medicine, St Marianna University School of Medicine, Yokohama-City Seibu Hospital, Yokohama, Japan.¹⁰⁷⁸Division of Hematology, Department of Internal Medicine, St Marianna University Yokohama-City Seibu Hospital, Yokohama, Japan.¹⁰⁷⁹Division of Pulmonary Medicine, Department of Medicine, Tokai University School of Medicine, Tokai University School of Medicine, Tokyo, Japan.¹⁰⁸⁰Division of Pulmonary Medicine, Department of Medicine, Tokai University School of Medicine, Tokyo, Japan.¹⁰⁸¹National Hospital Organization Kumamoto Medical Center, Kumamoto, Japan.¹⁰⁸²Department of Respiratory Medicine, Tokyo Medical University Hospital, Tokyo, Japan.¹⁰⁸³Department of Respiratory Medicine, Japanese Red Cross Medical Center, Tokyo, Japan.¹⁰⁸⁴JA Toride Medical Hospital, Toride, Japan.¹⁰⁸⁵Japan Organization of Occupational Health and Safety Okayama Rosai Hospital, Okayama, Japan.¹⁰⁸⁶Emergency and Disaster Medicine, Graduate School of Medicine, Gifu University School of Medicine, Gifu, Japan.¹⁰⁸⁷Niigata University, Niigata, Japan.¹⁰⁸⁸National Hospital Organization Kyoto Medical Center, Kyoto, Japan.¹⁰⁸⁹Research Institute for Diseases of the Chest, Graduate School of Medical Sciences, Kyushu University, Fukuoka, Japan.¹⁰⁹⁰Department of Medicine and Biosystemic Science, Kyushu University Graduate School of Medical Sciences, Fukuoka, Japan.¹⁰⁹¹Department of Emergency and Critical Care Medicine, Tsukuba University, Tsukuba, Japan.¹⁰⁹²Department of Nephrology, Faculty of Medicine, University of Tsukuba, Tsukuba, Japan.¹⁰⁹³Department of Hematology, Faculty of Medicine, University of Tsukuba, Tsukuba, Japan.¹⁰⁹⁴National Hospital Organization Tokyo Hospital, Tokyo, Japan.¹⁰⁹⁵Fujioka General Hospital, Fujioka, Japan.¹⁰⁹⁶Division of Respiratory Medicine and Allergology, Department of Medicine, School of Medicine, Showa University, Tokyo, Japan.¹⁰⁹⁷Department of Pulmonary Medicine, Fukushima Medical University, Fukushima, Japan.¹⁰⁹⁸Kansai Electric Power Hospital, Osaka, Japan.¹⁰⁹⁹Kumamoto City Hospital, Kumamoto, Japan.¹¹⁰⁰Department of Emergency and Critical Care Medicine, Tokyo Metropolitan Police Hospital, Tokyo, Japan.¹¹⁰¹Department of Respiratory Medicine, International University of Health and Welfare, Shioya Hospital, Narita, Japan.¹¹⁰²Department of Clinical Laboratory, International University of Health and Welfare, Shioya Hospital, Narita, Japan.¹¹⁰³National Hospital Organization Saitama Hospital, Saitama, Japan.¹¹⁰⁴Department of Respiratory Medicine, Gunma University Graduate School of Medicine, Maebashi, Japan.¹¹⁰⁵Department of Orthopedic Surgery, Tokyo Medical

University, Ibaraki Medical Center, Tokyo, Japan.¹¹⁰⁶Department of Internal Medicine, Kiryu Kosei General Hospital, Kiryu, Japan.¹¹⁰⁷Daini Osaka Police Hospital, Osaka, Japan.¹¹⁰⁸Department of Epidemiology, University Medical Centre Groningen, University of Groningen, Groningen, The Netherlands.¹¹⁰⁹Department of Psychiatry, University Medical Center Groningen, Groningen, The Netherlands.¹¹¹⁰Department of Genetics, University Medical Center Groningen, Groningen, The Netherlands.¹¹¹¹Centre for Heart Lung Innovation, University of British Columbia, Vancouver, British Columbia, Canada.¹¹¹²Division of Respiratory Medicine, Faculty of Medicine, University of British Columbia, Vancouver, British Columbia, Canada.¹¹¹³Institut Universitaire de Cardiologie et de Pneumologie de Québec, Université Laval, Québec, Québec, Canada.¹¹¹⁴Department of Genetics and Genomic Sciences, Icahn School of Medicine at Mount Sinai, New York, NY, USA.¹¹¹⁵University of Washington, Global Health, Seattle, WA, USA.¹¹¹⁶Gossamer Bio, San Diego, CA, USA.¹¹¹⁷Department of Pathology and Medical Biology, University Medical Centre Groningen, University of Groningen, Groningen, The Netherlands.¹¹¹⁸GRIAC Research Institute, University Medical Centre Groningen, University of Groningen, Groningen, The Netherlands.¹¹¹⁹Department of Pulmonary Diseases, University Medical Centre Groningen, University of Groningen, Groningen, The Netherlands.¹¹²⁰Center for Genomic Medicine, Massachusetts General Hospital, Boston, MA, USA.¹¹²¹Harvard Medical School, Cambridge, MA, USA.¹¹²²Program in Medical and Population Genetics, Broad Institute, Boston, MA, USA.¹¹²³Channing Division of Network Medicine, Department of Medicine, Brigham and Women's Hospital, Boston, MA, USA.¹¹²⁴Brigham and Women's Hospital, Boston, MA, USA.¹¹²⁵Psychiatric and Neurodevelopmental Genetics Unit, Center for Genomic Medicine, Massachusetts General Hospital, Boston, MA, USA.¹¹²⁶Department of Neurology, Massachusetts General Hospital, Boston, MA, USA.¹¹²⁷Division of General Internal Medicine, Massachusetts General Hospital and Department of Medicine, Boston, MA, USA.¹¹²⁸Department of Human Genetics, University of Michigan, Ann Arbor, MI, USA.¹¹²⁹Mount Sinai Clinical Intelligence Center, Department of Genetics and Genomic Sciences, Icahn School of Medicine at Mount Sinai, New York, NY, USA.¹¹³⁰Sema4, a Mount Sinai venture, Stamford, CT, USA.¹¹³¹Mount Sinai Clinical Intelligence Center, Charles Bronfman Institute for Personalized Medicine, New York, NY, USA.¹¹³²Department of Human Genetics, David Geffen School of Medicine at UCLA, Los Angeles, CA, USA.¹¹³³Icahn Institute of Data Science and Genomics Technology, Icahn School of Medicine, New York, NY, USA.¹¹³⁴Mount Sinai Clinical Intelligence Center, Icahn School of Medicine, New York, NY, USA.¹¹³⁵Department of Genetic and Genomic Sciences, Icahn School of Medicine at Mount Sinai, New York, NY, USA.¹¹³⁶Charles Bronfman Institute for Personalized Medicine, Icahn School of Medicine at Mount Sinai, New York, NY, USA.¹¹³⁷Institute for Genomic Health, Icahn School of Medicine at Mount Sinai, New York, NY, USA.¹¹³⁸The Mindich Child Health and Development Institute, Icahn School of Medicine at Mount Sinai, New York, NY, USA.¹¹³⁹Pamela Sklar Division of Psychiatric Genomics, Icahn School of Medicine at Mount Sinai, New York, NY, USA.¹¹⁴⁰Department of Psychiatry, Icahn School of Medicine at Mount Sinai, New York, NY, USA.¹¹⁴¹Icahn School of Medicine at Mount Sinai, New York, NY, USA.¹¹⁴²Department of Psychiatry, Department of Genetic and Genomic Sciences, Icahn School of Medicine at Mount Sinai, New York, NY, USA.¹¹⁴³Department of Environmental Medicine and Public Health, Icahn School of Medicine at Mount Sinai, New York, NY, USA.¹¹⁴⁴Department of Human Genetics, Center for Autism Research and Treatment, Institute for Precision Health, University of California Los Angeles, Los Angeles, CA, USA.¹¹⁴⁵The Hasso Plattner Institute of Digital Health at Mount Sinai, Icahn School of Medicine at Mount Sinai, New York, NY, USA.¹¹⁴⁶BioMe Phenomics Center, Icahn School of Medicine at Mount Sinai, New York, NY, USA.¹¹⁴⁷Department of Medicine, Icahn School of Medicine at Mount Sinai, New York, NY, USA.¹¹⁴⁸Regeneron Genetics Center, Tarrytown, NY, USA.¹¹⁴⁹Phenomic Analytics & Clinical Data Core, Geisinger Health System, Danville, PA, USA.¹¹⁵⁰Department of Population Health Sciences, Geisinger Health System, Danville, PA, USA.¹¹⁵¹Department of Molecular and Functional Genomics, Geisinger Health System, Danville, PA, USA.¹¹⁵²Department of Genetics, University of Pennsylvania Perelman School of Medicine, Philadelphia, PA, USA.¹¹⁵³Department of Biomedical Data Science, Stanford University, Stanford, CA, USA.¹¹⁵⁴Department of Psychiatry, University of North Carolina at Chapel Hill, Chapel Hill, USA.¹¹⁵⁵Department of Nutrition, University of North Carolina at Chapel Hill, Chapel Hill, USA.¹¹⁵⁶Institute of Neuroscience and Physiology, University of Gothenburg, Gothenburg, Sweden.¹¹⁵⁷Department of Medical Sciences, University of Turin, Turin, Italy.¹¹⁵⁸Department of Clinical and Biological Sciences, University of Turin, Orbassano, Italy.¹¹⁵⁹Department of Pediatrics, Department of Microbiology, Immunology and Molecular Genetics, University of California Los Angeles, Los Angeles, CA, USA.¹¹⁶⁰University of Genova, Genova, Italy.¹¹⁶¹Hopital Mont-Godinne, Yvoir, Belgium.¹¹⁶²Department of Molecular Medicine, University of Pavia, Pavia, Italy.¹¹⁶³Department of Public Health and Pediatric Sciences, University of Turin, Turin, Italy.¹¹⁶⁴Qatar Biobank for Medical Research, Qatar Foundation Research, Development and Innovation, Qatar Foundation, Doha, Qatar.¹¹⁶⁵Latvian Biomedical Research and Study Centre, Riga, Latvia.¹¹⁶⁶Department of Neuroscience, Karolinska Institutet, Stockholm, Sweden.¹¹⁶⁷Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany.¹¹⁶⁸Anaesthesiology and Intensive Care Medicine, Department of Surgical Sciences, Uppsala University, Uppsala, Sweden.¹¹⁶⁹Integrative Physiology, Department of Medical Cell Biology, Uppsala University, Uppsala, Sweden.¹¹⁷⁰Hedenstierna Laboratory, CIRRUS, Anaesthesiology and Intensive Care Medicine, Department of Surgical Sciences, Uppsala University, Uppsala, Sweden.¹¹⁷¹Department of Computer Science, School of Engineering, University of California Los Angeles, Los Angeles, CA, USA.¹¹⁷²University of California Los Angeles, Los Angeles, CA, USA.¹¹⁷³Department of Psychiatry and Biobehavioral Sciences, David Geffen School of Medicine at University of California Los Angeles, Los Angeles, CA, USA.¹¹⁷⁴Division of Immunology, Allergy, and Rheumatology, University of California Los Angeles, Los Angeles, CA, USA.¹¹⁷⁵Department of Psychiatry, University of California Los Angeles, Los Angeles, CA, USA.¹¹⁷⁶Department of Neurology, University of California Los Angeles, Los Angeles, CA, USA.¹¹⁷⁷Department of Computational Medicine, University of California Los Angeles, Los Angeles, CA, USA.¹¹⁷⁸Department of Pathology and Laboratory Medicine, University of California Los Angeles, Los Angeles, CA, USA.¹¹⁷⁹Bioinformatics IDP, UCLA, Los Angeles, CA, USA.¹¹⁸⁰Department of Neurology, David Geffen School of Medicine at UCLA, Los Angeles, CA, USA.¹¹⁸¹Department of Urology, David Geffen School of Medicine at UCLA, Los Angeles, CA, USA.¹¹⁸²Queen Mary University, London, UK.¹¹⁸³UCL Great Ormond Street Institute of Child Health, London, UK.¹¹⁸⁴University of Cambridge, Cambridge, UK.¹¹⁸⁵Big Data Institute, Nuffield Department of Population Health, Li Ka Shing Centre for Health Information and Discovery, University of Oxford, Oxford, UK.¹¹⁸⁶Experimental Medicine Division, Nuffield Department of

Medicine, John Radcliffe Hospital, University of Oxford, Oxford, UK. ¹²⁰²Public Health England, Field Service, Addenbrooke's Hospital, Cambridge, UK. ¹²⁰³Public Health England, Data and Analytical Services, National Infection Service, London, UK. ¹²⁰⁴Program in Bioinformatics and Integrative Genomics, Harvard Medical School, Boston, MA, USA. ¹²⁰⁵Program in Biological and Biomedical Sciences, Harvard Medical School, Boston, MA, USA. ¹²⁰⁷Department of Clinical Research and Leadership, George Washington University, Washington, DC, USA. ¹²⁰⁸Department of Human Genetics, The Wellcome Sanger Institute, Wellcome Genome Campus, Hinxton, Cambridge, UK. ¹²⁰⁹Strangeways Research Laboratory, The National Institute for Health Research Blood and Transplant Unit in Donor Health and Genomics, University of Cambridge, Cambridge, UK. ¹²¹⁰Department of Haematology, University of Cambridge, Cambridge Biomedical Campus, Cambridge, UK. ¹²¹¹British Heart Foundation Cardiovascular Epidemiology Unit, Department of Public Health and Primary Care, University of Cambridge, Cambridge, UK. ¹²¹²British Heart Foundation Centre of Research Excellence, University of Cambridge, Cambridge, UK. ¹²¹³The National Institute for Health Research Blood and Transplant Research Unit in Donor Health and Genomics, University of Cambridge, Cambridge, UK. ¹²¹⁴Health Data Research UK Cambridge, Wellcome Genome Campus and University of Cambridge, Cambridge, UK. ¹²¹⁵Department of Human Genetics, Wellcome Sanger Institute, Hinxton, UK. ¹²¹⁶Department of Epidemiology, Emory University Rollins School of Public Health, North Druid Hills, GA, USA. ¹²¹⁷Atlanta CA Health Care System, North Druid Hills, GA, USA. ¹²¹⁸Center for Population Genomics, MAVERIC, VA Boston Healthcare System, Boston, MA, USA. ¹²¹⁹MAVERIC, VA Boston Healthcare System, Boston, MA, USA. ¹²²⁰Stanford University, Stanford, CA, USA. ¹²²¹Palo Alto VA Healthcare System, Stanford, CA, USA. ¹²²²Department of Biostatistics, Boston University School of Public Health, Boston, MA, USA. ¹²²³Department of Haematology, Central Hospital of Bolzano (SABES-ASDAA), Bolzano, Italy. ¹²²⁴Laboratory of Clinical Pathology, Hospital of Bressanone (SABES-ASDAA), Bressanone, Italy. ¹²²⁶University of Alcalá, Centro de Investigación Biomédica en Red en Enfermedades Respiratorias (CIBERES), Madrid, Spain. ¹²²⁷Center for Applied Genomics, The Children's Hospital of Philadelphia, Philadelphia, PA, USA. ¹²²⁸Division of Human Genetics, Department of Pediatrics, The Perelman School of Medicine, University of Pennsylvania, Philadelphia, PA, USA. ¹²²⁹Faculty of Medicine, University of Iceland, Reykjavik, Iceland. ¹²³¹Infectious Disease Unit, Hospital of Massa, Massa, Italy. ¹²³²Department of Clinical Medicine, Public Health, Life and Environment Sciences, University of L'Aquila, L'Aquila, Italy. ¹²³³UOSD Laboratorio di Genetica Medica - ASL Viterbo, San Lorenzo, Italy. ¹²³⁴Unit of Infectious Diseases, S. M. Annunziata Hospital, Florence, Italy. ¹²³⁵Infectious Disease Unit, Hospital of Lucca, Lucca, Italy. ¹²³⁶Department of Clinical and Experimental Medicine, Infectious Diseases Unit, University of Pisa, Pisa, Italy. ¹²³⁸Clinic of Infectious Diseases, Catholic University of the Sacred Heart, Rome, Italy. ¹²³⁹Department of Diagnostic and Laboratory Medicine, Institute of Biochemistry and Clinical Biochemistry, Fondazione Policlinico Universitario A. Gemelli IRCCS, Catholic University of the Sacred Heart, Rome, Italy. ¹²⁴⁰Private University in the Principality of Liechtenstein, Triesen, Liechtenstein. ¹²⁴¹Digestive Diseases Unit, Virgen del Rocio University Hospital, Institute of Biomedicine of Seville, University of Seville, Seville, Spain. ¹²⁴²Department of Biochemistry, University Hospital Vall d'Hebron, Barcelona, Spain.

¹²⁴³University of Sevilla, Sevilla, Spain. ¹²⁴⁴Instituto de Biomedicina de Sevilla, Sevilla, Spain. ¹²⁴⁵Hospital Universitario Virgen del Rocio de Sevilla, Sevilla, Spain. ¹²⁴⁶Consejo Superior de Investigaciones científicas, Madrid, Spain. ¹²⁴⁷Humanitas Clinical and Research Center, IRCCS, Milan, Italy. ¹²⁴⁸Immunohematology Department, Banc de Sang i Teixits, Autonomous University of Barcelona, Barcelona, Spain. ¹²⁴⁹August Pi i Sunyer Biomedical Research Institute, Hospital Clinic, University of Barcelona, Barcelona, Spain. ¹²⁵⁰Department of Pathophysiology and Transplantation, Università degli Studi di Milano, Milan, Italy. ¹²⁵¹Internal Medicine Department, Virgen del Rocio University Hospital, Sevilla, Spain. ¹²⁵²Department of Biomedical Sciences, Humanitas University, Milan, Italy. ¹²⁵³Department Emergency, Anesthesia and Intensive Care, University Milano-Bicocca, Monza, Italy. ¹²⁵⁴Department of Medical Sciences, Università degli Studi di Torino, Turin, Italy. ¹²⁵⁵Department of Medical Microbiology, Clinic of Laboratory Medicine, St Olav's Hospital, Trondheim, Norway. ¹²⁵⁶Department of Infectious Diseases, St Olav's Hospital, Trondheim University Hospital, Trondheim, Norway. ¹²⁵⁷Department of Clinical and Molecular Medicine, NTNU, Trondheim, Norway. ¹²⁵⁸Department of Research, St Olav's Hospital, Trondheim University Hospital, Trondheim, Norway. ¹²⁵⁹Institute of Parasitology and Biomedicine Lopez-Neyra, Granada, Spain. ¹²⁶⁰Institute for Cardiogenetics, University of Lübeck, Lübeck, Germany. ¹²⁶¹German Research Center for Cardiovascular Research, partner site Hamburg-Lübeck-Kiel, Lübeck, Germany. ¹²⁶²University Heart Center Lübeck, Lübeck, Germany. ¹²⁶³Department of Research, Ostfold Hospital Trust, Gralun, Norway. ¹²⁶⁴Pediatric Department, Centro Tettamanti- European Reference Network (ERN) PaedCan, EuroBloodNet, MetabERN-University of Milano-Bicocca-Fondazione MBBM/Ospedale San Gerardo, Milan, Italy. ¹²⁶⁵Geminicenter for Sepsis Research, Institute of Circulation and Medical Imaging (ISB), NTNU, Trondheim, Norway. ¹²⁶⁶Clinic of Anesthesia and Intensive Care, St Olav's Hospital, Trondheim University Hospital, Trondheim, Norway. ¹²⁶⁷Clinic of Medicine and Rehabilitation, Levanger Hospital, Nord-Trøndelag Hospital Trust, Levanger, Norway. ¹²⁶⁸Stefan-Morsch-Stiftung, Birkenfeld, Germany. ¹²⁶⁹Center of Bioinformatics, Biostatistics, and Bioimaging, School of Medicine and Surgery, University of Milano Bicocca, Milan, Italy. ¹²⁷⁰Phase 1 Research Centre, ASST Monza, School of Medicine and Surgery, University of Milano-Bicocca, Milan, Italy. ¹²⁷¹Pneumologia ASST-Monza, University of Milano-Bicocca, Milano, Italy. ¹²⁷²School of Medicine and Surgery, University of Milano-Bicocca, Milano, Italy. ¹²⁷³Infectious Diseases Unit, San Gerardo Hospital, Monza, Italy. ¹²⁷⁴SODIR-VHIR research group, Barcelona, Spain. ¹²⁷⁵Bioinformatics area, Fundación progreso y Salud, Andalucía, Spain. ¹²⁷⁶Present address: Program in Metabolism, Broad Institute of MIT and Harvard, Cambridge, MA, USA. ¹²⁷⁷Present address: Program in Medical and Population Genetics, Broad Institute of MIT and Harvard, Cambridge, MA, USA. ¹²⁷⁸Present address: Diabetes Unit, Center for Genomic Medicine, Massachusetts General Hospital, Boston, MA, USA. ¹²⁷⁹Present address: Harvard Medical School, Boston, MA, USA. ¹²⁸⁰These authors contributed equally: Mari E. K. Niemi, Juha Karjalainen, Benjamin M. Neale, Mark Daly, Andrea Ganna. ¹²⁸¹Unaffiliated: Sangyoon Im, Jason Kendall, Michael MacMahon, Mark Peters, Robert Thompson, Martin Williams. ⁸³e-mail: bneale@broadinstitute.org; mark.daly@helsinki.fi; andrea.ganna@helsinki.fi

Methods

Contributing studies

All of the participants were recruited following protocols approved by local Institutional Review Boards; this information is collected in Supplementary Table 1 for all 46 studies. All protocols followed local ethics recommendations and informed consent was obtained when required. Information about sample numbers, sex and age from for each contributing study is given in Supplementary Table 1. In total, 16 studies contributed data to the analysis of critical illness due to COVID-19, 29 studies contributed data to hospitalized COVID-19 analysis and 44 studies contributed to the analysis of all cases of COVID-19. Each individual study that contributed data to a particular analysis met a minimum threshold of 50 cases, as defined by the phenotypic criteria, for statistical robustness. The effective sample sizes for each ancestry group shown in Fig. 1 were calculated for display using the formula: $((4 \times N_{\text{case}} \times N_{\text{control}}) / (N_{\text{case}} + N_{\text{control}}))$. Details of contributing research groups are provided in Supplementary Table 1.

Phenotype definitions

COVID-19 disease status (critical illness and hospitalization status) was assessed following the Diagnosis and Treatment Protocol for Novel Coronavirus Pneumonia³⁸. The critically ill COVID-19 group included patients who were hospitalized owing 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 owing to symptoms associated with laboratory-confirmed SARS-CoV-2 infection.

The reported SARS-CoV-2 infection 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 (for example, by questionnaire), with or without symptoms of any severity. Genetic-ancestry-matched control individuals 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. Additional information regarding individual studies contributing to the consortium are described in Supplementary Table 1.

Genome-wide association studies and meta-analyses

Each contributing study genotyped the samples and performed quality controls, data imputation and analysis independently, but following the consortium recommendations (information is available at <https://www.covid19hg.org/>). We recommended that genome-wide association study (GWAS) analyses were run using Scalable and Accurate Implementation of GEneralized mixed model (SAIGE)³⁹ on chromosomes 1–22 and X. The recommended analysis tool was SAIGE, but studies also used other software such as PLINK⁴⁰. The suggested covariates were age, age², sex, age × sex and the 20 first principal components. Any other study-specific covariates to account for known technical artefacts could be added. SAIGE automatically accounts for sample relatedness and case–control imbalances. Quality-control and analysis approaches for individual studies are reported in Supplementary Table 1.

Study-specific summary statistics were then processed for meta-analysis. Potential false positives, inflation and deflation were examined for each submitted GWAS. Allele frequency plots against gnomAD 3.0 genomes were manually inspected for each study. Standard error values as a function of the effective sample size were used to find studies that deviated from the expected trend. Summary statistics passing this manual quality control were included in the meta-analysis. Variants with an allele frequency of >0.1% and an imputation INFO score of >0.6 were carried forward from each study. Variants and alleles were lifted over to genome build GRCh38, if needed, and harmonized to

gnomAD 3.0 genomes⁴¹ by finding matching variants by strand flipping or switching the ordering of alleles. If multiple matching variants were included, the best match was chosen according to the minimum fold change in absolute allele frequency. Meta-analysis was performed using the inverse-variance-weighted (IVW) method on variants that were present in at least two-thirds of the studies contributing to the phenotype analysis. The method summarizes effect sizes across the multiple studies by computing the mean of the effect sizes weighted by the inverse variance in each individual study.

We report 13 meta-analysis variants that pass the genome-wide significance threshold after adjusting the threshold for multiple traits tested ($P < 5 \times 10^{-8}/3$). We report the unadjusted P values for each variant. We tested for heterogeneity between estimates from contributing studies using Cochran's Q -test^{42,43}. This is calculated for each variant as the weighted sum of squared differences between the effect sizes and their meta-analysis effect, the weights being the inverse variance of the effect size. Q is distributed as a χ^2 statistic with k (number of studies) minus one degrees of freedom. Two loci reached genome-wide significance but were excluded from the significant results in Supplementary Table 2 due to heterogeneity between estimates from contributing studies and missingness between studies at chr. 6: 31057940–31380334 and chr. 7: 54671568–54759789; however, these regions are not excluded from the corresponding summary statistics in data release 5 (COVID-19 HGI (<https://www.covid19hg.org/results/r5/>) and GWAS Catalog (study code GCST011074)). For each of the lead variants reported in Supplementary Table 2, we aimed to find loci specific to susceptibility or severity by testing whether there was heterogeneity between the effect sizes associated with hospitalized COVID-19 (progression to severe disease) and reported SARS-CoV-2 infection. We used the Cochran's Q measure^{42,43}, calculated for each variant as the weighted sum of squared differences between the two analysis effect sizes and their meta-analysis effect with the weights being the inverse variance of the effect size. A significant P value of $P < 0.004$ ($(0.05/13)$ loci) for multiple tests) indicates that the effect sizes for a particular variant are significantly different in the two analyses (Supplementary Table 2). For the nine loci, in which the lead variant effect size was significantly higher for hospitalized COVID-19, we carried out the same test again but comparing effect sizes from hospitalized COVID-19 with critically ill COVID-19 (Supplementary Table 4). Furthermore, we carried out the same test comparing meta-analysed hospitalized COVID-19 (population as controls) and hospitalized COVID-19 (SARS-CoV-2-positive but non-hospitalized as controls) (Supplementary Table 4). For these pairs of phenotype comparisons, we generated new meta-analysis summary statistics to use; including only those studies that could contribute data to both phenotypes that were under comparison.

Principal component projection

To project every GWAS participant into the same principal component (PC) space, we used pre-computed PC loadings and reference allele frequencies. For reference, we used unrelated samples from the 1000 Genomes Project and the Human Genome Diversity Project and computed PC loadings and allele frequencies for the 117,221 single-nucleotide polymorphisms (SNPs) that (1) are available in every cohort; (2) have a minor allele frequency of >0.1% in the reference; and (3) are LD-pruned ($r^2 < 0.8$; 500-kb window). We then asked each cohort to project their samples using our automated script provided at <https://github.com/covid19-hg/>. It internally uses the PLINK2⁴⁴ --score function with the variance-standardize option and reference allele frequencies (--read-freq); so that each cohort-specific genotype/dosage matrix is mean-centred and variance-standardized with respect to reference allele frequencies, but not cohort-specific allele frequencies. We further normalized the projected PC scores by dividing the values by a square root of the number of variants used for projection to account for a subtle difference due to missing variants.

Gene prioritization

To prioritize candidate causal genes reported in full in Supplementary Table 2, we used various gene prioritization approaches using both locus-based and similarity-based methods. Because we only describe the in silico gene prioritization results without characterizing the actual functional activity in vitro or in vivo, we aimed to provide a systematic approach to nominate potential causal genes in a locus using the following criteria.

(1) The closest gene: a gene that is closest to a lead variant by distance to the gene body.

(2) Genes in the LD region: genes that overlap with a genomic range containing any variants in LD ($r^2 > 0.6$) with a lead variant. For LD computation, we retrieved LD matrices provided by gnomAD v.2.1.1⁴¹ for each population analysed in this study (except for admixed American, Middle Eastern and South Asian genetic ancestry populations, for whom data are not available). We then constructed a weighted-average LD matrix by per-population sample sizes in each meta-analysis, which we used as a LD reference.

(3) Genes with coding variants: genes with at least one loss-of-function or missense variant (annotated by VEP⁴⁵ v.95 with GENCODE v.29) that is in LD with a lead variant ($r^2 > 0.6$).

(4) eGenes: genes with at least one fine-mapped *cis*-eQTL variant (PIP > 0.1) that is in LD with a lead variant ($r^2 > 0.6$) (Supplementary Table 5). We retrieved fine-mapped variants from the GTEx v.8²⁰ (<https://www.finucanelab.org/>) and eQTL catalogue⁴⁶. In addition, we looked up significant associations in the Lung eQTL Consortium²¹ ($n = 1,103$) to further support our findings in lung with a larger sample size (Supplementary Table 7). We note that, in contrast to the GTEx or eQTL catalogue, we only looked at associations and did not fine-map our data to the Lung eQTL Consortium data.

(5) V2G: a gene with the highest overall V2G score based on Open Targets Genetics (OTG)²⁶. For each variant, the overall V2G score aggregates differentially weighted evidence of variant–gene associations from several data sources, including molecular *cis*-QTL data (for example, *cis*-protein QTLs from ref.⁴⁷, *cis*-eQTLs from GTEx v.7 and so on), interaction-based datasets (for example, promoter capture Hi-C), genomic distance and variant effect predictions (VEP) from Ensembl. A detailed description of the evidence sources and weights used is provided in the OTG documentation (<https://genetics-docs.opentargets.org/our-approach/data-pipeline>)²⁶.

Phenome-wide association study

To investigate the evidence of shared effects of 15 index variants for COVID-19 and previously reported phenotypes, we performed a phenome-wide association study. We considered phenotypes in OTG obtained from the GWAS catalogue (this included studies with and without full summary statistics, $n = 300$ and 14,013, respectively)⁴⁸ and from the UK Biobank. Summary statistics for UK Biobank traits were extracted from SAIGE³⁹ for binary outcomes ($n = 1,283$ traits) and Neale v.2 ($n = 2,139$ traits) for both binary and quantitative traits (<http://www.nealelab.is/uk-biobank/>) and FinnGen Freeze 4 cohort (https://www.finnngen.fi/en/access_results). We report PheWAS results for phenotypes for which the lead variants were in high LD ($r^2 > 0.8$) with the 13 genome-wide significant lead variants from our main COVID-19 meta-analysis (Supplementary Table 6). This conservative approach allowed spurious signals primarily driven by proximity rather than actual colocalization to be removed (see Methods).

To remove plausible spurious associations, we retrieved phenotypes for GWAS lead variants that were in LD ($r^2 > 0.8$) with COVID-19 index variants.

Heritability

LD score regression v.1.0.1⁴⁹ was used to estimate the SNP heritability of the phenotypes from the meta-analysis summary statistic files. As this

method depends on matching the LD structure of the analysis sample to a reference panel, the summary statistics of European ancestry only were used. Sample sizes were $n = 5,101$ critically ill cases of COVID-19 and $n = 1,383,241$ control participants, $n = 9,986$ hospitalized cases of COVID-19 and $n = 1,877,672$ control participants, and $n = 38,984$ cases and $n = 1,644,784$ control participants for the analysis of all cases—all including the 23andMe cohort. Pre-calculated LD scores from the 1000 Genomes European reference population were obtained online (<https://data.broadinstitute.org/alkesgroup/LDSCORE/>). Analyses were conducted using the standard program settings for variant filtering (removal of non-HapMap3 SNPs, the HLA region on chromosome 6, non-autosomal, $\chi^2 > 30$, minor allele frequency of <1%, or allele mismatch with reference). We additionally report SNP heritability estimates for the all-ancestries meta-analyses, calculated using European panel LD scores, in Supplementary Table 8.

Partitioned heritability

We used partitioned LD score regression⁵⁰ to partition COVID-19 SNP heritability in cell types in our summary statistics for European ancestry only. We ran the analysis using the baseline model LD scores calculated for European populations and regression weights that are available online (<https://github.com/bulik/ldsc>). We used the COVID-19 summary statistics for European ancestry only for the analysis.

Genome-wide association summary statistics

We obtained genome-wide association summary statistics for 43 complex-disease, neuropsychiatric, behavioural or biomarker phenotypes (Supplementary Table 10). These phenotypes were selected based on their putative relevance to COVID-19 susceptibility, severity or mortality, with 19 selected based on the Centers for Disease Control list of underlying medical conditions associated with COVID-19 severity⁵¹ or traits reported to be associated with increased risk of COVID-19 mortality by OpenSafely⁵². Summary statistics generated from GWAS using individuals of European ancestry were preferentially selected if available. These summary statistics were used in subsequent genetic correlation and Mendelian randomization analyses.

Genetic correlation

LD score regression⁵⁰ was also used to estimate the genetic correlations between our COVID-19 meta-analysis phenotypes reported using samples of only European ancestry, and between these and the curated set of 38 summary statistics. Genetic correlations were estimated using the same LD score regression settings as for heritability calculations. Differences between the observed genetic correlations of SARS-CoV-2 infection and COVID-19 severity were compared using a z-score method⁵³.

Mendelian randomization

Two-sample Mendelian randomization was used to evaluate the potential for causal association of the 38 traits on COVID-19 hospitalization, on COVID-19 severity and reported SARS-CoV-2 infection using samples of only European ancestry. Independent genome-wide significant SNPs robustly associated with the exposures of interest ($P < 5 \times 10^{-8}$) were selected as genetic instruments by performing LD clumping using PLINK⁴⁰. We used a strict r^2 threshold of 0.001, a 10-Mb clumping window, and the European reference panel from the 1000 Genomes Project⁵⁴ to discard SNPs in LD with another variant with a smaller P -value association. For genetic variants that were not present in the hospitalized COVID-19 analysis, PLINK was used to identify proxy variants that were in LD ($r^2 > 0.8$). Next, the exposure and outcome datasets were harmonized using the R package TwoSampleMR⁵⁵. Namely, we ensured that the effect of a variant on the exposure and outcome corresponded to the same allele, we inferred positive-strand alleles and dropped palindromes with ambiguous allele frequencies, as well as incompatible alleles. Supplementary Table 10 includes the harmonized datasets used in the analyses.

The global test from Mendelian randomization pleiotropy residual sum and outlier (MR-PRESSO)⁵⁶ software was used to investigate overall horizontal pleiotropy. In brief, the standard IVW meta-analytic framework was used to calculate the average causal effect by excluding each genetic variant used to instrument the analysis. A global statistic was calculated by summing the observed residual sum of squares, that is, the difference between the effect predicted by the IVW slope excluding the SNP, and the observed effect of the SNP on the outcome. Overall horizontal pleiotropy was subsequently analysed by comparing the observed residual sum of squares, with the residual sum of squares expected under the null hypothesis of no pleiotropy. The MR-PRESSO global test was shown to perform well when the outcome and exposure GWASs are not disjoint (although the power to detect horizontal pleiotropy is slightly reduced by complete sample overlap). We also used the regression intercept in MR-Egger⁵⁷ to evaluate potential bias due to directional pleiotropic effects. This additional check was used in Mendelian randomization analyses with an I_{GX}^2 index surpassing the recommended threshold ($I_{GX}^2 > 90\%$)⁵⁸. Contingent on the MR-PRESSO global test results we analysed the causal effect of each exposure on COVID-19 hospitalization by using a fixed-effect IVW meta-analysis as the primary analysis, or, if pleiotropy was present, the MR-PRESSO outlier-corrected test. The IVW approach estimates the causal effect by aggregating the single-SNP causal effects (obtained using the ratio of coefficients method—that is, the ratio of the effect of the SNP on the outcome over the effect of the SNP on the exposure) in a fixed-effects meta-analysis. The SNPs were assigned weights based on their inverse variance. The IVW method confers the greatest statistical power for estimating causal associations⁵⁹, but assumes that all variants are valid instruments and can produce biased estimates if the average pleiotropic effect differs from zero. Alternatively, when horizontal pleiotropy was present, we used the MR-PRESSO outlier-corrected method to correct the IVW test by removing outlier SNPs. We conducted further sensitivity analyses using alternative Mendelian randomization methods that provide consistent estimates of the causal effect even when some instrumental variables are invalid, at the cost of reduced statistical power including: (1) Weighted median estimator (WME); (2) weighted mode-based estimator (WMBE); and (3) MR-Egger regression. Robust causal estimates were defined as those that were significant at an FDR of 5% and either (1) showed no evidence of heterogeneity (MR-PRESSO global test $P > 0.05$) or horizontal pleiotropy (Egger intercept $P > 0.05$); or (2) in the presence of heterogeneity or horizontal pleiotropy, the WME-, WMBE-, MR-Egger- or MR-PRESSO-corrected estimates were significant ($P < 0.05$). All statistical analyses were conducted using R v.4.0.3. Mendelian randomization analysis was performed using the 'TwoSampleMR' v.0.5.5 package⁵⁵.

Website and data distribution

In anticipation of the need to coordinate many international partners around a single meta-analysis effort, we created the COVID-19 HGI website (<https://covid19hg.org>). We were able to centralize information, recruit partner studies, rapidly distribute summary statistics and present preliminary interpretations of the results to the public. Open meetings are held on a monthly basis to discuss future plans and new results; video recordings and supporting documents are shared (<https://covid19hg.org/meeting-archive>). This centralized resource provides a conceptual and technological framework for organizing global academic and industry groups around a shared goal. The website source code and additional technical details are available at <https://github.com/covid19-hg/covid19hg>.

To recruit new international partner studies, we developed a workflow in which new studies are registered and verified by a curation team (<https://covid19hg.org/register>). Users can explore the registered studies using a customized interface to find and contact studies with similar goals or approaches (<https://covid19hg.org/partners>). This helps to promote organic assembly around focused projects that are

adjacent to the centralized effort (<https://covid19hg.org/projects>). Visitors can query study information, including study design and research questions. Registered studies are visualized on a world map and are searchable by institutional affiliation, city and country.

To encourage data sharing and other forms of participation, we created a rolling acknowledgements page (<https://covid19hg.org/acknowledgements>) and directions on how to contribute data to the central meta-analysis effort (<https://covid19hg.org/data-sharing>). Upon the completion of each data freeze, we post summary statistics, plots and sample size breakdowns for each phenotype and contributing cohort (<https://covid19hg.org/results>). The results can be explored using an interactive web browser (<https://app.covid19hg.org>). Several computational research groups carry out follow-up analyses, which are made available for download (<https://covid19hg.org/in-silico>). To enhance scientific communication to the public, preliminary results are described in blog posts by the scientific communications team and shared on Twitter. The first post was translated to 30 languages with the help of 85 volunteer translators. We compile publications and preprints submitted by participating groups and summarize genome-wide significant findings from these publications (<https://covid19hg.org/publications>).

Reporting summary

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

Data availability

Summary statistics generated by the COVID-19 HGI are available at <https://www.covid19hg.org/results/r5/> and are available in the GWAS Catalog (study code GCST011074). The analyses described here include the freeze-5 data. COVID-19 HGI continues to regularly release new data freezes. Summary statistics for non-European ancestry samples are not currently available due to the small individual sample sizes of these groups, but results for lead variants of 13 loci are reported in Supplementary Table 3. 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 lab (<http://www.nealelab.is/uk-biobank/>), Finucane lab (<https://www.finucanelab.org>), the FinnGen Freeze 4 cohort (https://www.finnngen.fi/en/access_results) and the eQTL catalogue release 3 (<http://www.ebi.ac.uk/eql/>).

Code availability

The code for summary statistics lift-over, the projection PCA pipeline including precomputed loadings and meta-analyses are available on GitHub (<https://github.com/covid19-hg/>) and the code for the Mendelian randomization and genetic correlation pipeline is available on GitHub at <https://github.com/marcoralab/MRcovid>.

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Author contributions Author contributions are provided within the author list.

Competing interests A full list of competing interests is supplied as Supplementary Table 13.

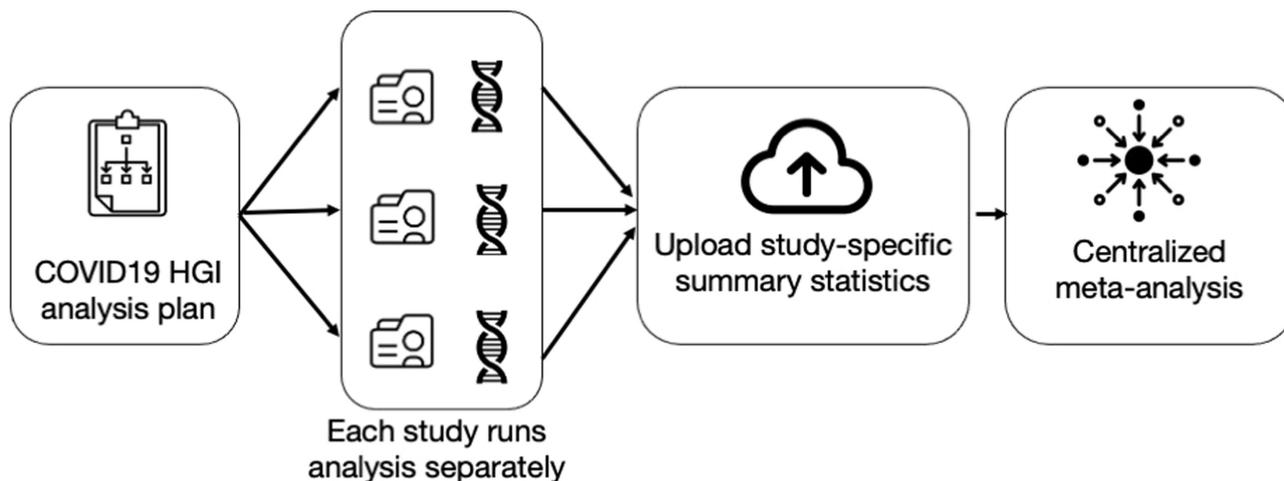
Additional information

Supplementary information The online version contains supplementary material available at <https://doi.org/10.1038/s41586-021-03767-x>.

Correspondence and requests for materials should be addressed to Benjamin M. Neale, Mark Daly, Andrea Ganna, Benjamin M. Neale or Mark Daly.

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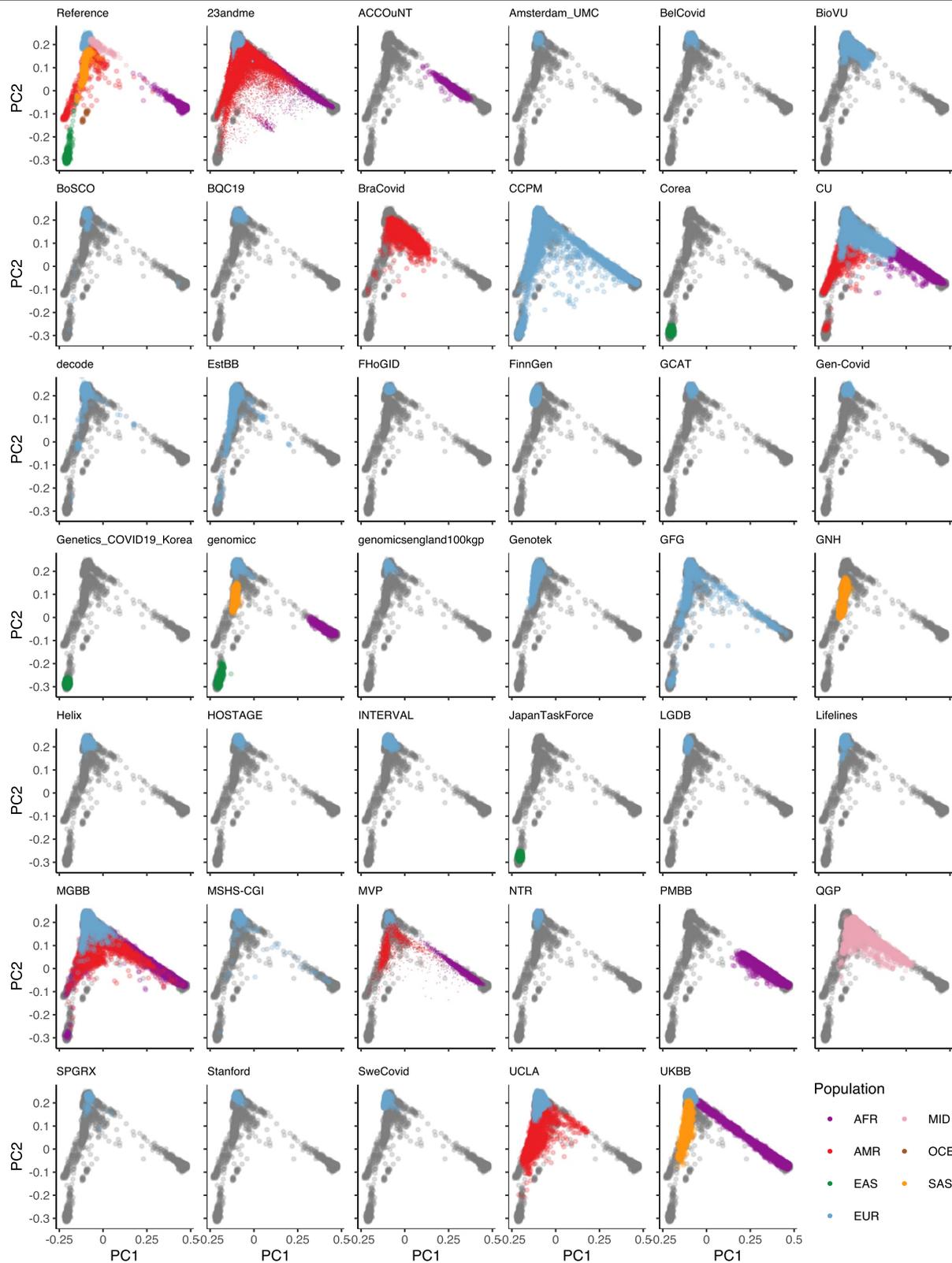
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	Critically ill COVID-19+	Hospitalized COVID-19+	Reported SARS-CoV-2 infection
Cases	Lab confirmed SARS-CoV-2 infection AND hospitalized for COVID-19 AND death OR respiratory support	Lab confirmed SARS-CoV-2 infection AND hospitalized for COVID-19	Lab confirmed SARS-CoV-2 infection OR Physician-reported COVID-19 OR self-reported COVID-19 via questionnaire
	N=6,179	N=13,641	N=49,562
Controls	Everybody that is not a case, e.g. population	Everybody that is not a case, e.g. population	Everybody that is not a case, e.g. population
	N=1,483,780	N=2,070,709	N=1,770,206
	↓	↓	↓
	6 loci	9 loci	7 loci
	13 unique loci		

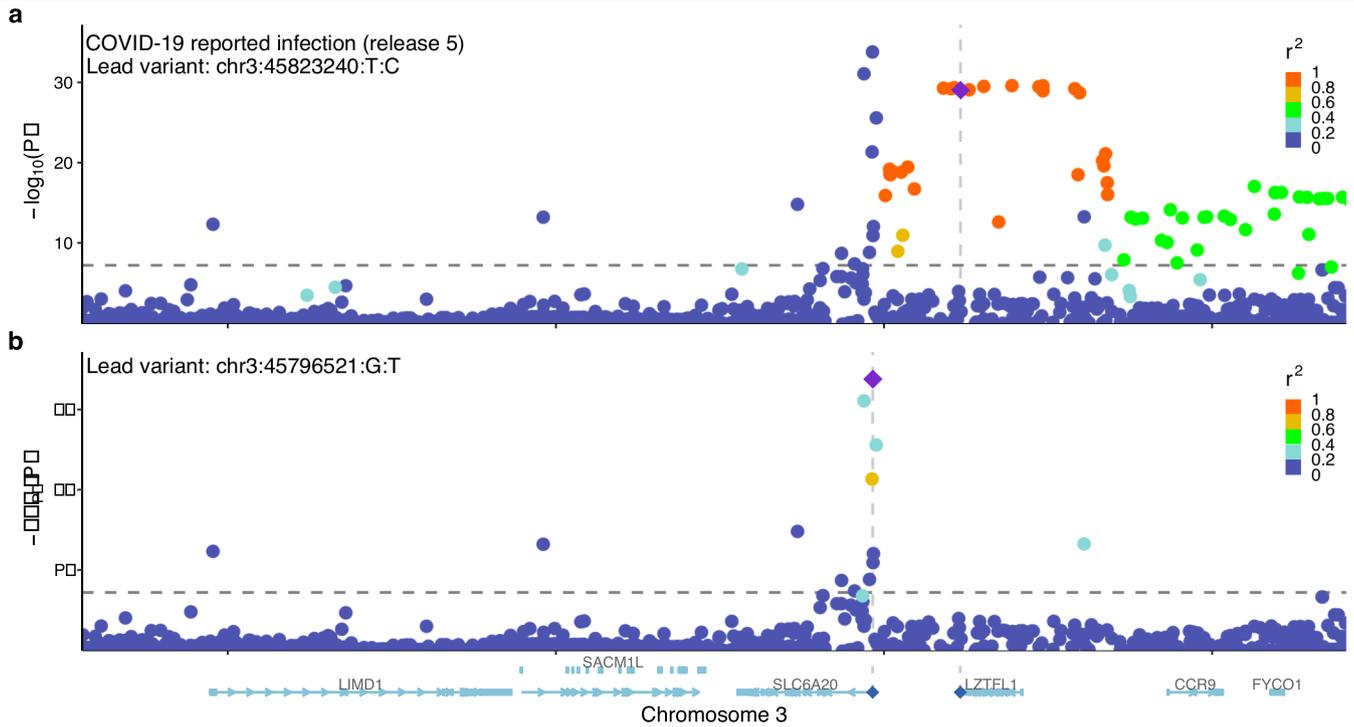
Extended Data Fig. 1 | Analytical summary of the COVID-19 HGI meta-analysis. Using the analytical plan set by the COVID-19 HGI, each individual study runs their analyses and uploads the results to the Initiative, who then runs the meta-analysis. There are three main analyses that each study can contribute summary statistics to: critically ill COVID-19, hospitalized COVID-19 and reported SARS-CoV-2 infection. The phenotypic criteria used to define cases are listed in the dark grey boxes, along with the numbers of cases

(*N*) included in the final all-ancestries meta-analysis. Controls were defined in the same way across all three analyses as everybody that is not a case—for example, population controls (light grey box). Sensitivity analyses—not reported in this extended data figure—also included mild and/or asymptomatic cases of COVID-19 as control individuals. Sample number (*N*) of control individuals differed between the analyses due to the difference in the number of studies contributing data to these.



Extended Data Fig. 2 | Projection of contributing studies samples into the same PC space. We asked participating studies to perform a PC projection using the 1000 Genomes Project and Human Genome Diversity Project as a reference, with a common set of variants. For each panel (except for the reference), coloured points correspond to contributed samples from each cohort, whereas grey points correspond to the reference samples from the 1000 Genomes Project. Colour represents a genetic population that each

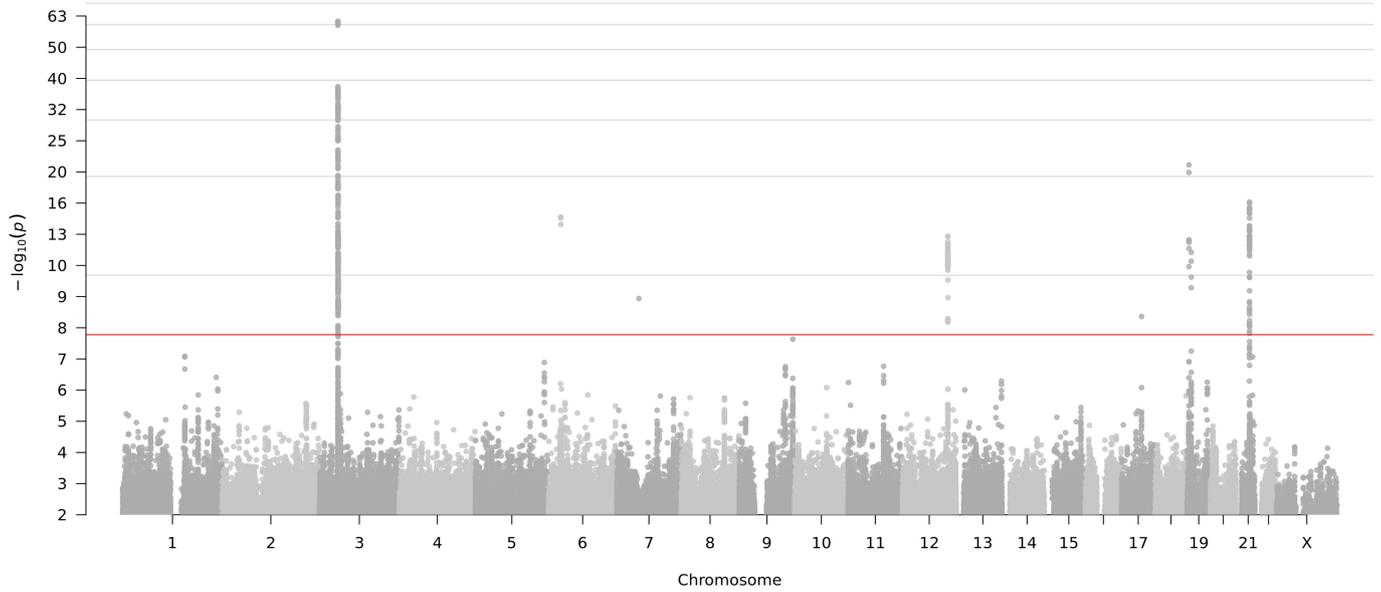
cohort specified. As 23andMe, Genomics England 100,000 Genomes Project (GenomicsEngland100kpg), and Million Veterans Program (MVP) only submitted PCA images, we overlaid their submitted transparent images using the same coordinates, instead of directly plotting them. Populations are defined as African (AFR), admixed American (AMR), East Asian (EAS), European (EUR), Middle Eastern (MID) and South Asian (SAS), Oceanian (OCE).



Extended Data Fig. 3 | Locus-zoom plots of the 3p21.31 region for reported SARS-CoV-2 infection. a, A standard plot without exclusion. Here, the severity lead variant rs10490770 (chr. 3: 45823240T:C) is shown as a lead variant.

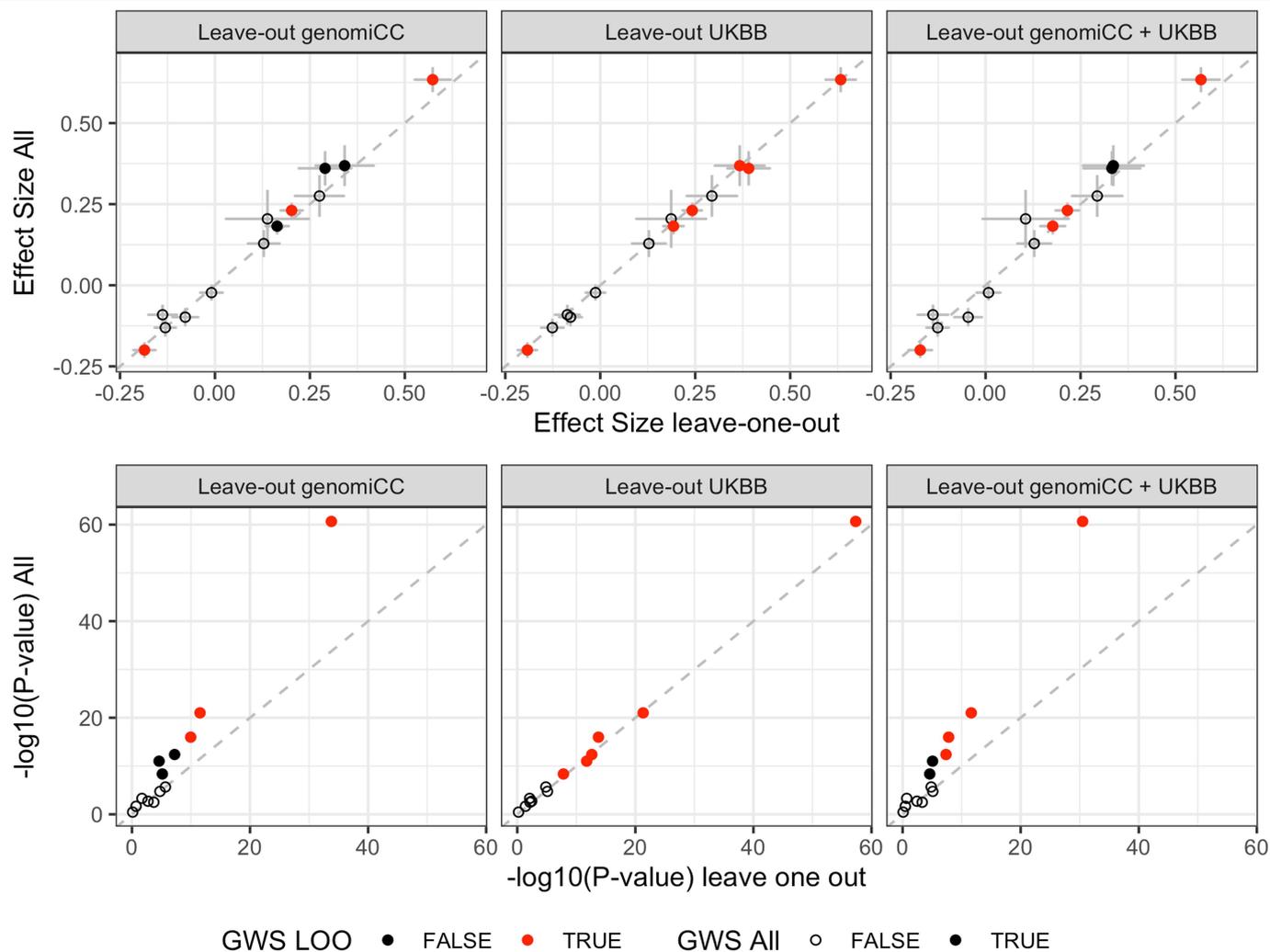
b, Additional independent susceptibility signal(s) after excluding variants with $r^2 > 0.05$ with rs10490770. The susceptibility lead variant rs2271616 (chr. 3: 45796521G:T) is highlighted.

Critically ill COVID-19+ (N.cases=6,179,N.controls=1,483,780)



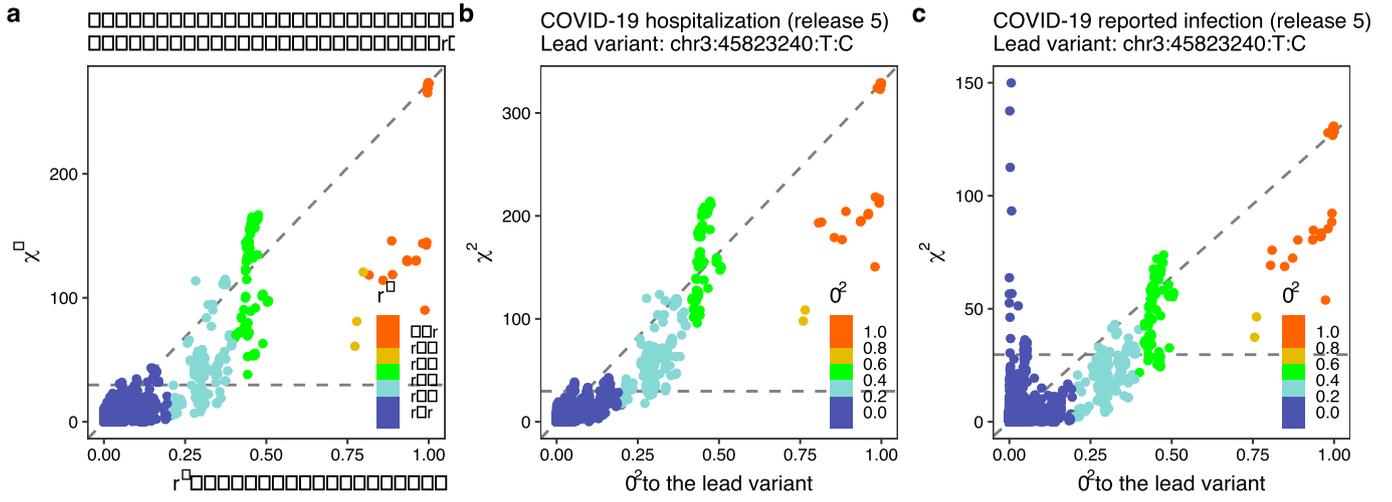
Extended Data Fig. 4 | Genome-wide meta-analysis association results for critical illness due to COVID-19. The locus on chromosome 6 is the HLA locus, which was removed from the list of reported loci in Supplementary Table 2 due to the high heterogeneity in effect size estimated between studies included in

the analysis. The locus on chromosome 7 was also not reported in Supplementary Table 2 due to missingness across studies—that is, the high number of studies in the meta-analysis that did not report summary statistics for this region. There are two association peaks on chromosome 19.



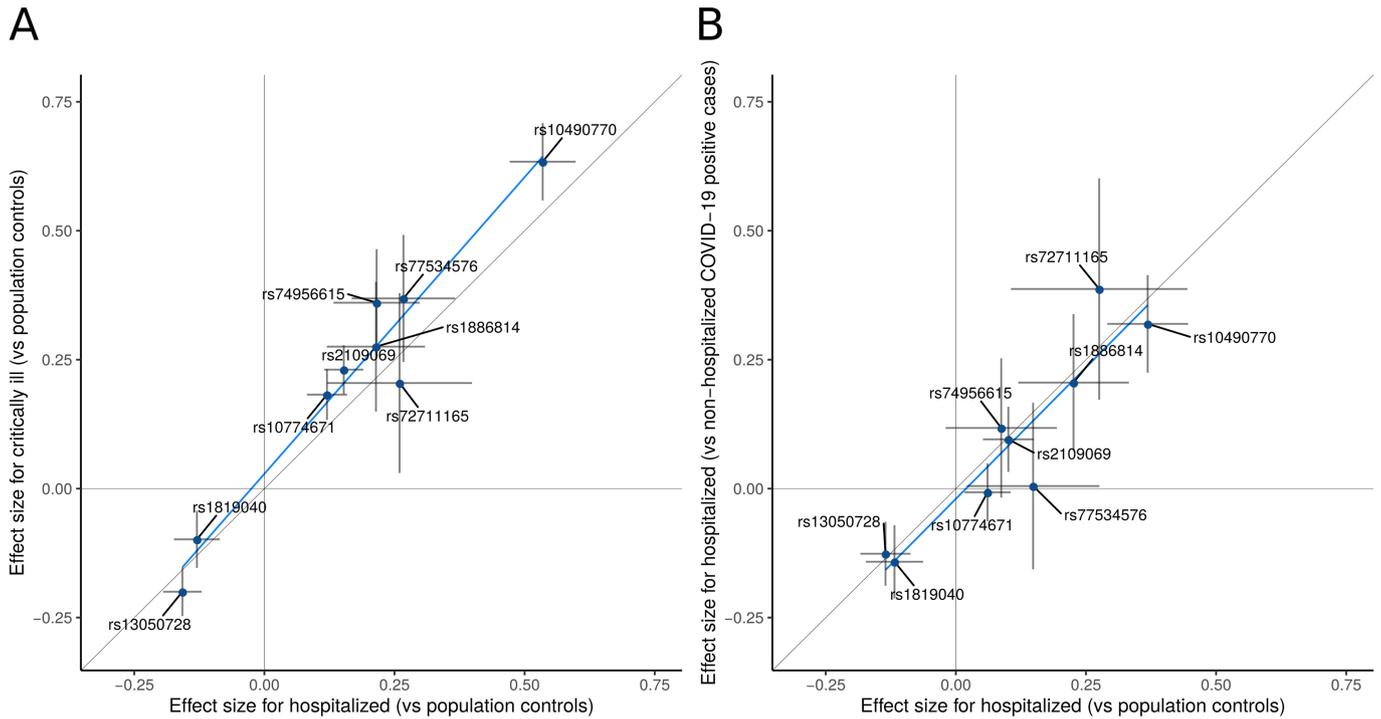
Extended Data Fig. 5 | Sensitivity analyses for overlapping controls in genomICC and UK Biobank. Comparison of the beta effect sizes (top) and unadjusted P values (bottom) of the 13 lead variants, using data from the COVID-19 critical illness meta-analysis in all the cohorts to leaving out genomICC (cases, $n = 4,354$; controls, $n = 1,474,655$; total, $n = 1,479,009$), leaving out the UK Biobank (UKBB; cases, $n = 5,870$; controls, $n = 1,155,203$; total, $n = 1,161,073$) and leaving out both genomICC and UK Biobank (cases, $n = 4,045$; controls, $n = 1,146,078$; total, $n = 1,150,123$) (from left to right, respectively). Top, dots and grey bars represent the beta effect size estimates \pm standard

error from the corresponding GWAS meta-analysis. Bottom, dots represent two-sided P values from the corresponding GWAS meta-analysis. Filled dots indicate variants that showed genome-wide significance in the full meta-analysis of critical illness due to COVID-19, and empty dots represent variants that were not significant for critical illness but were significant for either hospitalization due to COVID-19 or reported SARS-CoV-2 infection. Red dots represent variants that showed genome-wide significance in the leave-one-out analysis for genomICC, UK Biobank or genomICC and UK Biobank.



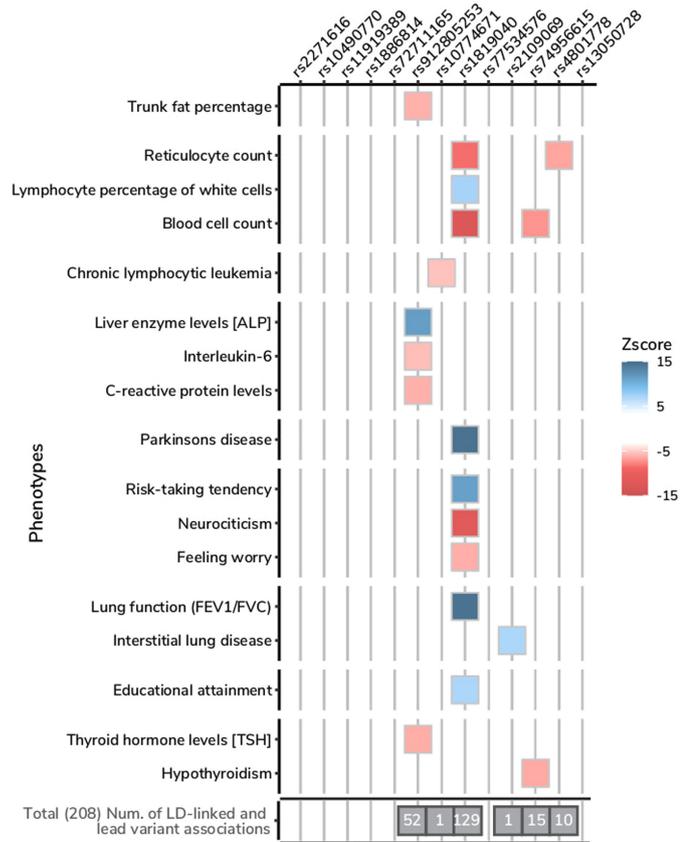
Extended Data Fig. 6 | Comparison of χ^2 statistics and r^2 values to the lead variant in the 3p21.31 region. a-c, Data are shown for critical illness (a), hospitalization (b) and reported SARS-CoV-2 infection (c). The left blue peak in

c, which is uncorrelated with the lead variants in the region, indicates that there are independent signals.



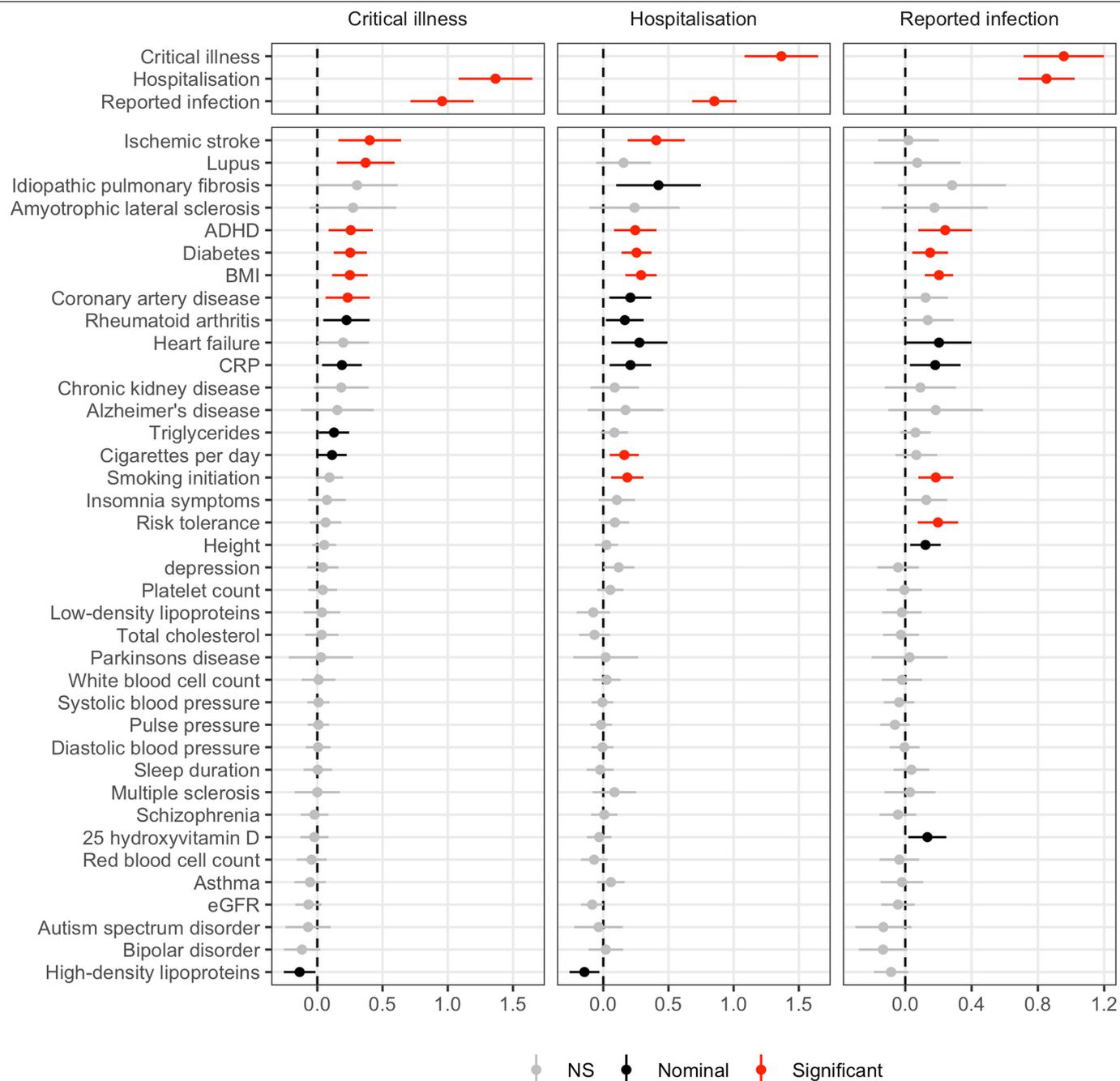
Extended Data Fig. 7 | Comparison of the effect sizes of lead variants between pairs of COVID-19 meta-analyses. Comparison of effect sizes for the nine variants associated with severity of COVID-19 disease. **a**, Comparing hospitalized cases of COVID-19 versus population controls ($n = 10,428$ cases and $n = 1,483,270$ controls) and critically ill cases of COVID-19 versus population controls ($n = 6,179$ cases and $n = 1,483,780$ controls). **b**, Hospitalized cases of COVID-19 versus population controls ($n = 5,806$ cases and $n = 1,144,263$ controls) and hospitalized cases of COVID-19 versus non-hospitalized cases of

COVID-19 ($n = 5,773$ cases and $n = 15,497$ controls). Sample sizes for hospitalized cases of COVID-19 versus population controls differ between **a** and **b** due to differences in the sampling of studies selected for the analysis. This selection included all studies that were able to contribute data to the respective analyses that the data were compared to (shown on the y axis) in each panel. Dots represent the effect size beta estimates, bars represent the 95% confidence interval of the estimates. Effect size estimates and P values for heterogeneity tests (Cochran's Q , two-tailed test) are reported in Supplementary Table 3.



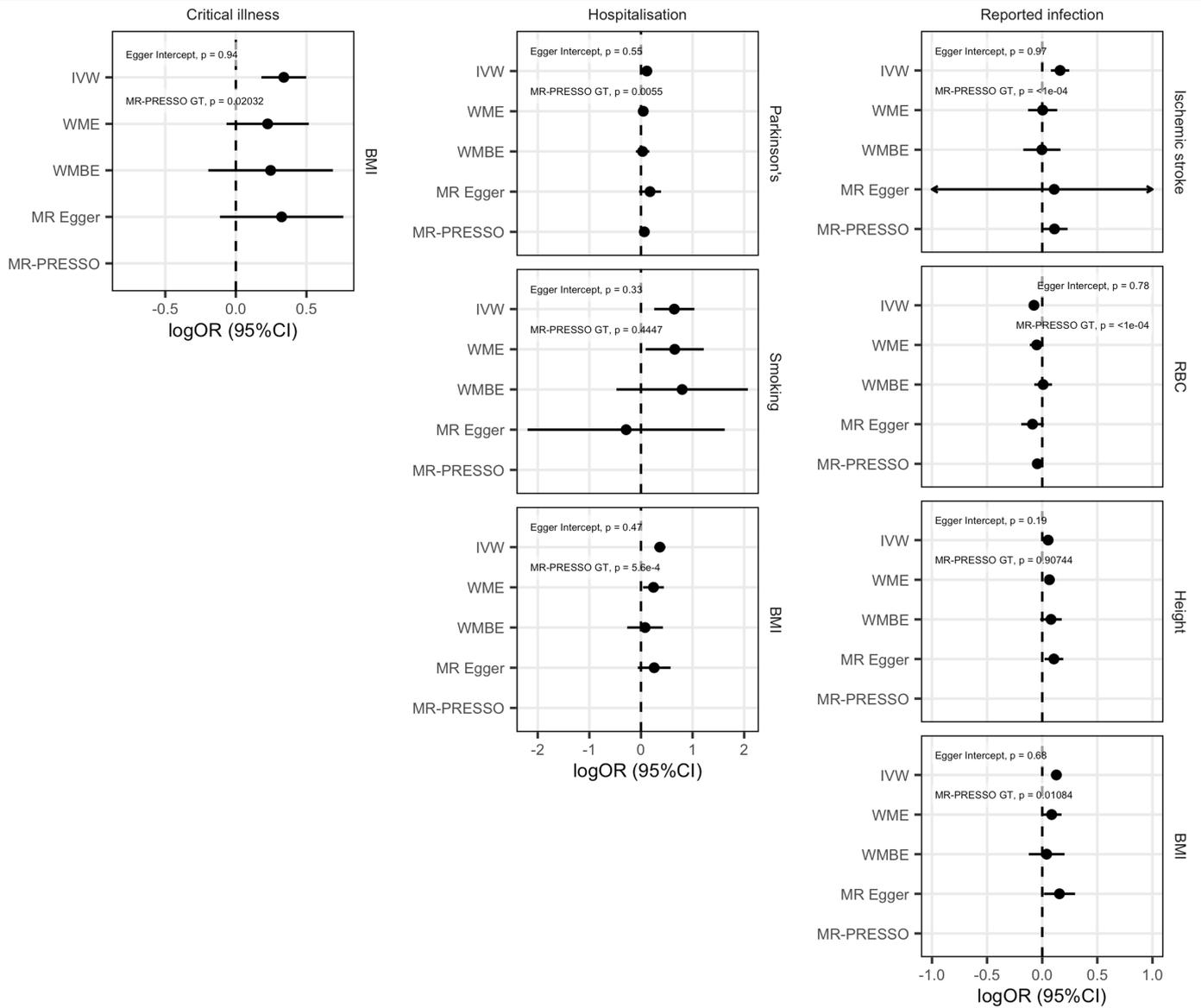
Extended Data Fig. 8 | PheWAS for genome-wide significant lead variants.

Selected phenotypes associated with genome-wide significant COVID-19 variants (see Supplementary Table 6 for a complete list). We report those associations for which a lead variant from a previous GWAS result was in high LD ($r^2 > 0.8$) with the index COVID-19 variants. The colour represents the z-scores of correlated risk increasing alleles for the trait. The total number of associations for each COVID-19 variant is highlighted in the grey box.



Extended Data Fig. 9 | Genetic correlation with COVID-19 phenotypes. Each column shows the genetic correlation results for the three COVID-19 phenotypes (European-ancestry analyses only): critical illness, hospitalization and reported SARS-CoV-2 infection. The traits that the genetic correlation is run against are listed on the left. Significant correlations (FDR < 0.05) are

shown with their 95% confidence intervals in red, nominally significant correlations ($P < 0.05$) are in black and non-significant correlations are in grey. Two-sided P values were calculated using LDSC for genetic correlations and exact estimates, unadjusted standard errors and two-sided P values are available in Supplementary Table 11.



Extended Data Fig. 10 | Mendelian randomization sensitivity analyses. Genetic correlations and Forest plots displaying the causal estimates for each of the sensitivity analyses used in the Mendelian randomization analysis for

trait pairs that were significant at an FDR of 5%. Two-sided *P* values were estimated using IVW, WME, WMBE and MR-PRESSO analyses. RBC, red blood cell count.

Reporting Summary

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Software and code

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

Data collection

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 did release 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.

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 Fixed-effects 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 liftover, projection PCA pipeline including precomputed loadings and meta-analysis are available at <https://github.com/covid19-hg/> and the code for Mendelian randomization and genetic correlation pipeline at <https://github.com/marcoralab/MRcovid>.

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Data availability statement:

Summary statistics generated by COVID-19 HGI are available at <https://www.covid19hg.org/results/r5/> and are available on GWAS Catalog (study code GCST011074). The analyses described here utilize the freeze 5 data. COVID-19 HGI continues to regularly release new data freezes. Summary statistics for non-European ancestry samples are not currently available due to the small individual sample sizes of these groups, but results for 13 loci lead variants are reported in Supplementary Table 3. 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 lab (<http://www.nealelab.is/uk-biobank/>), Finucane lab (<https://www.finucanelab.org>), FinnGen Freeze 4 cohort (https://www.finnngen.fi/en/access_results), and eQTL catalogue release 3 (<http://www.ebi.ac.uk/eqtl/>).

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Life sciences study design

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Sample size	The consortium meta-analysed genome-wide association study (GWAS) summary statistics from any individual study that had included a minimum of n=50 cases and n=50 controls in their analysis. The cutoff at n=50 cases and n=50 controls was aimed at reducing noise to the meta-analysis, but also to be inclusive of studies that had not yet accumulated large numbers of COVID-19 patient data. 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). 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, and Table 1 excludes two genome-wide significant loci that were deemed to have extremely heterogeneous effects, but these variants are reported in the released consortium summary statistics (with heterogeneity test values).
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. 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 ² + 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.

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Human research participants

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Population characteristics

Summary statistics from 46 independent studies were included in consortium meta-analyses. Mean age of cases across studies was 55.3 years. The effective sample size for genetic ancestry populations was: n=11,598 Middle Eastern; n=28,918 South Asian; 43,332 East Asian; 48,714 African; 70,902 Ad-mixed American; 738,538 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.