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Supplementary Material for

Spatiotemporal invasion dynamics of SARS-CoV-2 lineage B.1.1.7 emergence

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Other Supplementary Material for this manuscript includes the following:
(available at science.sciencemag.org/content/science.abj0113/DC1)

Materials and Methods

Human mobility data

We used two human mobility datasets in this study. The O2 dataset was available for February 2020 and very comprehensive (capturing ~21 million unique users (roughly 32% of the UK population (*58*) and 35% of smartphone users ((*59*)). However, this dataset was not available through time so we complemented it with weekly aggregated human mobility data from the Google COVID-19 Aggregated Mobility Research Dataset (*60*) which represents ~29.7 million smartphone users (calculated as the total number of smartphone users in the UK (*59*) multiplied by the proportion of Android users ((*61*). Both datasets exhibit a very strong correlation (Fig. S18, Pearson's r = 0.95, CI 0.95-0.95, $p < 0.001$).

Static human mobility data: We use anonymised and aggregated mobile data insights collected from the network operator, O2 in the UK. The O2 data is extrapolated to give a picture of movement trends of the UK population over the age of 12 and includes trips using all transport and purpose modes. Extrapolation was performed accounting for the number of unique users in each LAD. All trips were allocated to 'Local Authority Districts' (LADs) (https://geoportal.statistics.gov.uk/datasets/local-authority-districts-december-2019-boundaries-uk-bfc) based on cell tower overlaps. Data also includes Scotland, Wales, and Northern Ireland. Trips are recorded when a mobile device connects from one mobile cell mast to the next, non-overlapping, cell mast. This means that some shorter trips may not be included. Further, the size of the cells may vary depending on the population density of the region. The trips shown in this manuscript represent the average number of trips per weekday (Mon – Thu) in February 2020 between Kent and London and other LADs in the UK. For analyses that are performed at the UTLA level we aggregate movements from LAD level to UTLA using a standard conversion: https://geoportal.statistics.gov.uk/datasets/3e4f4af826d343349c13fb7f0aa2a307_0. Removing Hampshire (outlier on the left side in Figure 1c) when estimating the association between movements from Kent and London and B.1.1.7 detection results in only minor changes to the correlation coefficient (Pearson's r = -0.67, CI -0.53 : -0.78, $p < 0.001$).

Time-varying weekly human mobility data: We used the Google COVID-19 Aggregated Mobility Research Dataset (*60*), which contains anonymized relative mobility flows aggregated over users who have turned on the Location History setting, which is off by default. This is similar to the data used to show how busy certain types of places are in Google Maps — helping identify when a local business tends to be the most crowded. The mobility flux is aggregated per week, between pairs of approximately $5km^2$ cells worldwide and for the purpose of this study aggregated for LADs in the United Kingdom for the time period August 31st, 2020 to January 12th, 2021 (https://geoportal.statistics.gov.uk/datasets/local-authority-districts-december-2019-boundaries-uk-bfc).

To produce this dataset, machine learning is applied to log data to automatically segment it into semantic trips. To provide strong privacy guarantees, all trips were anonymized and aggregated using a differentially private mechanism to aggregate flows over time (see https://policies.google.com/technologies/anonymization). This research is done on the resulting heavily aggregated and differentially private data. No individual user data was ever manually inspected, only heavily aggregated flows of large populations were handled.

All anonymized trips are processed in aggregate to extract their origin and destination locations and times. For example, if users traveled from location *a* to location *b* within time interval *t*, the corresponding cell (*a,b,t*) in the tensor would be $n \pm err$, where *err* is Laplacian noise. The automated Laplace mechanism adds random noise drawn from a zero-mean Laplace distribution and yields (ϵ, δ)-differential privacy guarantee of $\epsilon = 0.66$ and $\delta = 2.1 \times 10^{-29}$. The parameter ϵ controls the noise intensity in terms of its variance, while δ represents the deviation from pure ϵ-privacy. The closer they are to zero, the stronger the privacy guarantees. Each user contributes at most one increment to each partition. If they travel from one region, *a* , to another region, *b*, multiple times during the same week, they only contribute once to the aggregation count.

These results should be interpreted in light of several important limitations. First, the Google mobility data is limited to smartphone users who have opted in to Google's Location History feature,

which is off by default. These data may not be representative of the population as whole, and furthermore, their representativeness may vary by location. Importantly, these limited data are only viewed through the lens of differential privacy algorithms, specifically designed to protect user anonymity and obscure fine details. Moreover, comparisons across, rather than within, locations (countries) are only descriptive since these regions can differ in substantial ways.

We converted the relative number of trips in the Google mobility data to trip numbers by multiplying relative trips by the slope of a linear regression between the monthly relative Google movements between pairs of locations and corresponding monthly O2 movements in February. Weekend day movements were calculated as 77.6% of weekday movements based on insights from the O2 data, where daily human mobility data was available. Weekday to weekend movements vary only slightly across LADs in the UK (mean 0.776, median 0.78, 50% CI 0.76 - 0.80). We note that a trip is reported when there was a 'significant stop' in a location. For example if someone travels from location A to C through B only A to C is reported. If someone travels from A to B (decides to make a significant stop there for roughly >15 minutes) and then continues to C the matrix shows one trip from A to B and another from B to C (no report of A to C).

Epidemiological case data

Daily new cases by specimen date were downloaded from https://coronavirus.data.gov.uk/details/download. Data was last accessed on January 29th, 2020. Additionally we used line-list data provided and collected by Public Health England (PHE). These data include additional information about the SGTF test result status. There were multiple entries of the same unique identifiers in the SGTF test results, which prevented directly mapping the SGTF test results to the full line list (where the unique identifiers are truly unique). Specifically, there were 50,357 "individuals" with multiple test results, of which 48,599 had the same result, i.e., they were both negative or both positive, and could be readily merged with the full line list. However, 1758 did not match, i.e., one result was positive and the other negative, and these cases were subsequently excluded from all analyses. The total excluded cases were <0.15% of the total unique individuals that tested positive and were present in the line list dataset. This data was available at the resolution of LTLAs.

Coronavirus (COVID-19) Infection Survey UK

We use data from the COVID-19 Infection Survey from the Office of National Statistics (ONS) from January 29th, 2021 (*62*). Surveys are designed to estimate the daily percentage of the population (non-symptomatic) to test positive across regions in the UK. To calculate the relative rate of exportation of B.1.1.7 from London to locations elsewhere we multiply the unrounded, modelled daily rates of the estimated percentage of the population of Greater London testing positive for COVID-19 with the estimated weekly number of movements from Greater London to UTLAs and LADs across the United Kingdom. Together, we call this the estimated exportation intensity (EEI). We split the EEI into B.1.1.7 and non-B.1.1.7 components using the weekly proportion of B.1.1.7 genomes in Greater London.

Genomic data

Sequences were aligned as part of the grapevine pipeline (https://github.com/COG-UK/grapevine/) which processes COG and GISAID data every day. Using pangolin (https://github.com/cov-lineages/pangolin), we identified sequences that are part of the B.1.1.7 lineage, and extracted corresponding cleaned metadata. The genomic data contain the date a sample was collected, which was used as reference in the analyses. We then use the line list data to calculate the average delay between specimen collection date and date of onset of symptoms which was 2.206 days (rounded to 2 days). On average infectiousness is highest around the start of symptom onset. We therefore further subtract 1 day and use that as the date when the individual became infectious (*63*).

Metadata: The location data for sequences is cleaned as part of the grapevine pipeline (https://github.com/COG-UK/grapevine/), and is available at the administrative level 2 level, see Table S2. Custom Python scripts were used to match UTLAs and LADs to adm2 and adm3 regions from the Global Administrative Database (GADM, https://gadm.org/) for mapping and analysis. Some

adm2 areas which are commonly thought to be part of larger areas were grouped into that larger region (e.g. Leicester was changed to Leicestershire).

Continuous phylogeographical analysis

The dataset used was a subset of the genomic dataset described for the other analyses. Those sequences from pillar two (i.e. surveillance) sequencing, and those with correct postcode district (outer postcode) were used, resulting in a dataset of 17,741 sequences. These sequences were exclusively from England, as there were either no sequences or no usable postcode district data in pillar two sequences of the lineage B.1.1.7 from this time period present for the other constituent nations. The number of sequences per postcode in this dataset is shown in Fig. S19, and the correlation between the number of sequences and the number of SGTF positive cases is shown in Fig. S6.

These sequences were extracted from the master COG alignment, an approximately maximum likelihood (ML) tree was built using FastTree (*64*) which was then used as a starting tree for building a more reliable ML tree using the HKY substitution model (*65*) in IQTree (*66*). The resulting tree was passed into TreeTime (*67*) to generate a time-scaled phylogeny. After examining the root-to-tip plot, 23 molecular clock outliers were removed (*68*). Two additional sequences were also removed for being a known partial B.1.1.7 genome (MILK-B154B6) and a known recombinant (CAMC-CBA018). The final dataset therefore had 17,716 sequences. The ML and time-scaled tree were used as the inputs for a variation on a common Bayesian phylogenetic analysis using the BEAST software package (see (*16*) for details) with a strict clock model and a nonparametric skygrid coalescent prior (*69*). The tree with the highest likelihood from this analysis was used as the empirical tree for the continuous phylogeographic analysis, shown in Fig. S5.

We performed the continuous phylogeographic analysis using a relaxed random walk (RRW) diffusion model (*26*) available in BEAST 1.10 (*70*), and a Cauchy distribution to model the among-branch heterogeneity in diffusion velocity. This model infers the locations of the internal nodes in the tree. Branch movements are defined as the path travelled across the map by a branch in the phylogenetic tree from the ancestral to descendent nodes. Because the phylogeographic inference under the RRW diffusion model does not allow identical sampling coordinates assigned to sampled sequences, we avoided assigning sampling coordinates using the centroid point of each administrative area of the origin postcode location. For a given sampled sequence, we instead retrieved geographic coordinates from a point randomly sampled within its postcode area of origin (using shapefiles from (*71*)), which is the maximal level of spatial precision available for the samples. Phylogeographic results may be biased when early dispersals are more likely to lead to substantial onward transmission than later exports. The tree then may capture a slightly higher fraction of earlier translocations than later ones which may explain the observed difference between early exports from the phylogeographic results compared to those estimates from the SGTF data. Visualisation was performed using a custom R script, which can be found at https://github.com/COG-UK/B.1.1.7_spatial_analysis_UK.

Estimate of case growth rates

To estimate the daily epidemic growth rates in each LTLA/UTLA, we fit a mixed effects GLM of log new daily case counts in sliding 6-day windows (fixed effect; approximately the generation time of COVID-19) and a random effect for each LTLA/UTLA on the slope and intercept, using the R package lme4 v.1.1-21 (*72*). Daily case counts were determined using the date of specimen collection. Qualitatively similar results were obtained by estimating the epidemic doubling time across each LTLA/UTLA using mixed-effects Poisson and negative binomial GLMs. The growth rates included in subsequent models used to estimate the effects of mobility, etc. on B.1.1.7 growth rates are the median value of these sliding window estimates.

Estimation of SGTF and Non-SGTF growth rates: To calculate the instantaneous growth rates for both SGTF and non-SGTF cases, we fit a mixed effects log-linear GLM of new daily case counts (fixed effect) - stratified by SGTF test results - and a random effect for each LTLA/UTLA on the slope and intercept, using the R package lme4 v.1.1-21 (*72*). Growth rates were calculated in sliding 6-day windows. We estimate the total S- and S+ in each LTLA/UTLA and day by adjusting counts upwards in proportion to total cases reported in each LTLA/UTLA and day.

Excess growth rate regressions: We calculate the excess growth rate by simply subtracting the estimated growth rate for non SGTF cases from SGTF cases at each day between 15th November and December 20th (for sensitivity we extended that period to January 5th, 2021). We then use estimates from the phylogeographic reconstruction on the number of estimated imports of B.1.1.7 from Greater London and estimates of the number of expected imports using prevalence data (ONS) and estimated daily human mobility as predictors of the excess growth rate. We performed univariate and multivariate analyses because of collinearity of the predictors. Results are robust across both models.

$$ExcessGRate_{ij} = \beta_{0j} + \beta_1 * log_e(EII)_{ij} + \beta_2 * B117Imports_{ij} + \varepsilon_{ij}$$

$\beta_{0j} = \beta_0 + u_{0j}$ (random intercept for LTLAs)
$\varepsilon_{ij} \sim N(0, \sigma_e^2)$
$u_{0j} \sim N(0, \sigma_u^2)$

where i = day; j = LTLA regions

Estimate of drivers of the increase in frequency of B.1.1.7 and SGTF

Genome sequence data analysis: For all genomes sampled in Kent, ~55% were assigned lineage B.1.1.7 between 5th November and 2nd December. Using a Beta prior (0.1,1) that assumes the pre-lockdown frequencies of B.1.1.7 to be low, we can update the estimated frequency using sampling data from the periods *pre-lockdown* (prior to November 5th), *lockdown* (November 5th - December 2nd), *post-lockdown* (December 3rd - 16th), late December (after December 16th) and most recent (after January 1st, 2021). When updating the posteriors for the subsequent sampling period, we take as priors the posteriors from the previous period (down-weighted to prevent more recent data from being overwhelmed by earlier samples). We observe consistent increases in the frequency of B.1.1.7 across the sampling periods (Fig. 5a). Specifically, we see increases in Medway and Kent in the initial phase, and rapid increases in East Sussex and Swindon after the lockdown ended (Fig. 5a). Other locations exhibit slower increases, for example Norfolk (Fig. S16).

SGTF data analysis: Using SGTF data we also find consistent increases in frequency among locations across the sampling periods (Fig. 5b; differences between genome data and SGTF data are not statistically significant). However, we note that SGTF observations may be biased in October and November due to the co-circulation of lineages other than B.1.1.7 that can also lead to SGTF (Fig. S17). Using SGTF as a proxy for B.1.1.7 is therefore time-dependent and depends on the background diversity of co-circulating lineages.

Mobility, case, and B.1.1.7/SGTF frequencies were aggregated up to each UTLA to ease comparison between all of the different data sources. To determine the relationship between these variables, we fit multi-GLM regressions to natural-log transformed data using base R. Model selection was used to confirm these results by exhaustive search with BIC in the R package glmulti v. 1.0.7.1 (*73*). For each time window included in our study, we included the following possible predictors: mobility from Greater London, within-UTLA mobility, SARS-CoV-2 incidence prior to the November lockdown, estimated arrival time of B.1.1.7, proportion of the population under age 20, median growth rate (all cases, SGTF, and non-SGTF), and B.1.1.7/SGTF frequency in the previous time window.

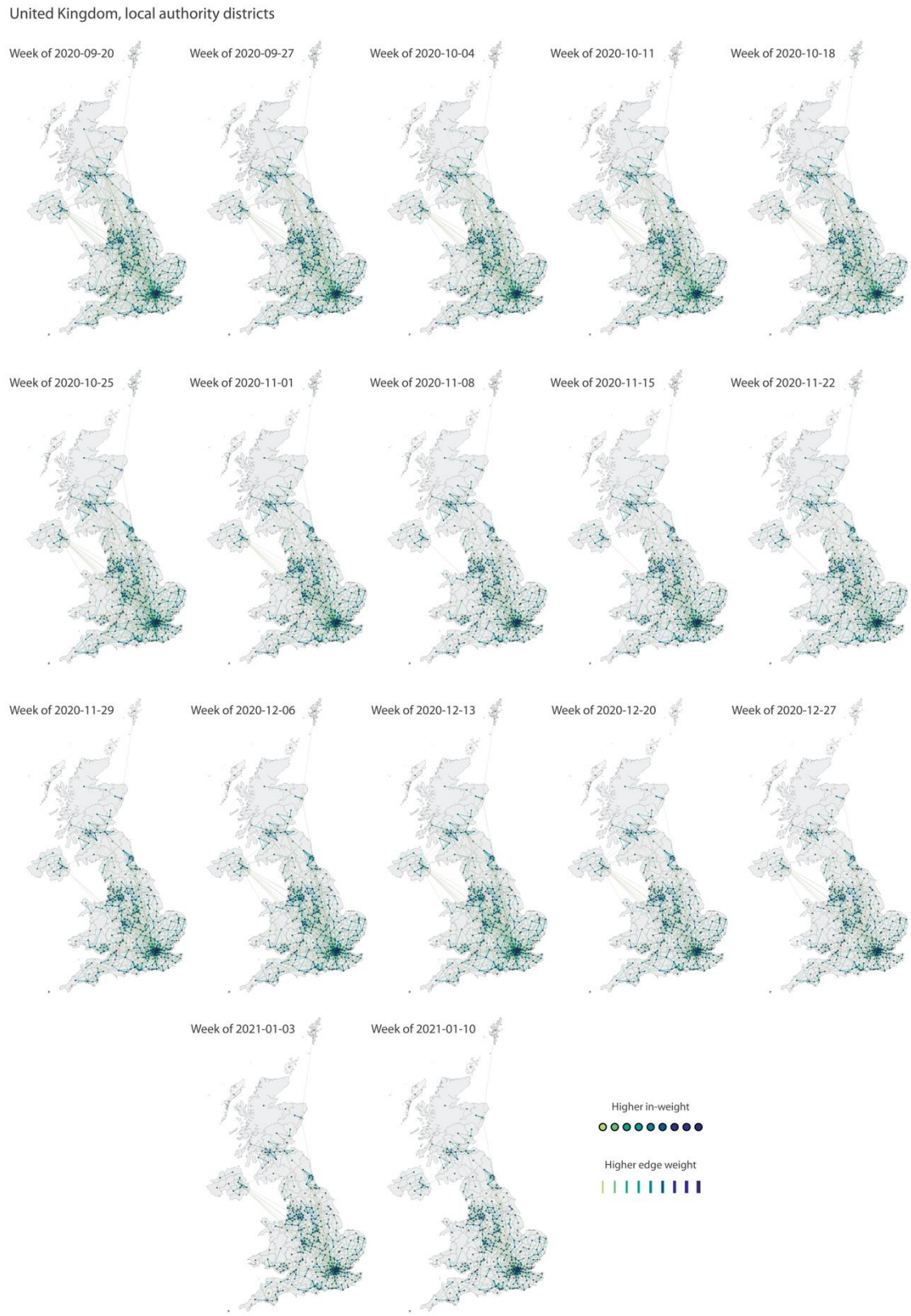

Fig. S1.

Human mobility at the UK Local Authority District Level (LTLA) during the epidemiological weeks 20th September - 15th January. Thicker lines (edges) represent greater relative movement intensity between regions. Nodes with larger absolute incoming movements are shown with darker colours.

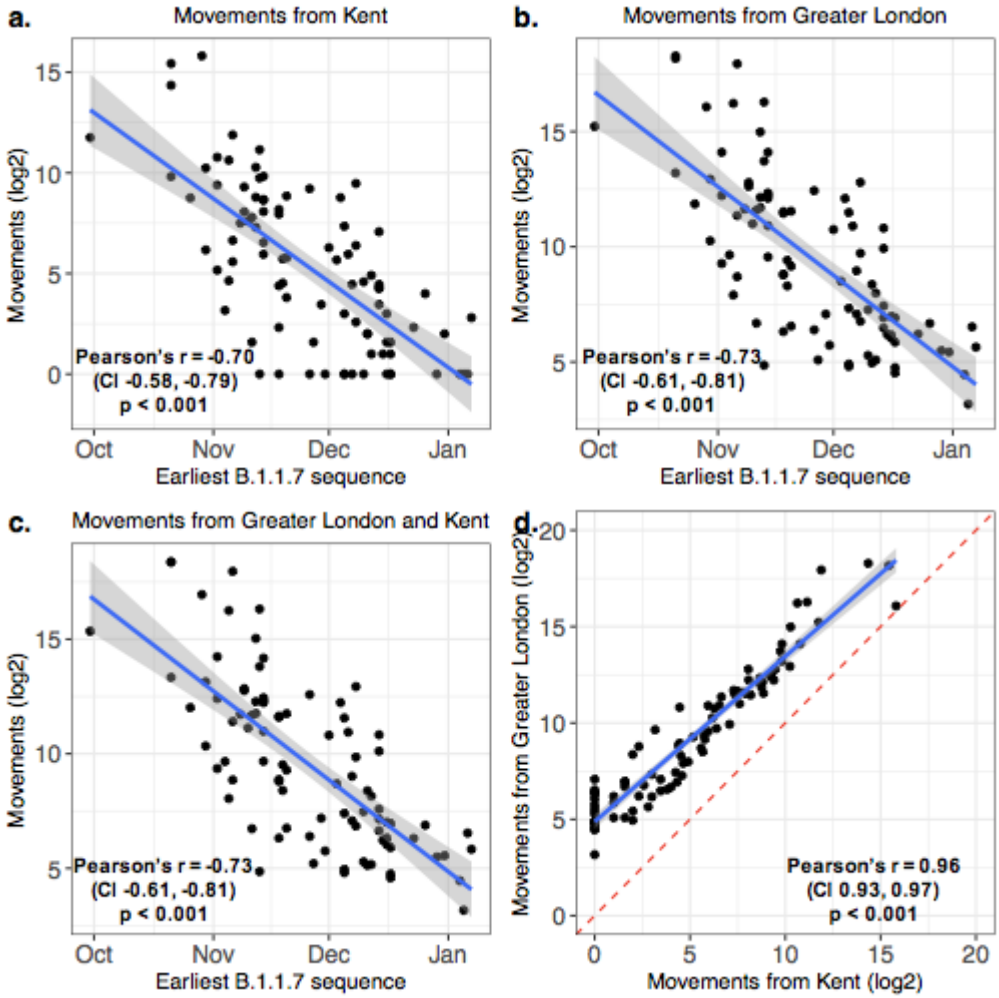

Fig. S2.

Correlation between the earliest detection date of B.1.1.7 in each UTLA and movements from Greater London (**a**), Kent (**b**) and Greater London and Kent combined **(c)** to that UTLA during February 2020. The correlations show that similar results are obtained for both Kent and Greater London. (**d**) There is a strong correlation between movements from Kent and movements from Greater London.

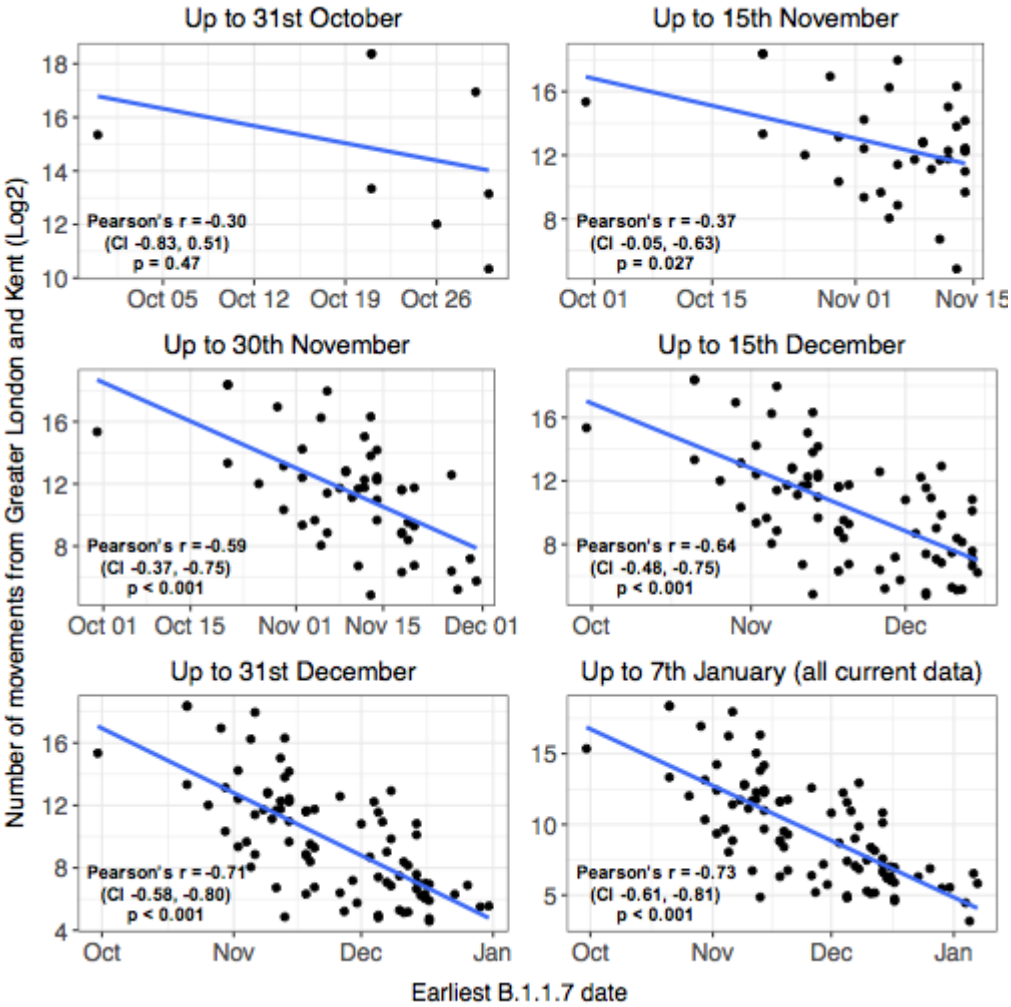

Fig. S3.

The change through time in the relationship between the date of detection of B.1.1.7 and movements from Greater London and Kent. Anonymised and aggregated data insights on human mobility is from February 2020 and does not change through time (see Materials & Methods).

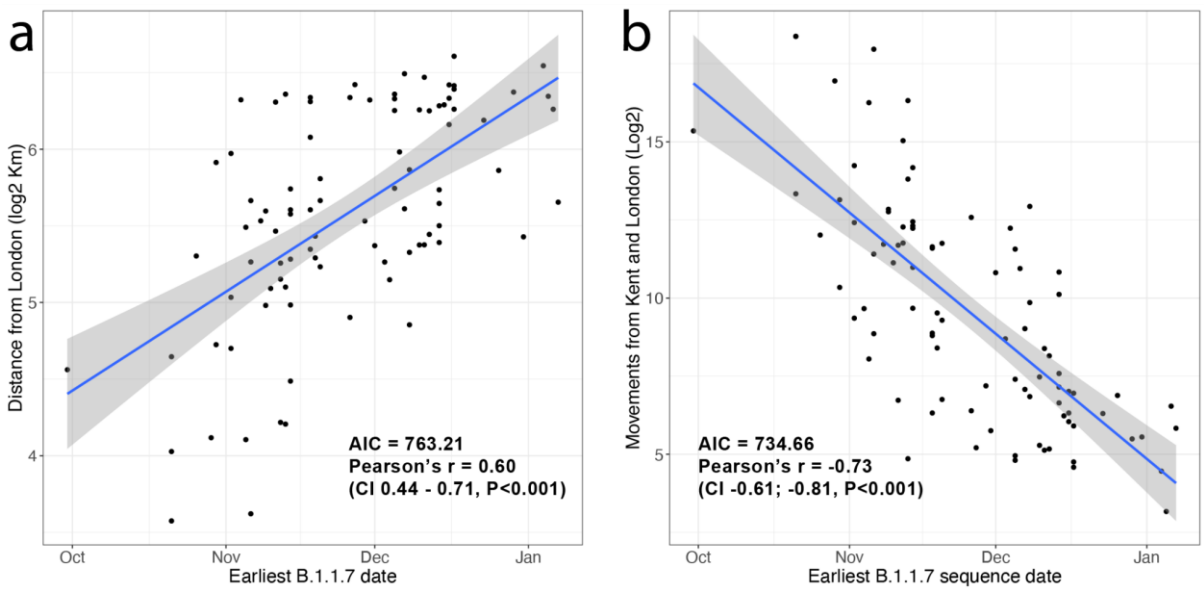

Fig. S4.

Predictors of the arrival time of B.1.1.7 across UTLAs in the UK. a) distance to London vs. earliest date (date of sample) of B.1.1.7, b) human movements from Greater London and Kent vs. earliest date (date of sample) of B.1.1.7.

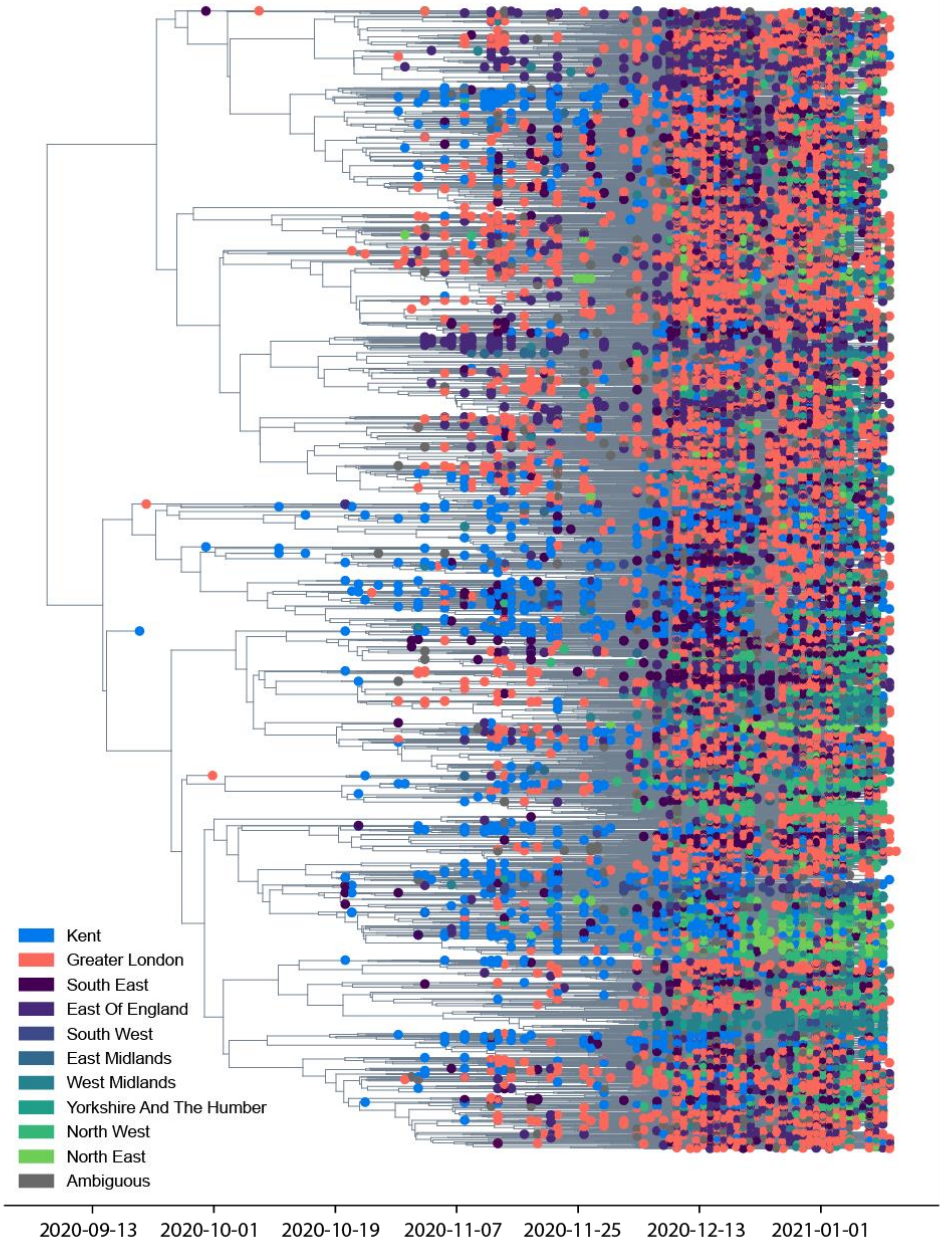

Fig. S5.
Time-scaled phylogeny of 17,716 B.1.1.7 sequences from England used as input for the continuous phylogeographic analysis. Tips are coloured by NUTS1 administrative region, or highlighted separately if from Kent. Visualised using Baltic (https://github.com/evogytis/baltic).

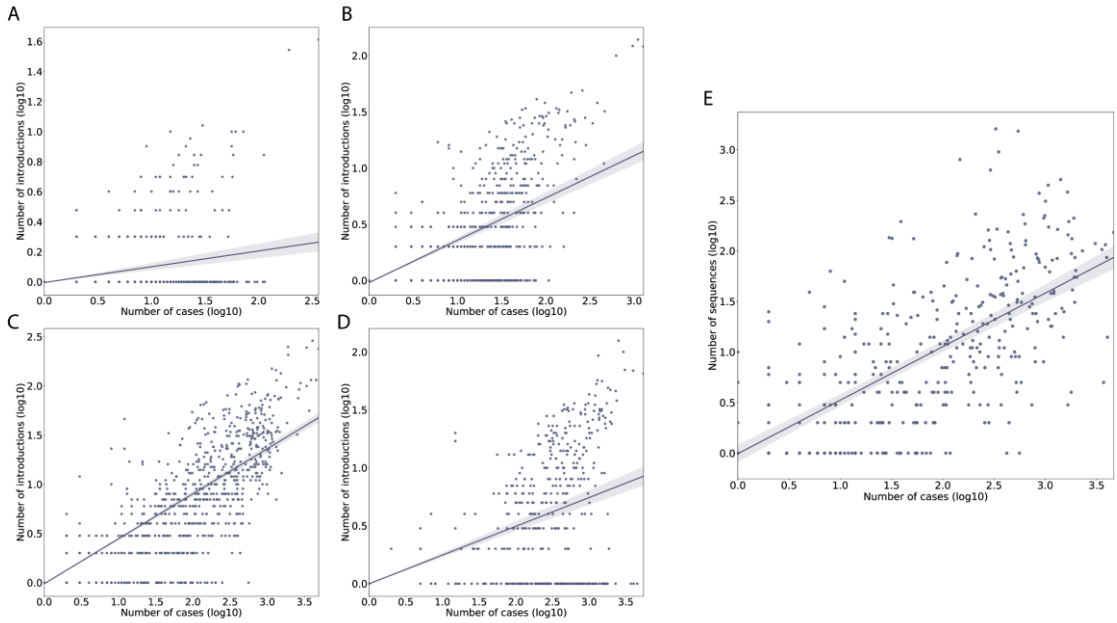

Fig. S6.

Correlation between the number of imports of B.1.1.7 into a UTLA per week and the number of B.1.1.7 cases in the same UTLA and same week in October (**a**, Pearson's r = 0.41, 95% CI: 0.38 - 0.44), November (**b**, Pearson's r = 0.76, 95% CI: 0.74 - 0.77), December (**c**, Pearson's r = 0.91, 95% CI: 0.90 - 0.92) and the first two weeks of January (**d**, Pearson's r = 0.73, 95% CI: 0.71 - 0.92). **(e)** Correlation between the logged number of sequences used in the dataset for the continuous phylogeography and the logged number of SGTF positive cases per location and over time (Pearson's r = 0.69, 95% CI: 0.63 - 0.73, p-value < 0.001).

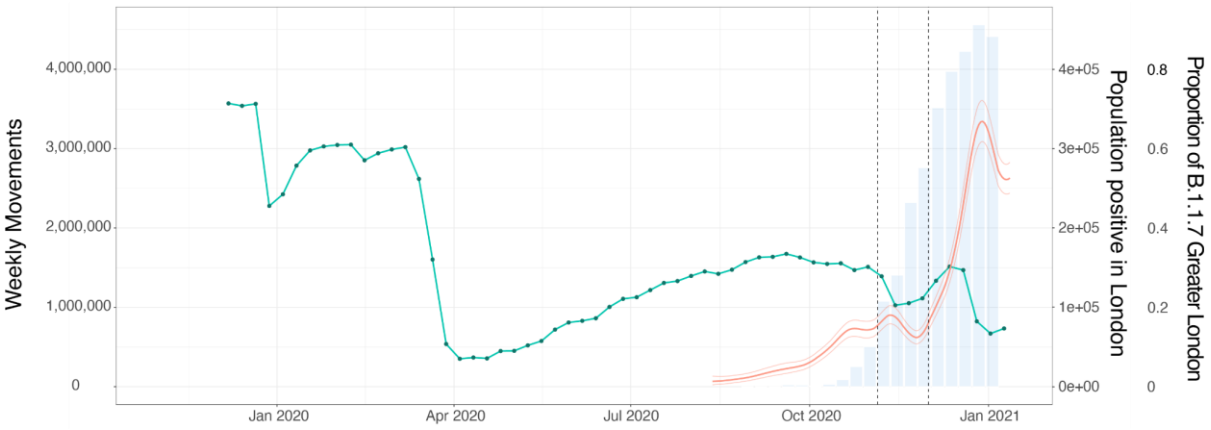

Fig. S7.

Number of weekly movements from Greater London (green), number of individuals testing positive in Greater London (red) and frequency of B.1.1.7 (blue) per week in Greater London. The dashed lines indicate the second English lockdown (5th November to 2nd December, 2020).

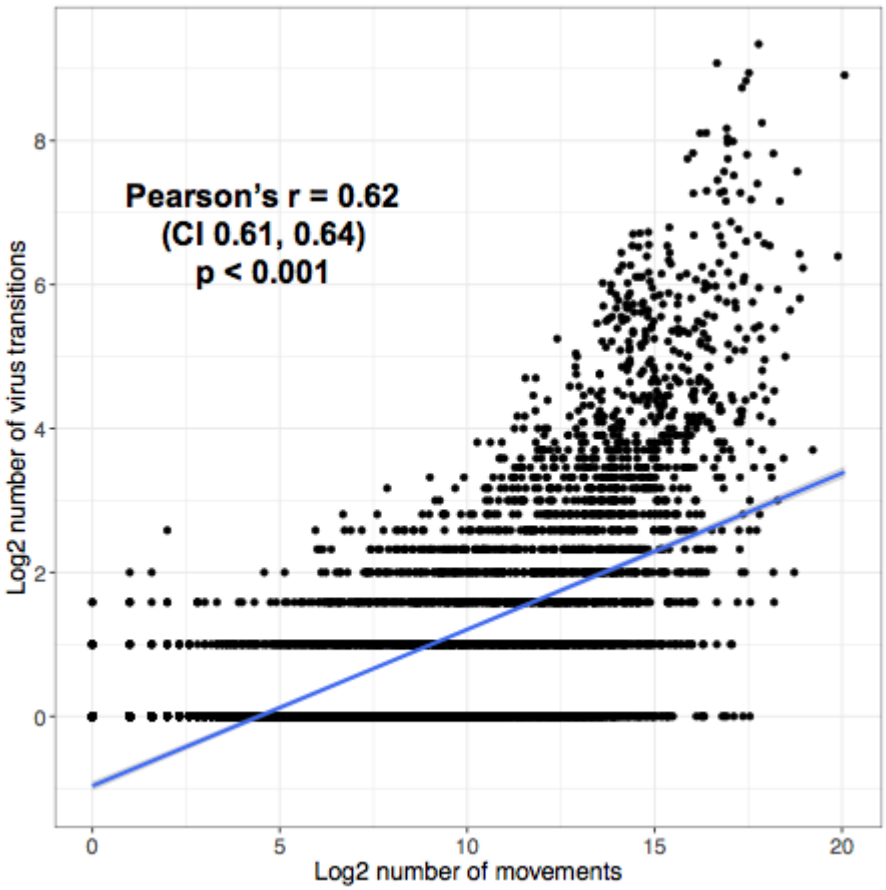

Fig. S8.
Correlation between the number of directional movements (from O2 movement data) and the number of virus transitions (from continuous phylogeography) between UTLA pairs.

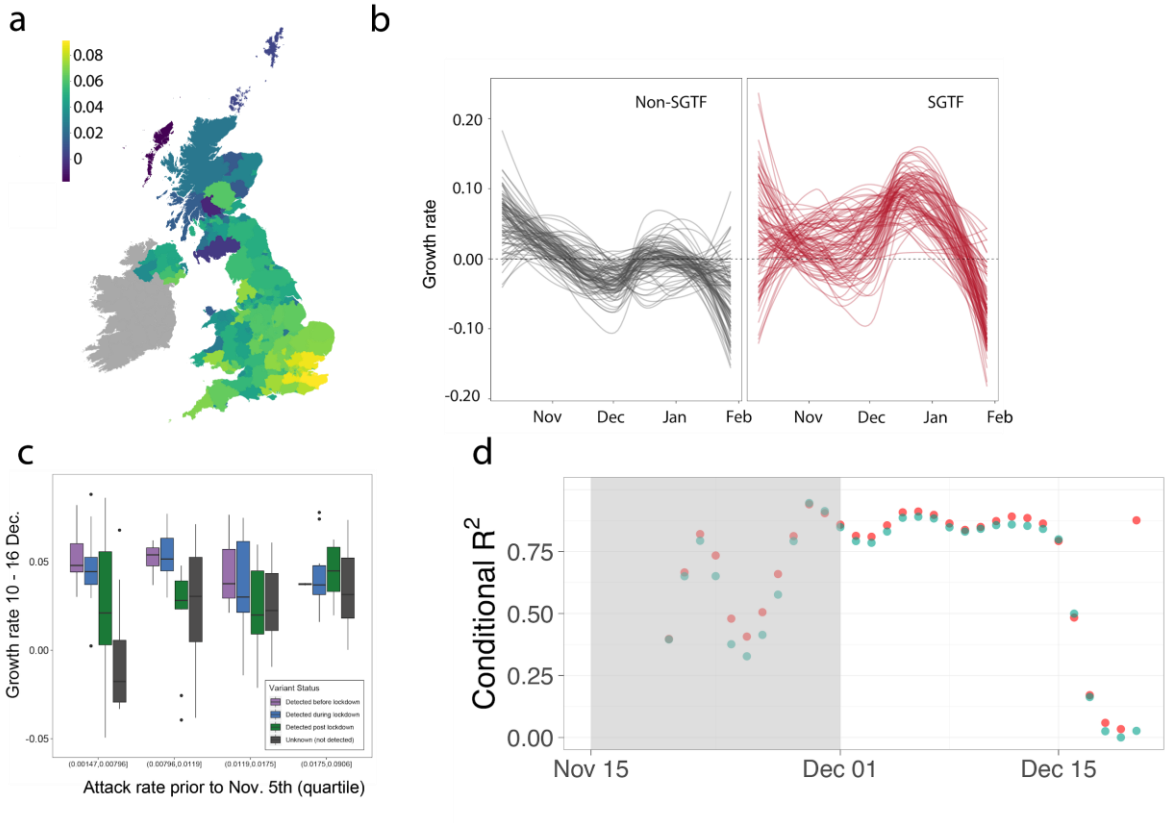

Fig. S9.

(a) Map of the rolling 7-day average of daily case growth rates in all UTLAs in the week December 10th - 16th 2020. **(b)** Rolling 7-day average growth rates of non-SGTF cases (grey) and SGTF cases at the UTLA level (each line represents a UTLA) in the UK. **(c)** Relationship between the first detection date of B.1.1.7 and case growth rate during 10th-16th December across all UTLAs, stratified by attack rate prior to November 5th, 2020. Each boxplot represents growth rates in UTLAs that had detected B.1.1.7 before November 5th (purple), between November 6th - December 2nd (blue), December 3rd - 29th (green) or not detected by December 29th(grey). The x-axis is grouped by attack rates (quartiles) prior to the second English lockdown (cases before November 5th). **(d)** Relationship between case growth rates of SGTF cases and mobility from London and Kent alone (blue) and combined with the numbers of introductions measured by phylogeographic models (red).

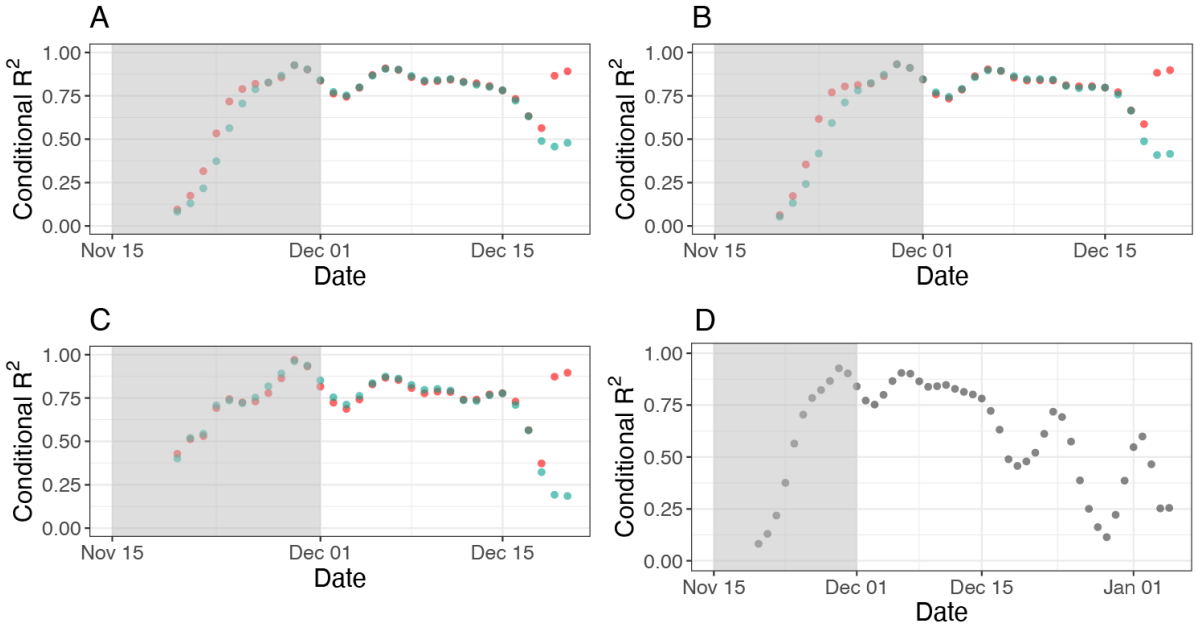

Fig. S10.
(a) Association between per-region (LTLA) difference between SGTF and non-SGTF case growth rates and number of importations as measured by estimated number of importations from prevalence surveys and human mobility (blue dots) and as measured by the genomic data (red dots). Grey area shows the time of the second English lockdown. **(b)** Same as (a) but only keeping subsequent rows for a given LTLA once 0.2 threshold of daily SGTF count/(SGTF count + non-SGTF count) is crossed. **(c)** Same as (a) but only keeping subsequent rows for a given LTLA once 0.6 threshold of daily SGTF count/(SGTF count + non-SGTF count) is crossed. **(d)** Association between per-region (LTLA) difference between SGTF and non-SGTF case growth rates and number of imports from Greater London (using genomic data) and prevalence data (see Materials and Methods) beyond December 20th.

Fig. S11.

Weekly average growth rates per LTLA for SGTF+ and SGTF- cases. Symbols represent weeks between November 15 (week 1) and December 20 (week 6) and colors represent LTLAs.

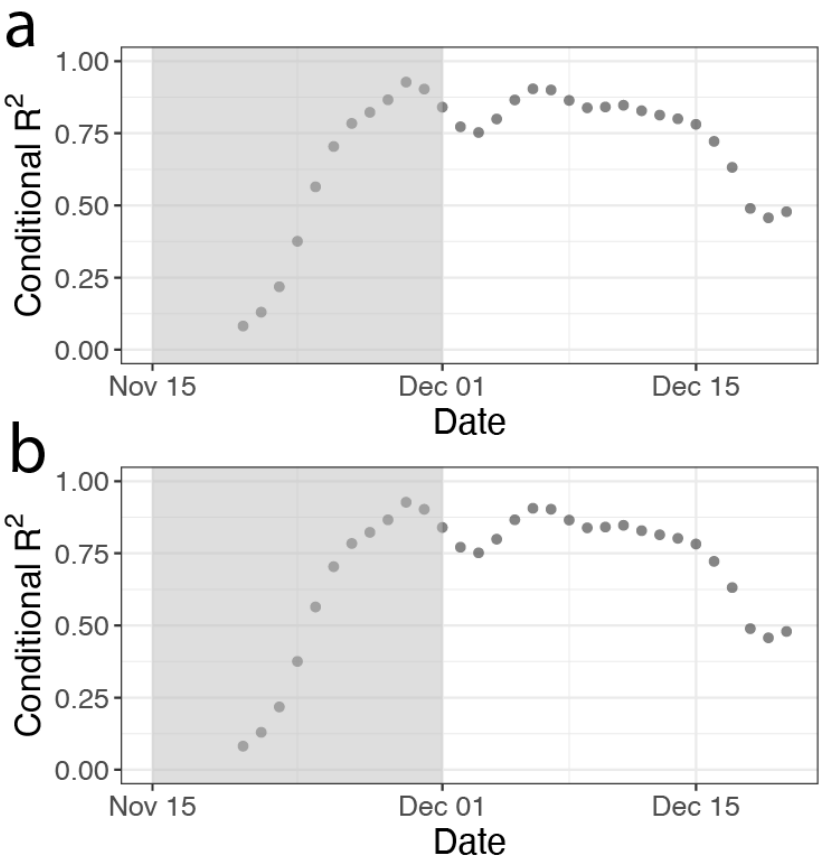

Fig. S12.
Estimates of the relationship between SGTF+ excess growth rates and the estimated number of importations of B.1.1.7 from Greater London using the upper **(a)** and lower **(b)** bounds of the ONS Infection Survey estimates.

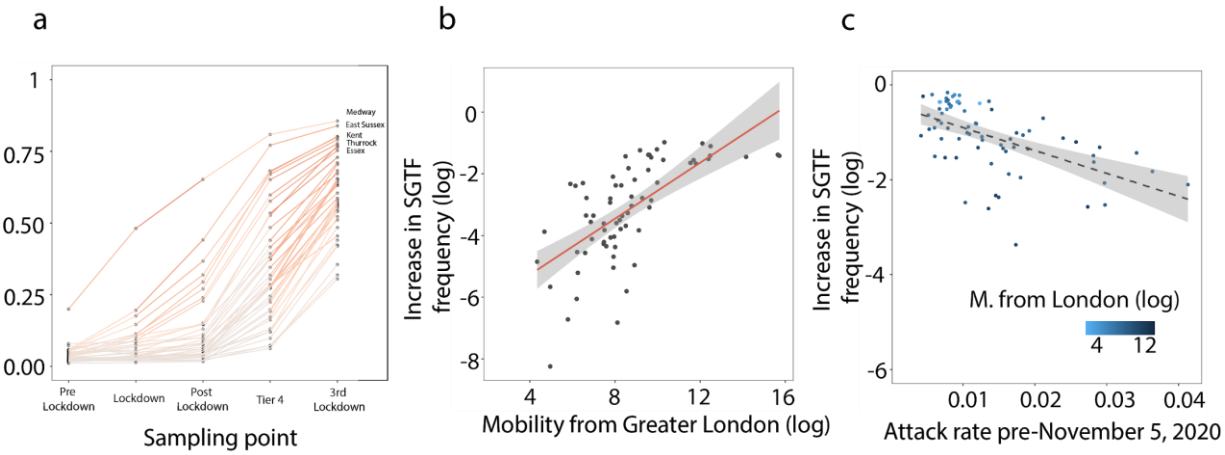

Fig. S13.

(a) Frequency of SGTF at the UTLA level at different sampling times (pre-lockdown refers to dates prior to 5th November; lockdown 5th - 30th November; post-lockdown 1st - 15th December; Tier 4, 16th - 31st December; and the most recent sampling point 1st - 12th January, Materials & Methods). (**b)** Increase in the frequency of SGTF at the end of the lockdown between 2nd - 16th December is associated with mobility from Greater London. (**c**) Increase in the frequency of SGTF as it relates to previous attack rates.

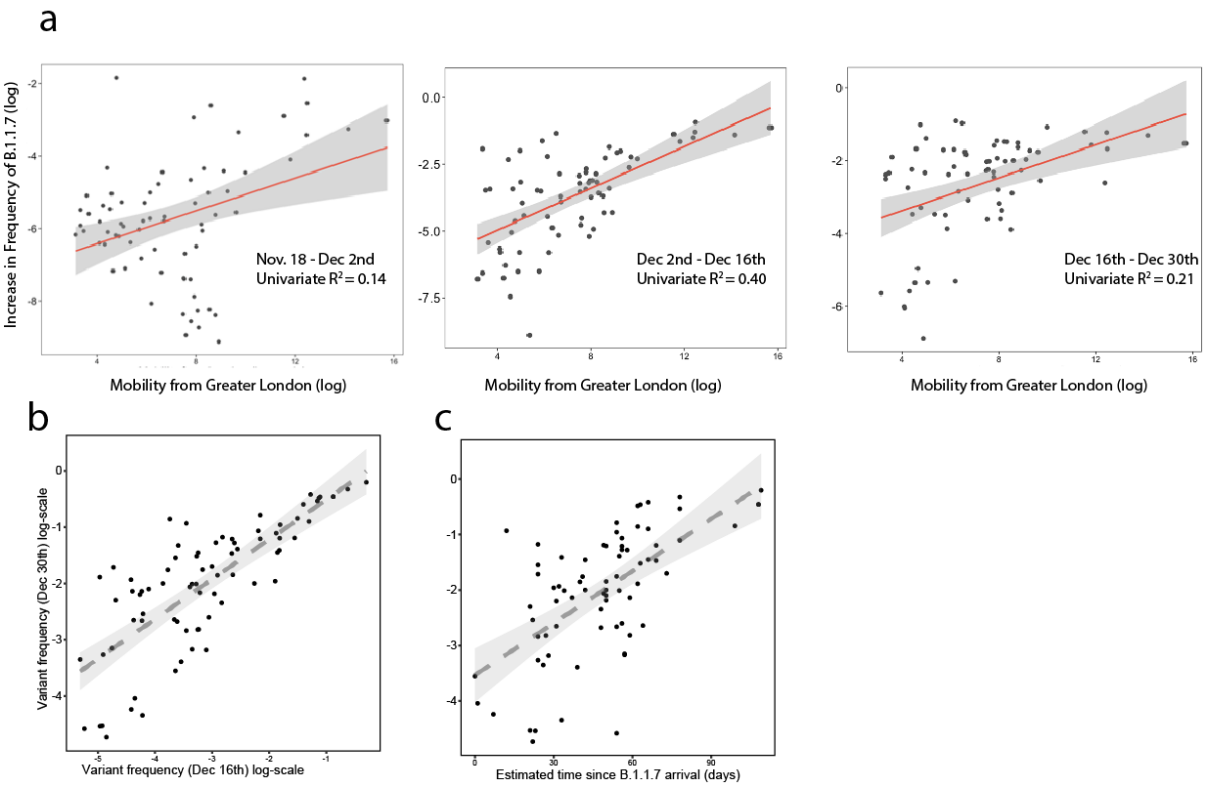

Fig. S14.
(**a)** Increase in the frequency of SGTF (UTLA) between (i) November 18th- December 2nd (ii) December 2nd - December 16th (iii) December 16th - December 30th vs. human mobility from Greater London. **(b)** Frequency of B.1.1.7 genomes (UTLA) amongst all sampled genomes between December 17th and December 30th. **(c)** Frequency of B.1.1.7 (UTLA) as it relates to the estimated time since B.1.1.7 was first detected in the corresponding UTLA.

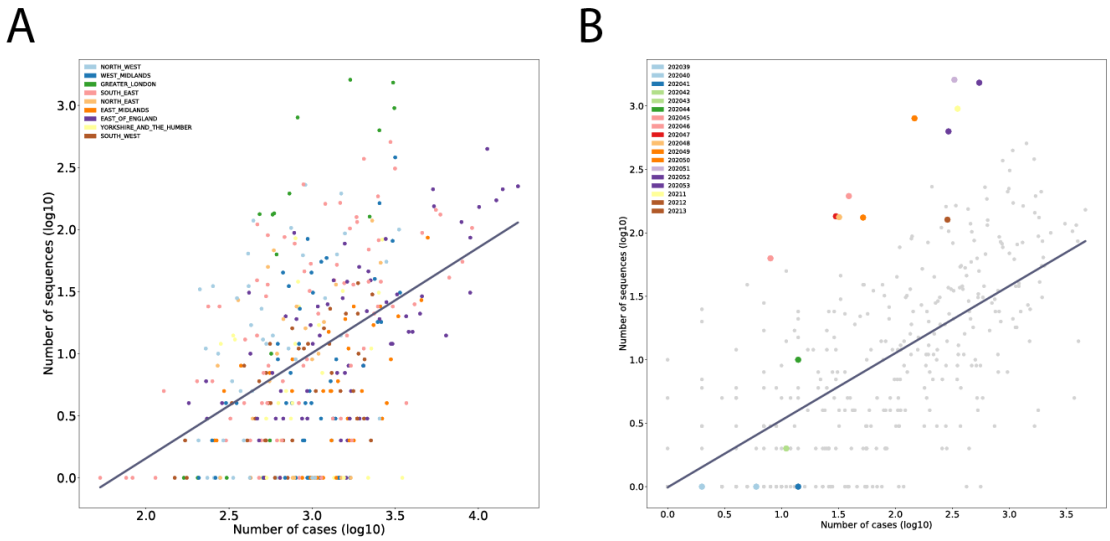

Fig. S15.
Correlation between numbers of cases (SGTF) and number of sampled B.1.1.7 genomes across UTLAs in England, coloured by NUTS1 region (A). NB Kent is part of the South East region. One such bias that was noted when regressing the number of SGTF cases against the number of B.1.1.7 sequences in each UTLA was that Greater London had a higher proportion of samples sequenced than other parts of England. This is highlighted in B, coloured by epiweek.

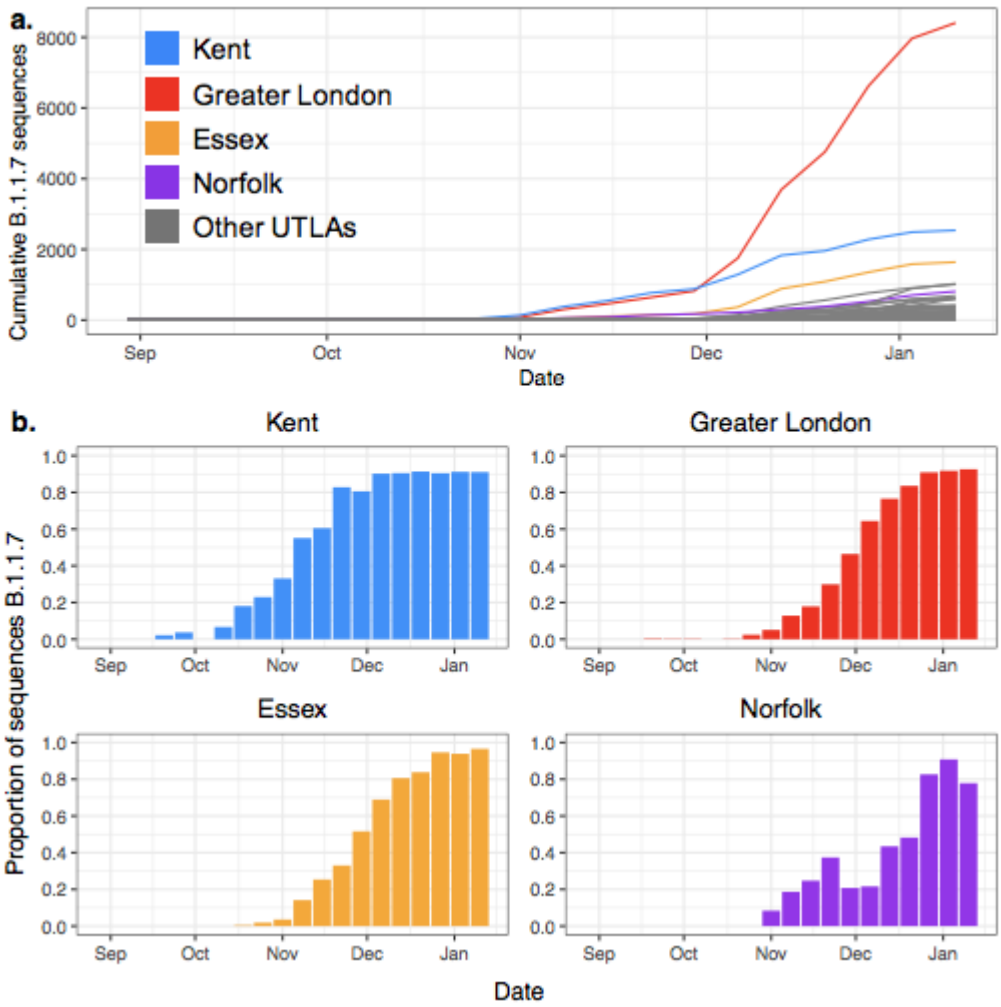

Fig. S16.

(a) The cumulative number of B.1.1.7 sequences up to and including each week in each UTLA. (b) The proportion of genomes sequenced each week that are B.1.1.7 (raw proportions shown here).

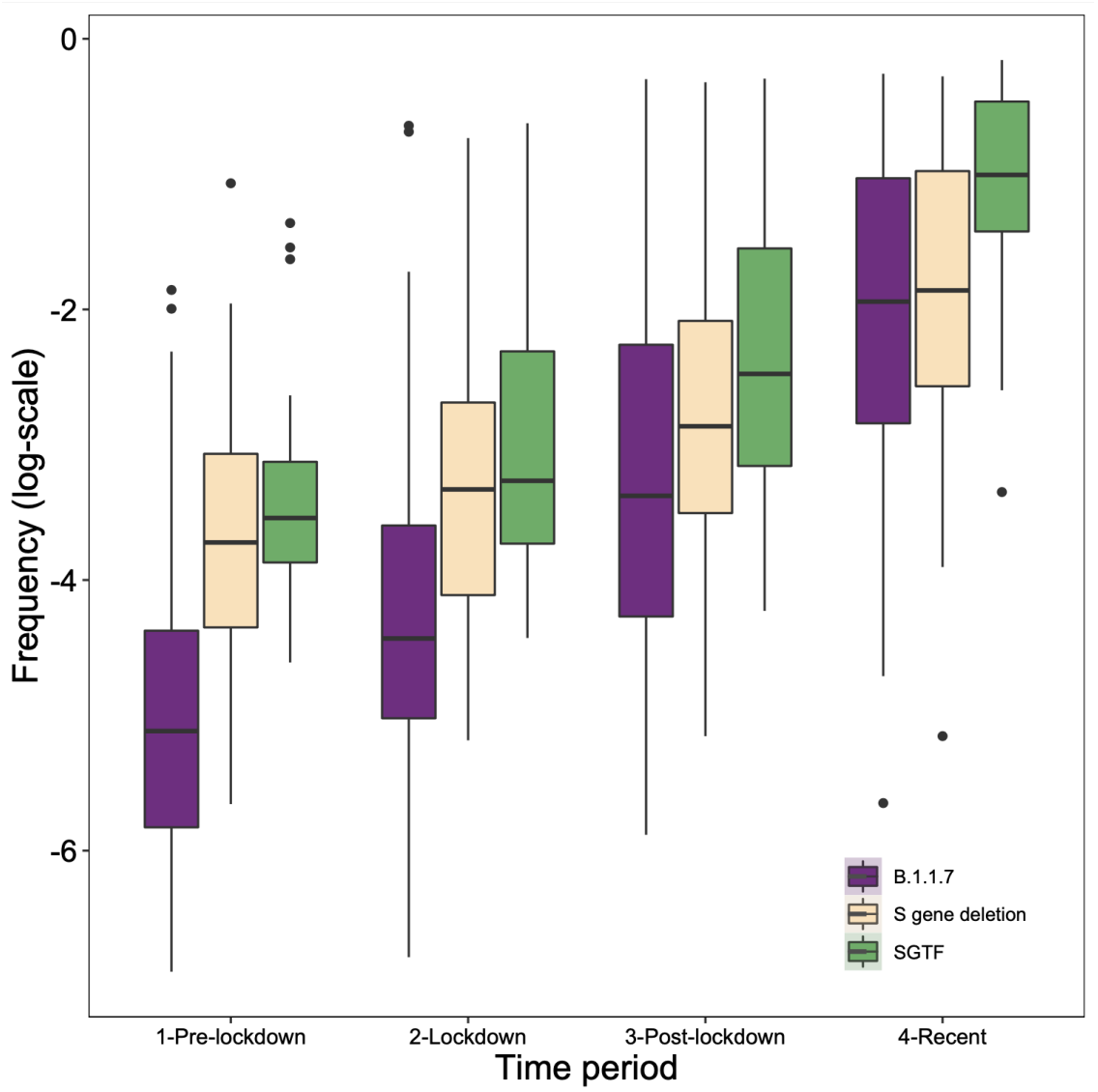

Fig. S17.
The frequency of the B.1.1.7 lineage (purple), the 20 lineages currently known to carry the 21765_6 S gene deletion (tan), and S-gene target failures (green) were estimated for each UTLA and aggregated into four time periods. Briefly, to estimate the frequency of each type, we used a Beta prior (0.1,1) on the proportion of the novel variant to account for sampling intensity, we estimated frequency using sampling data from pre-lockdown (prior to Nov. 5th), lockdown (Nov. 5st - Dec. 3rd), post-lockdown (Dec. 4th - Dec. 17th), and recent (after Dec. 17th). Following the first time period, when updating the posteriors, we take as priors the posteriors from the early period (down-weighted by 50% to prevent more recent data from being overwhelmed by earlier samples).

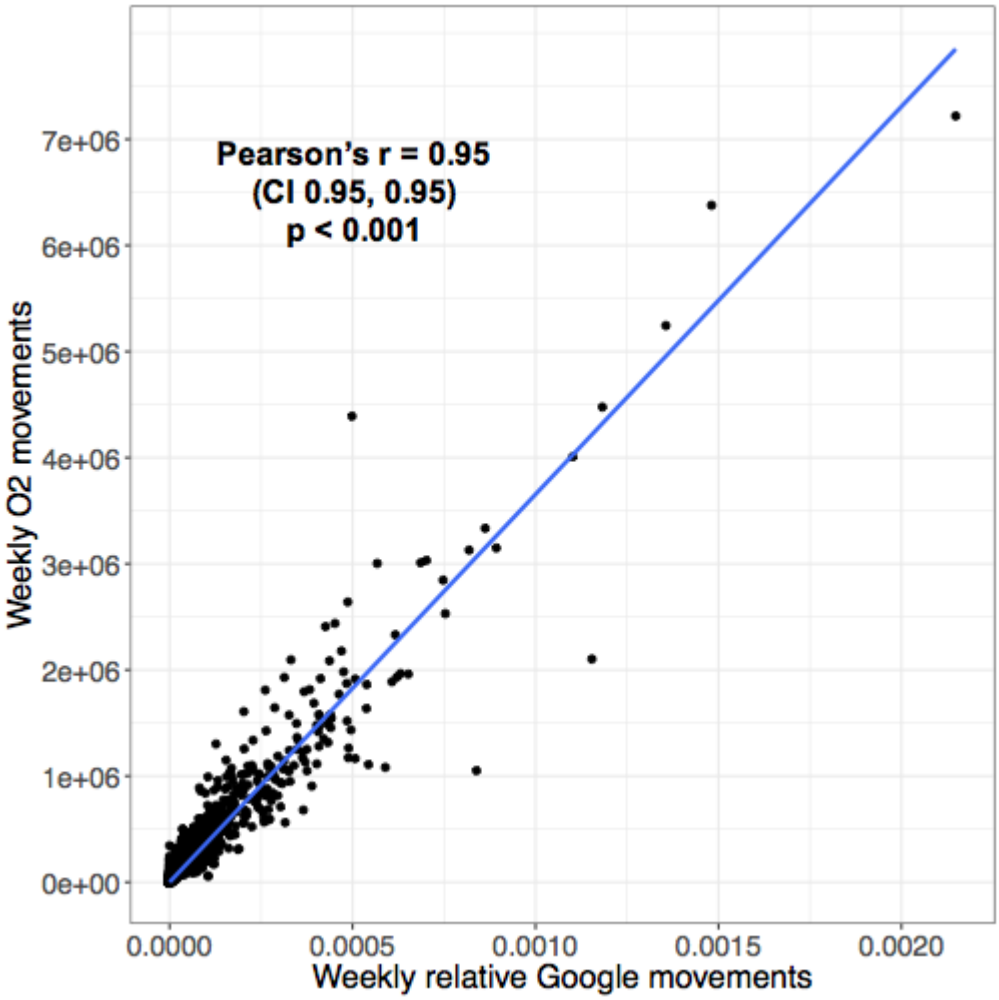

Fig. S18.
Comparison between human mobility data from O2 and Google in February 2020. Each point represents the directional movements between one LAD pair.

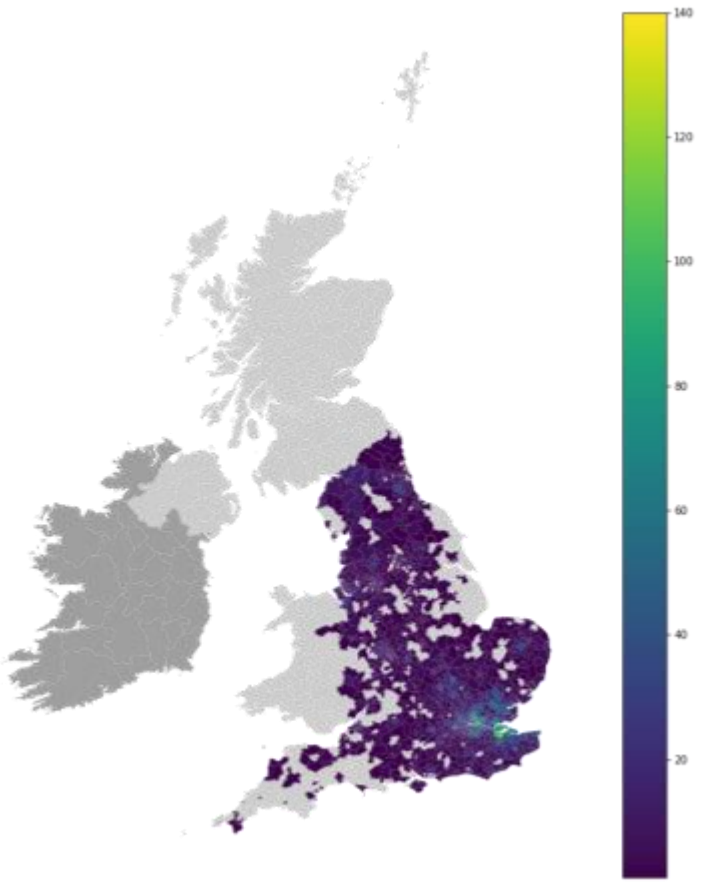

Fig. S19.
Map showing the number of sequences in each postcode region that are B.1.1.7 and from pillar two sequencing facilities. Locations in light grey have no sequences meeting these criteria, and the Republic of Ireland is shown in dark grey.

Table S1.
Percentage of transition events from Greater London and Kent through time.

Date window	Percent of transition events origin = Greater London (destination, not Greater London)	Percent of transition events origin = Greater London and Kent (destination not Greater London or Kent)
01.09.2020 - 05.11.2020	8.1	11.8
05.11.2020 - 01.12.2020	4.5	8.2
01.12.2020 - 20.12.2020	3.8	5.5
20.12.2020 - 12.01.2021	4.6	5.9

Table S2.
Descriptions of geographical units used in analysis. Note that data were routinely converted between the different units using custom scripts for different elements of the analysis, and that the exact components of each unit change regularly.

Unit	Acronym	Description	Data available	Examples
Upper tier local authority area	UTLA	Counties, metropolitan counties, inner/outer London, unitary authorities	None - used as a common level to unify all data sources	Inner London, Greater Manchester, Stoke-on-Trent
Lower tier local authority area	LTLA	Local authority districts, unitary authorities, metropolitan districts, London boroughs	Case data, SGTF data	Hackney, Lambeth, Camden, Bolton, Bury, Stockport, Stoke-on-Trent
Local authority district	LAD	One type of LTLA	O2 mobility data, Google mobility data	Same as LTLA examples
Administrative level 2	adm2	Roughly equivalent to UTLA, but often larger counties (such as Greater Manchester) are split into constituent parts	Sequence metadata	Greater London, Bolton, Bury, Stockport, Stoke-on-Trent

Table S3.

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