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## Title:

# Phylogenetic analyses of SARS-CoV-2 B.1.1.7 lineage suggest a single origin followed by multiple exportation events versus convergent evolution

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Abstract. The emergence of new variants of SARS-CoV-2 herald a new phase of the pandemic. This study used state-of-the-art phylodynamic methods to ascertain that the rapid rise of B.1.1.7 "Variant of Concern" most likely occurred by global dispersal rather than convergent evolution from multiple sources.

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Following phylogenetic and epidemiological investigations, the SARS-CoV-2 genetic lineage B.1.1.7 is suspected to be associated with an increase human-to-human viral transmissibility[1,2], and was classified as a “Variant of Concern” (VOC B.1.1.7) on December 18, 2020[3]. The variant was first discovered in Kent, United Kingdom (UK) on September 21, 2020, and has since been identified in over 29 countries across the world, including the United States[3,4]. We sought to evaluate whether the breadth of VOC B.1.1.7 identification represents convergent evolution[5] or rapid local and global dispersal after this lineage's genesis.

On January 7’ 2021, we downloaded all B.1.1.7 lineage SARS-CoV-2 genomic sequences available on the GISAID public database[6] (8,786 full length genome sequences across 29 countries, **Supplementary Table 1**). The vast majority were from the UK (96.4%, *n*=8468), but 318 sequences were from other countries, including 13 from North America (8 from USA and 5 from Canada; **Figure 1**).

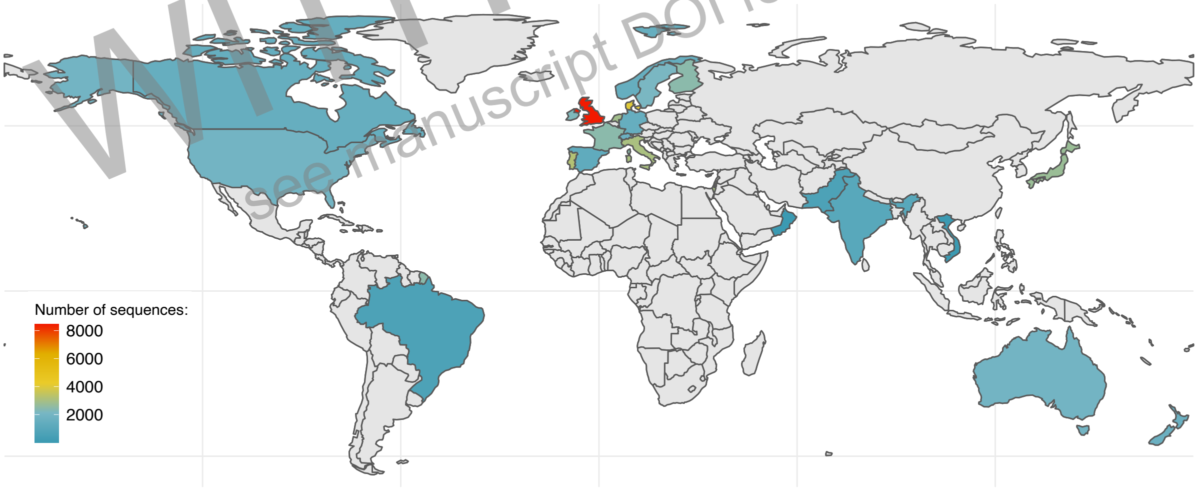

**Figure 1. Map of the B.1.1.7 genomic sequences available on GISAID as of January 7, 2020.** Countries are colored based on the number of publicly available B.1.1.7 sequences.

We combined these B.1.1.7 sequences with a representative set of non-B.1.1.7 sequences (*n*=3,163) based on sequence homology (see Supplementary). The final set of 11,949 sequences was aligned with MAFFT[7] and a Maximum Likelihood phylogeny was inferred using IQ-TREE v2.1.2[8]. The resulting phylogeny showed that all available B.1.1.7 samples cluster together with high support (0.99 Shimodaira Hasegawa [SH] support[9-11]). Non-UK VOC B.1.1.7 sequences intermix within those from the UK (**Figure 2**). As convergent evolution can induce incorrect clustering[12], the same approach was repeated after excluding variable positions that define the

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B.1.1.7. lineage (**Supplementary Table 2**), which yielded a similar picture. These patterns are in line with the view that this variant succesfully spread around the world after it arose in the UK.

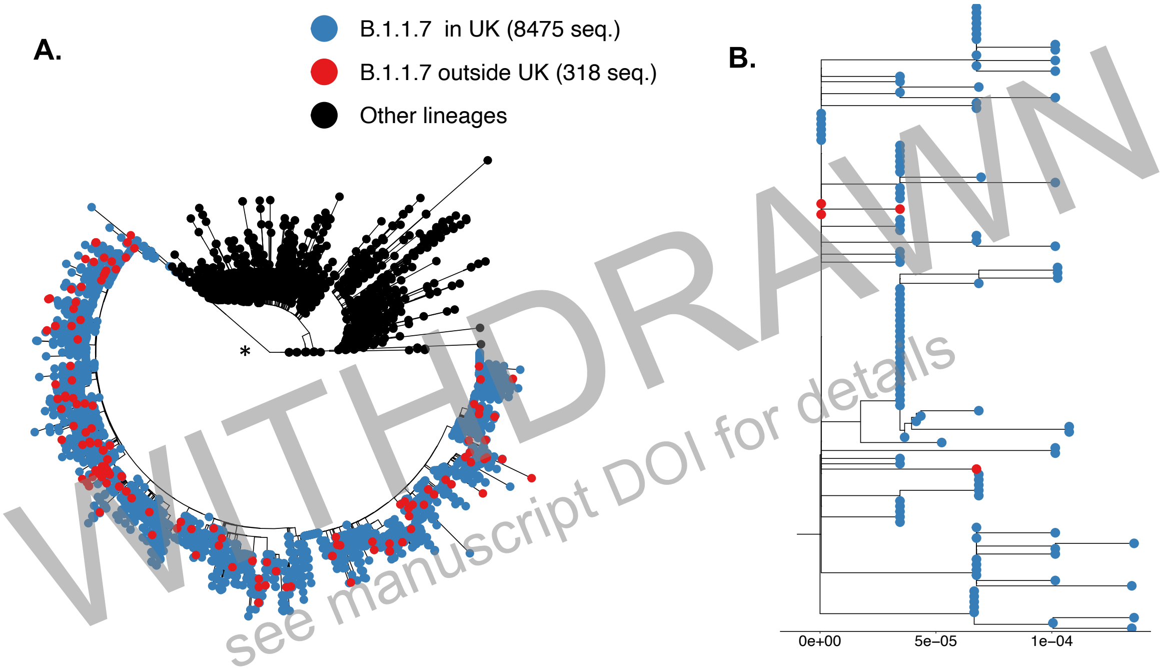

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**Figure 2. SARS-CoV-2 variant B.1.1.7 arose in the UK and spread globally from there.** Tips in the phylogeny are colored according to lineage and country of origin (blue denotes taxa from UK, red denotes taxa from outside UK, and black corresponds to other lineages). (*) The branch leading tot the VOC B.1.1.7 clade has close to perfect suppport (0.99 Shimodaira Hasegawa (SH) branch support[9-11]). **A.** All sequences included. **B.** Illustrative subset of B 1.1.7 taxa from UK (in blue) and other countries (in red). The branch length scale (s/s/y) is indicated at the bottom. Tree display was obtained with the R package "ggtree"[13].

To estimate the timing of introduction of B.1.1.7 variants outside the UK, we applied a multistep analytic approach as previously described by our group for HIV[14,15] (see Supplementary Information). We identified a total of 30 clades of size ≥2 for a total of 152 sequences (ranging from 2 to 21) including only B.1.1.7 variants from outside the UK. More than two-thirds (22/30) were European clusters (**Supplementary Table 1**).

The earliest estimated seeding of B.1.1.7 from the UK dates to September 23rd, and the most recent to December 23rd, see **Supplementary Table 3** and **Figure 3A**). The number of weekly

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introductions (**Figure 3B**) peaked on the week of November 16th, while the peak of detection was in mid-December.

In response to the rapid increase in viral infections and spread, UK officials announced a lockdown on October 31st that came into force on November 5th and ended on December 5th. Given time to the most recent common ancestor (TMRCA) estimates, we determined that 20% (6/30) of the exportation events that gave rise to detectable non-UK VOC B1.1.7 transmission lineages occurred during this period (the remaining 80% occurred before or after these dates). The emergence and rapid dispersal of this new VOC led to the implementation of a new national strict lockdown on January 4, 2021[16].

As previously described by du Plessis *et al.*[17], we next used the TMRCA of each non-UK clade to estimate the genomic "detection lag" for each cluster, which represents the duration that a transmission lineage went undetected before it was first sampled by genome sequencing. The mean detection lag was ~10 days (IQR= 4-9.5). This largely agrees with detection lag-time estimates from SARS-CoV-2 importation *into* the UK in the first months of the pandemic[17], which was on average 8 days (IQR=3-15, ~10 days for lineages comprising ≤10 genomes and <1 day for lineages of >100 genomes).

Of note, virus genome sequences have been determined for only a fraction of infections. Even in the UK, where the by far largest sequencing effort is done, only an estimated 4.3% (129,939 available sequences out of 3,039,797 cases reported on January 7th)[18] of infections have been sequenced. For this reason, and also because not all sequenced SARS-CoV-2 genomes are being deposited in the GISAID repository, many B.1.1.7 variants that succesfully established transmission chains outside of the UK likely remain undetected (for now). Our estimated number of B.1.1.7 exportation events from the UK thus represents an underestimate. The sparse sampling and sequencing also poses limits to the accuracy with which introduction events can be dated (see du Plessis and colleagues[19] for a more detailed explanation).

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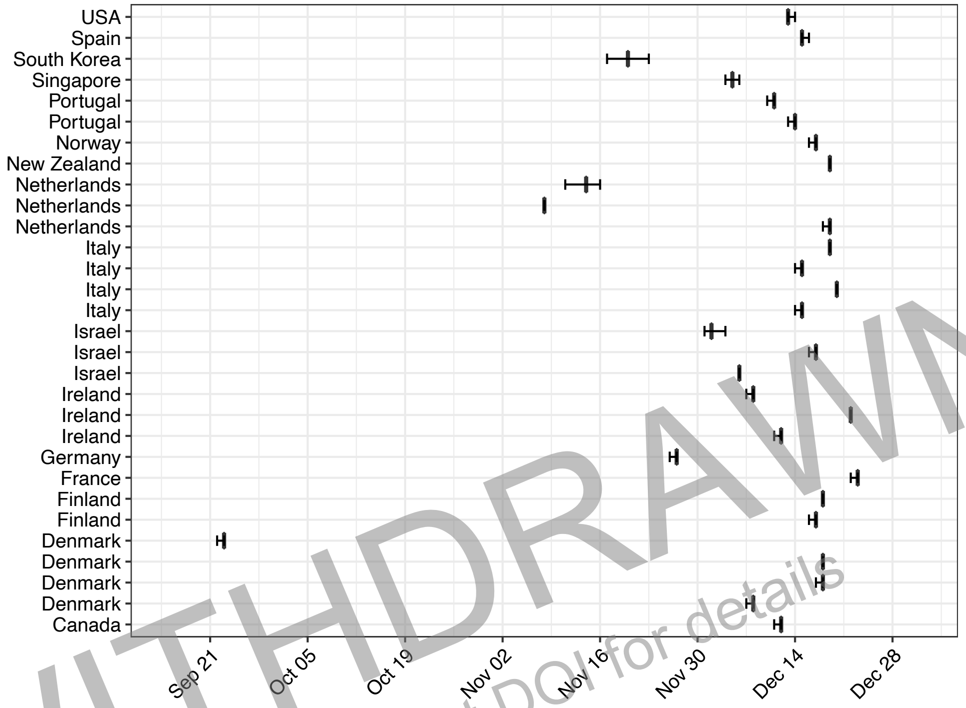

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**Figure 3A**. **Timing of introduction of each non-UK VOC B.1.1.7**. For each non-UK VOC lineage, we estimated the timing of introduction by performing molecular clock estimation on 100 replicates based on the clock rate distribution from Plessis *et al*[19] (see Supplementary Information). Each horizontal bar represent a non-UK cluster. Mean, lower and upper 95% CI are shown. Country of origin of these clusters is indicated on the y axis.

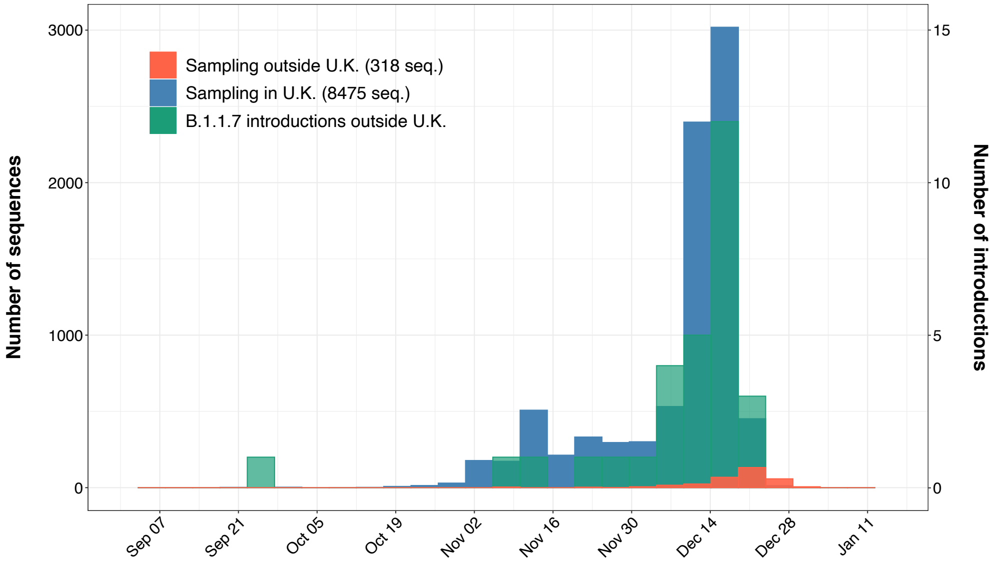

**Figure 3B. Number of introduction of B.1.1.7 outside UK.** Vertical green bar represents the biweekly number of introduction (right y axis). Red bars represent the number of B1.1.7 sequences collected through time.

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Our results do not suggest that the canonical mutations of VOC B.1.1.7 evolved independently in different locations. Instead, our analyses point to an origin in and spread of the VOC B.1.1.7 from the UK. As for the virus' initial[20] and subsequent[21,22] spread, global connectedness and high levels of human mobility undoubtedly facilitated VOC B.1.1.7 dissemination. The swift global spread of VOC B.1.1.7 illustrates that current restrictions are insufficient to prevent the spread of new and emerging variants[23-29]. Similar to Ebola[30], HCV[31,32] and HIV[15], countermeasures to SARS-CoV-2 spread should be developed with a broader perspective than the national level. Otherwise, without population immunity, successful local reductions in SARS-CoV-2 burden will be counteracted by imported infections that set off new waves of viral spread, possibly exacerbated by novel phenotypic characteristics of the imported strains.

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## Supplementary Information

*Data collection and preparation.* All publicity available full-length SARS-CoV2 genomic sequences were collected from GISAID on January 7, 2020. Sequences were aligned using MAFFT and highly homoplasic sites were masked[33]. To reduce the data set size while maintaining an appropriate set of epidemiologically relevant background sequences, we used BLAST[34,35] to identify the 50 closest non-B.1.1.7 variants to each of the 8,786 B.1.1.7 genomic sequences in the data set[17,36]. After keeping one copy of duplicated entries that ranked among the 50 best hits, a total of 3,163 sequences out of the 284,666 non-B1.1.7 sequences available on GISAID were kept for further analyses and combined with the B.1.1.7 dataset.

*Identification of non-UK B.1.1.7 clades*. From a Maximum Likelihood (ML) phylogeny inferred using IQ-TREE v 2.1.2[8], B.1.1.7 clusters of size ≥2 including only non-UK sequences were identified in R[37].

*Timing of introduction*. For each non-UK clade, the phylogeny was rescaled into units of time with treedater[13], assuming a strict molecular clock with the rate of SARS-CoV-2 genome evolution drawn from an externally-estimated distribution as described by du Plessis *et* al[19]. Specifically, for the rate a normal distribution was specified with mean $9.41\times10^{-4}$ nucleotide substitutions per site per year and a standard deviation of $4.99\times10^{-5}$. To incorporate uncertainty in the estimated clock rate, molecular clock estimation was replicated 100 times for each non-UK B.1.1.7 clade.

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## Supplementary Tables.

### Supplementary table 1. Sampling distribution of B.1.17 sequences.

| Country | Count (n) | Percentage (%) |
|---|---|---|
| Australia | 8 | 0.091 |
| Brazil | 2 | 0.023 |
| Canada | 5 | 0.057 |
| Denmark | 74 | 0.842 |
| Finland | 14 | 0.159 |
| France | 14 | 0.159 |
| Germany | 5 | 0.057 |
| Gibraltar | 1 | 0.011 |
| Hong Kong | 3 | 0.034 |
| India | 3 | 0.034 |
| Ireland | 11 | 0.125 |
| Israel | 25 | 0.285 |
| Italy | 26 | 0.296 |
| Japan | 19 | 0.216 |
| Luxembourg | 3 | 0.034 |
| Netherlands | 22 | 0.25 |
| New Zealand | 6 | 0.068 |
| Norway | 5 | 0.057 |
| Oman | 1 | 0.011 |
| Pakistan | 2 | 0.023 |
| Portugal | 31 | 0.353 |
| Singapore | 6 | 0.068 |
| South Korea | 3 | 0.034 |
| Spain | 4 | 0.046 |
| Sweden | 10 | 0.114 |
| Switzerland | 6 | 0.068 |
| **United Kingdom** | **8468** | **96.381** |
| **USA** | **8** | **0.091** |
| Vietnam | 1 | 0.011 |
| **Total** | **8786** | **100** |

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**Supplementary table 2.** Non-synonymous mutations and deletions to occur on the phylogenetic branch leading to lineage B.1.1.7.[1]

| gene | nucleotide | amino acid |
|---|---|---|
| ORF1ab | C3267T | T1001I |
|  | C5388A | A1708D |
|  | T6954C | I2230T |
|  | 11288-11296 deletion | SGF 3675-3677 deletion |
| spike | 21765-21770 deletion | HV 69-70 deletion |
|  | 21991-21993 deletion | Y144 deletion |
|  | A23063T | N501Y |
|  | C23271A | A570D |
|  | C23604A | P681H |
|  | C23709T | T716I |
|  | T24506G | S982A |
|  | G24914C | D1118H |
| Orf8 | C27972T | Q27stop |
|  | G28048T | R52I |
|  | A28111G | Y73C |
| N | 28280 GAT->CTA | D3L |
|  | C28977T | S235F |

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**Supplementary table 3**. Characteristics of the non-UK clusters identified.

| **continent** | **country (region)** | **cluster size** | **Estimated time of introduction, mean [95%CI]** | **detection lag in days [95%CI]** |
|---|---|---|---|---|
| Asia | Israel (NA) | 19 | 2020-12-02 [2020-12-01 - 2020-12-04] | 23 |
|  | Israel (NA) | 2 | 2020-12-06 [2020-12-06 - 2020-12-06] | 11 |
|  | Israel (NA) | 2 | 2020-12-17 [2020-12-16 - 2020-12-17] | 4 |
|  | Singapore (NA) | 3 | 2020-12-05 [2020-12-04 - 2020-12-06] | 15 |
|  | South Korea (Southkorea) | 3 | 2020-11-20 [2020-11-17 - 2020-11-23] | 33 |
| Europe | Denmark (Nordjylland) | 64 | 2020-09-23 [2020-09-22 - 2020-09-23] | 48 |
|  | Denmark (Sjaelland) | 2 | 2020-12-18 [2020-12-18 - 2020-12-18] | 4 |
|  | Denmark (Hovedstaden) | 2 | 2020-12-08 [2020-12-07 - 2020-12-08] | 7 |
|  | Denmark (Nordjylland) | 2 | 2020-12-18 [2020-12-17 - 2020-12-18] | 4 |
|  | Finland (Uusimaa) | 3 | 2020-12-18 [2020-12-18 - 2020-12-18] | 5 |
|  | Finland (Uusimaa) | 2 | 2020-12-17 [2020-12-16 - 2020-12-17] | 6 |
|  | France (Nouvelle-Aquitaine) | 2 | 2020-12-23 [2020-12-22 - 2020-12-23] | 4 |
|  | Germany (Lowersaxony) | 2 | 2020-11-27 [2020-11-26 - 2020-11-27] | 4 |
|  | Ireland (Wexford) | 3 | 2020-12-08 [2020-12-07 - 2020-12-08] | 10 |
|  | Ireland (Dublin) | 2 | 2020-12-22 [2020-12-22 - 2020-12-22] | 0 |
|  | Ireland (Dublin) | 2 | 2020-12-12 [2020-12-11 - 2020-12-12] | 7 |
|  | Italy (Campania) | 4 | 2020-12-19 [2020-12-19 - 2020-12-19] | 2 |
|  | Italy (Abruzzo) | 2 | 2020-12-15 [2020-12-14 - 2020-12-15] | 4 |
|  | Italy (Marche) | 2 | 2020-12-15 [2020-12-14 - 2020-12-15] | 4 |
|  | Italy (Campania) | 2 | 2020-12-20 [2020-12-20 - 2020-12-20] | 1 |
|  | Netherlands (Noord-Holland) | 8 | 2020-11-14 [2020-11-11 - 2020-11-16] | 30 |
|  | Netherlands (Noord-Holland) | 2 | 2020-11-08 [2020-11-08 - 2020-11-08] | 22 |
|  | Netherlands (Gelderland) | 2 | 2020-12-19 [2020-12-18 - 2020-12-19] | 4 |
|  | Norway (Vestland) | 2 | 2020-12-17 [2020-12-16 - 2020-12-17] | 6 |
|  | Portugal (NA) | 2 | 2020-12-14 [2020-12-13 - 2020-12-14] | 4 |
|  | Portugal (NA) | 2 | 2020-12-11 [2020-12-10 - 2020-12-11] | 5 |
|  | Spain (Madrid) | 2 | 2020-12-15 [2020-12-15 - 2020-12-16] | 7 |
| North America | Canada (Ontario) | 2 | 2020-12-12 [2020-12-11 - 2020-12-12] | 4 |
|  | USA (California) | 3 | 2020-12-13 [2020-12-13 - 2020-12-14] | 8 |
| Oceania | New Zealand (Auckland) | 2 | 2020-12-19 [2020-12-19 - 2020-12-19] | 1 |
| **Summary** |  | **152** | **2020-12-08 [2020-09-23 - 2020-12-23]** | **10 [I1 - 37]** |

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