



OPEN ACCESS

EDITED AND REVIEWED BY
Anne Kupczok,
Wageningen University and Research,
Netherlands

*CORRESPONDENCE

Daniel B. Weissman
daniel.weissman@emory.edu
Aris Katzourakis
aris.katzourakis@biology.ox.ac.uk

SPECIALTY SECTION

This article was submitted to
Viral Diversification and Evolution,
a section of the journal
Frontiers in Virology

RECEIVED 18 September 2022

ACCEPTED 26 September 2022

PUBLISHED 07 October 2022

CITATION

Ghafari M, Liu Q, Dhillon A,
Katzourakis A and Weissman DB
(2022) Corrigendum: Investigating the
evolutionary origins of the first three
SARS-CoV-2 variants of concern.
Front. Virol. 2:1047852.
doi: 10.3389/fviro.2022.1047852

COPYRIGHT

© 2022 Ghafari, Liu, Dhillon, Katzourakis
and Weissman. This is an open-access
article distributed under the terms of
the [Creative Commons Attribution
License \(CC BY\)](https://creativecommons.org/licenses/by/4.0/). The use, distribution
or reproduction in other forums is
permitted, provided the original
author(s) and the copyright owner(s)
are credited and that the original
publication in this journal is cited, in
accordance with accepted academic
practice. No use, distribution or
reproduction is permitted which does
not comply with these terms.

Corrigendum: Investigating the evolutionary origins of the first three SARS-CoV-2 variants of concern

Mahan Ghafari¹, Qihan Liu², Arushi Dhillon², Aris Katzourakis^{1*}
and Daniel B. Weissman^{2*}

¹Department of Biology, University of Oxford, Oxford, United Kingdom, ²Department of Physics, Emory University, Atlanta, GA, United States

KEYWORDS

SARS – CoV – 2, evolution, fitness landscape, mutation, variants of concern (VOCs), chronic infection

A Corrigendum on

Investigating the evolutionary origins of the first three SARS-CoV-2 variants of concern

by Ghafari M, Liu Q, Dhillon A, Katzourakis A and Weissman DB (2022) *Front. Virol.* 2:942555.
doi: 10.3389/fviro.2022.942555

In the published article, there was an error in the legend of [Figure 3](#) as published. The words "1.2% and 3.8%" should be "9.1% and 2.9%" respectively.

The corrected legend appears below.

"FIGURE 3 Evolution between hosts on a single-mutation landscape ($K = 1$) rarely reproduces the observed VOC dynamics, even with extreme overdispersion. (A) Total number of established VOC lineages (M) measured under varied levels of overdispersion, k , such that $IFR=1.5\%$, $\mu=0.87 \times 10^{-5}$, $K=1$, and $s=0.4$. The inset shows M with respect to the waiting time for the establishment of the first VOC lineage since the start of the pandemic, T_0 . The region corresponding to the waiting time for the emergence of the first three SARS-CoV-2 VOC is highlighted in red. Under low levels of overdispersion (blue, $k=0.2$), too many VOC lineages are produced very early on in the pandemic. On the other hand, as we increase overdispersion (orange and green), fewer VOCs can establish in the population. It also takes them much longer to establish and reach high frequencies in the population. (B) Evaluating the temporal clustering of the first three VOC lineages. For each simulation run, represented by a point on the graph, we measure T_0 and the time difference between the establishment of the first and third successful VOC lineages. The red dashed rectangle shows the region corresponding to the emergence of the first three SARS-CoV-2 VOCs with the cross sign ("X") representing the mean value. We see that as the level of overdispersion increases, the emergence time of VOCs are more scattered and rarely exhibit temporal clustering in late 2020 – Only

9.1% and 2.9% of the evolutionary dynamics corresponding to overdispersion $k=0.005$ and $k=0.001$ fall inside the enclosed area, respectively. The inset shows that 33.2% and 79.2% of the runs for $k=0.005$ and $k=0.001$ scenarios produce fewer than three successful VOC lineages by the end of the simulation period. Each run stops once the frequency of the VOC population reaches 75%. See also [Supplementary Figure 1](#)."

In the published article, there was an error in the legend of [Figure 5](#) as published. The words "K=4 (magenta)" should be "K=5 (magenta)".

The corrected legend appears below.

"FIGURE 5 Between-host evolution on an additive fitness landscape can match the observed VOC dynamics, but only by having intermediate mutants reach unrealistically high frequencies. (A) Total number of established VOC lineages (M) for different number of mutations, K , involved in the production of a VOC. For the $K=2$ scenario (blue), $IFR=1.5\%$, $\mu=0.87 \times 10^{-5}$, $k=0.05$, and $s=0.3$. For the $K=3$ scenario (orange), $IFR=0.5\%$, $\mu=0.87 \times 10^{-5}$, $k=0.05$, and $s=0.5$. For both the $K=4$ (green) and $K=5$ (magenta) scenarios, $IFR=0.2\%$, $\mu=2 \times 10^{-5}$, $k=0.2$, and $s=1.0$. The inset shows M with respect to the waiting time for the establishment of the first VOC lineage since the start of the pandemic, T_0 . Under $K=2$ and 3, a very large number of successful VOC lineages are produced by late 2020, with the $K=2$ scenario producing, on average, more than 20 VOC lineages that establish in the population. On the other hand, for the $K=5$ scenario, on average, fewer than three lineages are produced. It also takes much longer for them to establish in the population. (B) Evaluating the temporal clustering of the first three VOC lineages. For each simulation run, represented by a point on the graph, we measure the time that it takes for a single adaptive mutation to establish in the population and the time difference between the establishment of the first and third successful VOC lineage. The red dashed rectangle shows the region of the parameter space corresponding to the emergence of the first three SARS-CoV-2 VOCs with the cross sign ("X")

representing the mean value. We see a noticeable overlap between the $K=2$ and 4 scenarios and the red rectangle suggesting that a larger fraction of the simulation runs exhibit temporal clustering dynamics for VOC emergence. The inset shows that 10.3% of the runs for the $K=4$ scenario produce fewer than three successful VOC lineages by the end of the simulation period. Each run stops once the frequency of the VOC population reaches 75%. (C) A typical evolutionary trajectory corresponding to the $K=4$ scenario highlighted with a bold green circle in panel (B). The graph shows the background population in gray and the i -mutant populations ($1 < i \leq K$) in different shades of green from light (fewer mutations) to dark (more mutations). Note that for the $K=4$ scenario, there are four single-mutant, six double-mutant, four triple-mutant, and one quadruple-mutant genotypes. The dashed lines show the dynamics of all the established VOC lineages over time. Red vertical arrows show the establishment time of the first three VOCs. We can see that some of the intermediate mutant genotypes reach close to fixation before giving rise to the VOC population. See also [Supplementary Figure 3](#)."

In the published article, there was an error with [Figure 8A](#). The incorrect figure was used. A correction has been made to the section [Figure 8A](#) and the correct figure can be seen below.

The authors apologize for this error and state that this does not change the scientific conclusions of the article in any way. The original article has been updated.

Publisher's note

All claims expressed in this article are solely those of the authors and do not necessarily represent those of their affiliated organizations, or those of the publisher, the editors and the reviewers. Any product that may be evaluated in this article, or claim that may be made by its manufacturer, is not guaranteed or endorsed by the publisher.

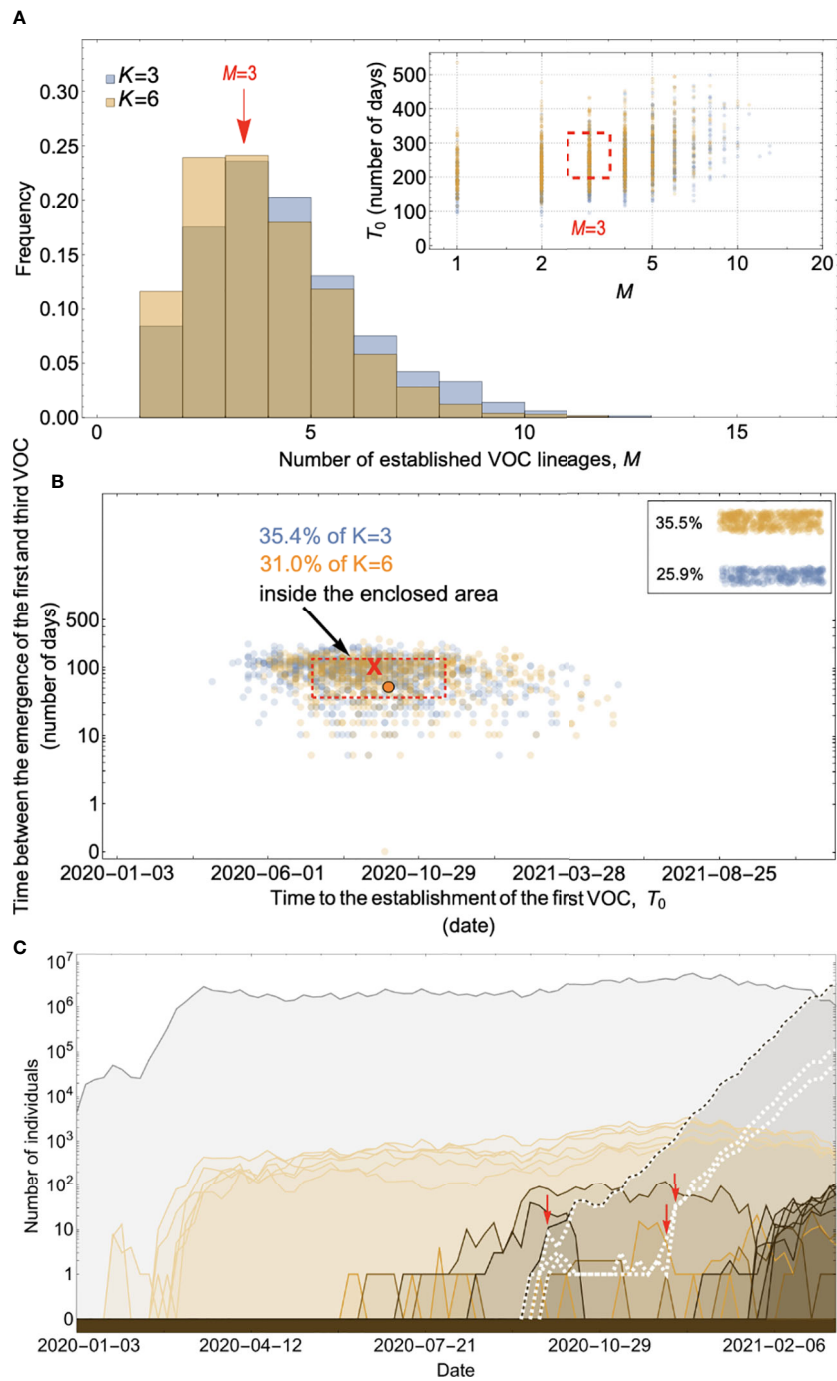


FIGURE 8 (Continued)

FIGURE 8 | Within-host evolution on a fitness plateau can match the observed VOC dynamics for a large range of plateau widths. **(A)** Total number of established VOC lineages (M for different number of mutations, K , involved in the production of a VOC. For $K=3$ (blue), the within-host parameters are $P_f=2 \times 10^{-8}$, and $\mu_C=0.1$. For $K=6$ (orange), $P_f=4.5 \times 10^{-8}$, and $\mu_C=0.25$. In both scenarios, the between-host parameters $\mu=1 \times 10^{-5}$, $IFR=0.5\%$, $k=0.1$, and $s=0.7$ are the same. The inset shows M with respect to the waiting time for the establishment of the first VOC lineage since the start of the pandemic, T_0 . The region corresponding to the waiting time for the emergence of the first three SARS-CoV-2 VOC is highlighted in red. Both scenarios produce roughly the same number of VOC lineages. However, on average, T_0 is slightly longer for the $K=6$ scenario. **(B)** Evaluating the temporal clustering of the first three VOC lineages. For each simulation run, represented by a point on the graph, we measure the time that it takes for a single adaptive mutation to establish in the population and the time difference between the establishment of the first and third successful VOC lineage. The red dashed rectangle shows the region of the parameter space corresponding to the emergence of the first three SARS-CoV-2 VOCs with the cross sign ("X") representing the mean value. We can see that a noticeable fraction of simulation runs for both scenarios yield a temporal clustering that matches the emergence of the first three VOCs in late 2020 (i.e., they fall inside the enclosed area). The inset shows that 35.5% and 25.9% of the runs for $K=3$ and 6 scenarios produce fewer than three successful VOC lineages by the end of the simulation period, respectively. Each run stops once the frequency of the VOC population reaches 75%. **(C)** A typical evolutionary trajectory corresponding to the $K=6$ scenario highlighted with a bold orange circle in panel **(B)**. The graph shows the background population in gray and the i -mutant populations ($1 < i \leq K$) in different shades of orange from light (fewer mutations) to dark (more mutations). The dashed lines show the dynamics of all the established VOC lineages over time. Red vertical arrows show the establishment time of the first three VOCs. We can see that the single-mutant genotypes (lines in light orange) are produced via the between-host pathway from very early on in the pandemic but are at very low prevalence before the emergence of the VOCs (white dashed lines). See also [Supplementary Figure 6](#).