

Narrative review

Severe zoonotic viruses carried by different species of bats and their regional distribution

Zegang Liu, Qinlu Liu, Huifang Wang, Xinsheng Yao*

Department of Immunology, Center of Immunomolecular Engineering, Innovation & Practice Base for Graduate Students Education, Zunyi Medical University, Zunyi City, China

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ABSTRACT

Background: Bats have garnered increased attention in the field of life sciences for their typical biological characteristics of carrying a variety of zoonotic viruses without disease, long lifespans, low tumorigenesis rates, and high metabolism. When it was found that bats can carry the rabies virus, over 60 years of research revealed that bats host over 4100 distinct viruses, including Ebola virus and SARS-CoV.

Objectives: This paper primarily reviews the profiles of zoonotic viruses carried by bats across various regions globally. The review aims to provide a foundation and reference for future research on monitoring zoonotic viruses in diverse global regions and bat species, exploring the coevolutionary relationship between bats and viruses, understanding the tolerance mechanisms of bat B cells, prevention, and treatment of zoonotic diseases caused by bats.

Sources: The search used 'bat', 'bats', 'rabies virus', 'Dengue virus', 'West Nile virus', 'Zika virus', 'St. Louis encephalitis virus', 'Japanese encephalitis virus', 'Hantavirus', 'Novel hantavirus', 'Rift Valley fever virus', 'Crimean Congo hemorrhagic fever virus', 'Paramyxovirus', 'Nipah virus', 'Hendra virus', 'Menangle virus', 'Tioman virus', 'Marburg Virus', 'Bombali virus', 'Ebola virus', 'Influenza A virus', 'coronavirus', 'Hepatitis B virus', and 'Hepatitis E virus' as text in PubMed.

Content: A total of 147 references were obtained. Surveys on severe zoonotic virus carriage have been limited to only 83 bat species belonging to nine families, which are distributed all over the world. We also briefly describe the antibody responses and B-cell molecules in bats.

Implications: Several viruses have been found in different species of bats. This suggests that bats may be important hosts for future viral infectious diseases. Particularly in recent years, the close correlation between human infection pandemics caused by coronaviruses and bats highlights the pressing need to comprehend the species, tolerance, and coevolutionary mechanisms of zoonotic viruses carried by different bat species. **Zegang Liu, Clin Microbiol Infect 2024;30:206**

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Introduction

Bats are the only mammals capable of sustained flight, comprise over 1200 species belonging to 20 families, accounting for approximately 20% of all mammalian species [1]. As highly social mammals, bats provide an optimal environment for the transmission and persistence of pathogens within their populations, some bats will fly a long distance in their seasonal migration, with

more than 4100 bat-associated animal viruses detected from 196 bat species in 69 countries worldwide [2]. Bats are now widely recognized as potential hosts for a large number of known and unknown viruses, some of which possess the ability to transmit to both animal and human populations. Since the discovery of the rabies virus in bats without clinical symptoms in 1955 [3], various severe zoonotic viruses have been detected in different regions and species of bats. For these zoonotic viruses, many bat species are considered to be important hosts, efficient transmitters, or even directly responsible for transmission. This paper reviews a detailed survey overview of the 83 bat species belonging to nine families that have been carried out, carrying severe zoonotic viruses

* Corresponding author. Xinsheng Yao, Department of Immunology, Center of Immunomolecular Engineering, Innovation & Practice Base for Graduate Students Education, Zunyi Medical University, Zunyi City, China.

E-mail address: immunology@126.com (X. Yao).

(Table S1), from a wide range of global areas including South America, Africa, and Asia (Fig. 1).

Materials and methods

The main 24 search terms (sources of abstract) were combined with the Boolean operators, AND and OR. Searches were carried out in PubMed. A total of 3698 references were obtained. The screening criteria were direct isolation of the virus from bats, detection of viral nucleic acids and specific antibodies, etc. By reading the abstract and full text, a total of 147 references were obtained, of which 111 were included in the bat-carrying viruses section of the summary.

Different species of bats carry severe zoonotic viruses

Detection and identification of bats carrying zoonotic viruses dates back to 1955, Enright et al. [3] detected rabies virus in *Tadarida brasiliensis* from California using mouse inoculation techniques. During the next 60 years, numerous laboratories have conducted studies to detect and identify severe zoonotic viruses in bats around the world. We describe in detail the names of the bats, the areas from which they were collected, and the methods used to detect or identify the virus, in chronological order, according to the types of zoonotic viruses found in different species of bats (Table S1).

Rabies virus

Because of the high mortality rate of rabies virus infections in humans and animals, researchers pay more attention to it more than other zoonotic infections. As early as the 1930s, Pawan et al. reported for the first time that vampire bats can transmit rabies to humans and other mammals [4,5]. In 1948, Pawan [6] reported on the association of Fruit-eating bats with paralytic rabies. Subsequently, several laboratories have conducted studies on bats

carrying rabies virus (Table S1, Refs. 1–36), it was found that rabies outbreaks caused by vampire bats have led to human deaths in Latin America. To date, rabies virus has been detected in bat samples from different regions of the world, a small proportion of these bat samples come from the United Kingdom, Ukraine, and Thailand, and most come from a number of neighbouring countries in the Americas, with the largest number of bats coming from Brazil. These samples encompass 20 bat species from four families: *Molossidae*, *Phyllostomidae*, *Pteropodidae*, and *Vespertilionidae*.

The researchers detected rabies virus in the same bat species from different areas and different bats from the same area, suggesting that different species of bats may share the same mechanism of rabies virus tolerance. Currently, a limited number of bat species for which rabies virus has been detected, and studies on the co-evolution of bats and rabies virus and immune tolerance mechanisms need to be carried out in more areas and more bat species.

Flaviviridae

The main types of Flaviviridae viruses that can cause severe zoonosis include Dengue virus, West Nile virus, Zika virus, St. Louis encephalitis virus, and Japanese encephalitis virus. As early as 1966, Sulkin et al. [7] isolated the St. Louis encephalitis virus in *Tadarida brasiliensis* from Texas, the bats were collected during an outbreak of encephalitis in Texas in 1964, suggesting that the encephalitis outbreak may be related to bats. To date, five major Flaviviridae viruses have been detected in at least 18 bat species from five families (Table S1, Refs. 37–51).

Japanese encephalitis virus has been detected in eight bat species belonging to three families, these bats are mainly from China and Indonesia. Currently, seven bat species have been found to carry Dengue virus, all belonging to the family *Phyllostomidae*, and all from the Americas, with five bat species from Mexico and two from Colombia; only five bat species have been found to carry West Nile virus, belonging to four families: *Phyllostomidae*, *Pteropodidae*,

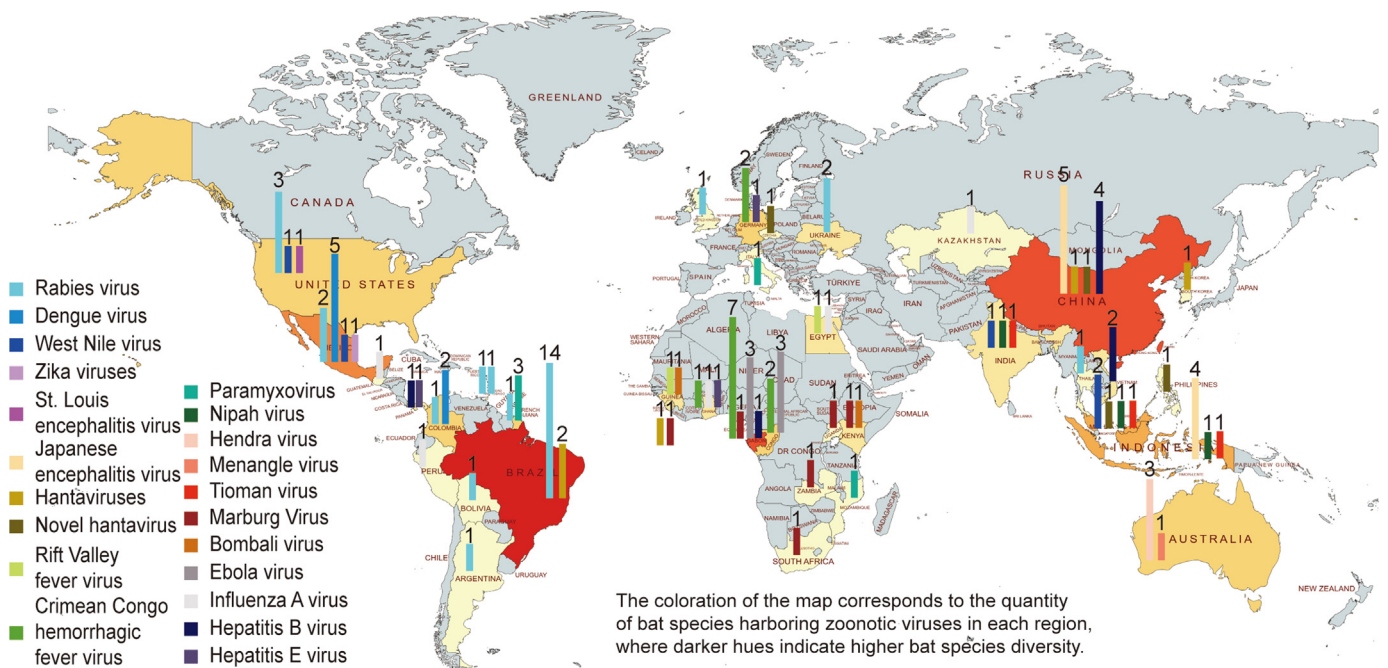


Fig. 1. Regional distribution of bats carrying severe zoonotic viruses. The numbers on the bar graph represent the number of bat species in the area that carry the corresponding zoonotic virus.

Rhinolophidae, and *Vespertilionidae*, which are fewer in number but more widely distributed, such as the United States, Mexico, India, and Malaysia. However, there are fewer studies on bats carrying Zika virus and St. Louis encephalitis virus, which have been found in *Artibeus jamaicensis* from Mexico and *Tadarida brasiliensis* from the United States, respectively.

Bunyaviridae

The main types of Bunyaviridae viruses that can cause severe zoonosis include Hantaviruses, Novel Hantavirus, Rift Valley fever virus, and Crimean Congo haemorrhagic fever virus. Since 1994, when Kim et al. [8] identified hantaviruses of *Rhinolophus ferrumequinum* from Korea, several laboratories have detected the above four major Bunyaviridae viruses in at least 23 bat species from seven families (Table S1, Refs. 52–63).

Crimean Congo haemorrhagic fever virus has been detected in 12 bat species belonging to four families, seven of which are from Gabon, and the rest from Ghana, Congo, and Germany. Hantaviruses have been detected in five bat species from three families with a wide range of distributions, including China, Korea, Brazil, and Sierra Leone. The novel hantavirus has been found in only four bat species but is widely distributed, including the Czech Republic, the Philippines, Malaysia, and China. There is a relative lack of research on bats carrying the Rift Valley fever virus, which has only been found in two bat species in Egypt and Guinea.

Paramyxoviridae

The main types of Paramyxoviridae viruses that can cause severe zoonosis include Nipah virus, Hendra virus, Menangle virus, and Tioman virus. Investigation of bats carrying the Paramyxoviridae began relatively late, several laboratories have detected all four major types of Paramyxoviridae virus in 11 bat species across five families (Table S1, Refs. 64–77). In contrast to surveys of bats carrying other viruses, the same bat-carrying Paramyxoviridae virus may also carry various other zoonotic viruses, in 2021, Hoarau et al. [9] detected Paramyxoviridae, coronaviruses, and astroviruses in *Paratriaenops furculus* from Mozambique, they found that 2.4% of the bats were infected with at least two viruses.

Only two bat species have been found to carry Nipah virus, both belonging to the family *Pteropodidae*, from India, Malaysia, and Indonesia; three bat species have been found to carry Tioman virus, all belonging to the family *Pteropodidae*, also from India, Malaysia, and Indonesia. Three bat species, all from Australia, have been found to carry Hendra virus. Currently, Menangle virus has only been found in *Pteropus Alecto* from Australia.

Filoviridae

The main types of Filoviridae viruses that can cause severe zoonosis include Marburg Virus, Bombali virus, and Ebola virus. Currently, the above three main Filoviridae viruses have been detected in five bat species belonging to three families (Table S1, Refs. 78–86). Highlights the finding that the common *Rousettus aegyptiacus* may be the primary natural host of Marburg virus, provides evidence of Marburg virus transmission in West Africa, indicating the possibility of spillover to humans.

Currently, Marburg Virus has been found in *Rousettus aegyptiacus* from Sierra Leone, Gabon, Uganda, Kenya, the Republic of South Africa, and Zambia. Relatively few studies have been conducted on bats carrying Bombali virus, the virus has been found in *Mops condylurus* from Guinea and Kenya. Ebola virus has been found in three bat species from Gabon and Congo, all belonging to the family *Pteropodidae*.

Influenza A virus

In 1979, L'vov et al. [10] isolated complex influenza virus (H3N2) in *Nyctalus noctula* from Kazakhstan. Currently, six bat species have been found to carry Influenza A virus, belonging to three families: *Vespertilionidae*, *Phyllostomidae*, and *Pteropodidae* (Table S1, Refs. 87–92), these bats come from all over the world, including Peru, Brazil, Guatemala, Kazakhstan, Egypt, and Ghana. Influenza A virus is the most important virus causing disease in humans, but bats have been relatively poorly studied for carrying and transmitting influenza A virus. Further exploration is necessary to determine whether bats have played a crucial role in the co-evolution of Influenza A virus.

Coronaviridae

The main types of Coronaviridae virus that can cause severe zoonosis include SARS-like coronavirus, Alpha coronavirus, and Beta coronavirus. After the SARS-COV outbreak in 2003, numerous laboratories initiated searches for the natural host of SARS-like coronavirus. In 2013, Ge et al. [11] and Hu et al. [12] detected SARS-like coronavirus in *Rhinolophus sinicus* and *Rhinolophus pusillus* from China. After the SARS-COV-2 outbreak in 2019, Zhou et al. [13] reported that the RaTG13 virus, found in *Rhinolophus affinis*, shared 96.2% similarity with SARS-COV-2. In 2022, it was found that BANAL virus, which belongs to the *Sarbecovirus* of Beta coronavirus, isolated from three different species of the *Rhinolophus* genus, shared 96.8% similarity with SARS-COV-2 [14]. Currently, four bat species have been found to carry SARS-like coronavirus, all belonging to the family: *Rhinolophidae* (Table S1, Refs. 101–104), from Russia, Thailand, and China (Fig. 2). These results imply that both SARS pandemics that occurred in humans, namely SARS-COV in 2003 and SARS-COV-2 in 2019, most likely originated from bats.

Currently, Alpha coronavirus and/or Beta coronavirus have been detected in 18 bat species belonging to five families (Table S1, Refs. 93–100, 105–107) from a wide range of locations around the world, including the United States, Mexico, India, China, South Korea, Indonesia, Italy, the Republic of South Africa, Sri Lanka, Myanmar, and Russia (Fig. 2). Different from investigations of bats carrying other viruses, the same bat species was found to carry multiple types of Alpha coronavirus and Beta coronavirus, this may promote an increase in the frequency of virus mutations, thereby accelerating virus evolution. Conducting studies on the mutation of coronaviruses in bats in the wild or captivity, as well as studies on the synergistic evolution of various coronavirus strains, may provide clues to the origin of SARS-COV/COV-2 and provide preventive and control solutions for the future coronavirus outbreak.

Hepatitis B virus and E virus

In 2013, Drexler et al. [15] detected Hepatitis B virus DNA in *Hipposideros ruber* from Gabon, indicating that bats may harbour Hepatitis B virus. Currently, Hepatitis B virus and E virus have been detected in ten bat species from three families, respectively (Table S1, Refs. 108–111), seven bat species carry Hepatitis B virus belonging to the families *Hipposideridae* and *Vespertilionidae* from Gabon, Panama, China, and Vietnam, and three bat species carry Hepatitis E virus belonging to the families *Hipposideridae*, *Phyllostomidae*, and *Vespertilionidae*, from Germany, Ghana, and Panama. For a long time, it was believed that only humans were natural hosts for Hepatitis B and E viruses. However, the detection of these viruses in several bat species provides a new tool for establishing and applying hepatitis disease models, and for studying the mechanisms, mutations, and evolution of cells infected with Hepatitis B and E viruses, which has been troubling virologists.

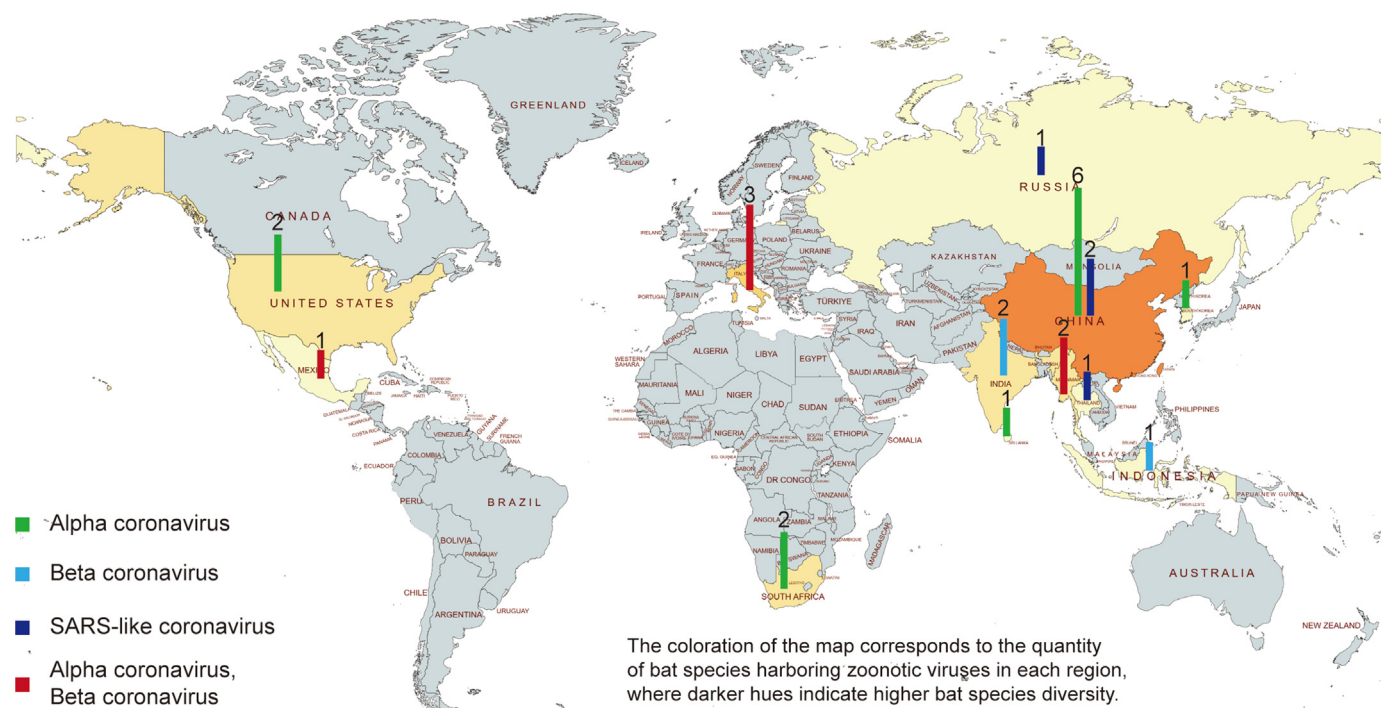


Fig. 2. Regional distribution of bats carrying coronaviruses. The numbers on the bar graph represent the number of bat species in the area that carry the corresponding coronaviruses.

The discovery of different species of coronaviruses in bats of the same family suggests that bat carriage has an important role in viral evolution. However, there is a lack of evolutionary studies such as genome sequencing of the same virus (or different viruses) carried by bats in different regions, which could provide valuable insights into their genetic diversity, origins, and zoonotic potential.

In addition to bat hosts, zoonotic viruses have a wide range of hosts. We have summarized the other animal reservoirs and host range (Table S1). How to compare and analyse the genomic changes of the same virus between different hosts, centred around bat hosts, will be an important direction in the study of virus origin and evolution.

Different species of bats from different regions can carry the same virus, suggesting the existence of a common mechanism of virus tolerance in bats. However, on the basis of the current large differences in immune cells and molecules of different bat species [16,17], the metabolism, body temperature, and behavioural patterns of bats may play an important role in their ability to tolerate viruses. Meanwhile, the investigation discovered that the same bat from different regions can carry multiple types of viruses simultaneously without exhibiting any clinical symptoms. This finding suggests that bats have a unique innate and adaptive immune system which is fundamentally different from other mammals in terms of response or tolerance mechanisms.

Compared with the more than 1200 bat species in 20 families that are widely distributed worldwide, the current investigation of bats carrying viruses is significantly limited in scope. Urgent collaboration is needed among multiple laboratories in different regions, as well as investment in human and material resources by organizations such as the WHO and public health departments in various countries. In particular, SARS-COV/COV-2, and some rare zoonotic viruses (e.g. Chikungunya virus) [18] have been found in different species of bats. This suggests that bats may be important hosts for future viral infectious diseases. The expansion of the study on viruses carried by different bat species in different regions is a prerequisite for exploring the co-evolution of viruses and bats,

which can provide a basis for the prevention and treatment of zoonotic viruses.

Antibody responses and B-cell molecules of bats

Regarding the adaptive response of bats, several laboratories have conducted studies on zoonotic virus antibodies secreted by bat B cells and the B-cell molecule (Table S2). There are more studies on rabies virus antibodies, Hendra virus antibodies, and Nipah virus antibodies; however, there are fewer studies on antibodies to other viruses, but a wide variety of viruses, including Marburg virus antibodies, Ebola virus antibodies, West Nile virus, and Japanese encephalitis virus. The researchers also observed and characterized bat cells using techniques such as electron microscopy and monoclonal antibodies, suggesting that mammalian-like B lymphocytes are present in bats and demonstrating that bat B cells are functional. The study on B cell receptor (BCR) genes of bats started relatively late, the annotation and comparison of BCR genes of a few bat species completed so far are very limited, it is difficult to understand the conservation and variation of the BCR genes within diverse bat populations.

Conclusion and prospects

In this paper, we reviewed severe zoonotic viruses carried by bats and analyse the different types of viruses carried by the same species of bats, the selection of different species of bats as hosts by the same virus, this demonstrates the breadth and complexity of the synergistic evolution of viruses and bats. With the rapid development of bat genome sequencing [19], models such as the study from viral gene fusion to the bat genome [20] will provide new ideas for the synergistic evolution of both.

Studies on the virus tolerance mechanisms in bats have mainly focused on the metabolic and innate immune responses of bats, such as Toll-like receptors, interferon (IFN), and complement,

aiding coexistence with the virus through early control of virus replication [21,22]. Considering the adaptive immune response of bats carrying severe zoonotic viruses, studies have shown that one bat species can secrete multiple antibodies to different viruses, and one type of virus antibody can be produced in different bat species, suggesting the existence of a common mechanism for virus tolerance in bats, further research should be directed towards clarifying whether bat virus antibodies primarily function in virus clearance or in modulating immune tolerance towards viruses.

Elucidating the intricate mechanism of virus antibody production in bats hinges on the advancement in studying bat B cells, as well as their associated molecules and genes. As more bat genomes are sequenced and assembled, there is an opportunity to annotate and compare the BCR VDJC gene (variable gene segment, diversity gene segment, joining gene segment, constant gene segment) composition of different bat species. Analysing the possible molecular mechanisms of bat B-cell regulation, response, and tolerance to viruses from the perspective of BCR CDR3 repertoire interacting with viral antigenic epitopes. This will provide new technologies and direction for experts in immunology, virology, and infectious diseases who have been struggling with the research on how bats can carry viruses without being infected by them.

Because of the widespread distribution and diversity of bat species, very limited studies have been accomplished. International collaboration and timely data sharing among laboratories are urgently required to investigate the origins and mutations of prevalent zoonotic viruses, improvements in diagnosis and treatment, and control epidemics of unknown viral infectious diseases. Research should focus particularly on bat families or species that are currently underrepresented. The establishment and application of bat stem cell sequencing [23], development of bat transcriptome [24], and single-cell sequencing [25], as well as the establishment of various disease models in captive bats, these advances in technology are particularly important.

Author contributions

XY and ZL completed the design and paper writing. QL and HW completed part of paper writing and collated references.

Transparency declaration

Conflict of interest

The authors declare that they have no conflicts of interest.

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Data availability

All data are available in the main text.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.cmi.2023.09.025>.

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