



Nipah Virus Transmission at the Human-Animal Interface: A One Health Scoping Review

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ABSTRACT

Nipah Virus (NiV) is a highly pathogenic zoonotic virus with pandemic potential but has limited synthetic evidence on its epidemiology, transmission dynamics, and One Health dimensions. This scoping review was conducted according to PRISMA-ScR guidelines to identify literature from PubMed, Google Scholar, and Semantic Scholar databases from 1998 to 2025. Of the 988 studies screened, 55 studies met the inclusion criteria. The geographic distribution is centred around Bangladesh with 20 studies and India with 12 studies. Outbreaks occurred with distinct patterns: the Malaysia-Singapore outbreak with pig as the animal host, Bangladesh-India with date palm sap as the transmission agent, and the Philippines with horse as the animal host. Pteropus bats were identified as the primary animal host with 17 primary studies confirming their role as the reservoir host. Human-to-human transmission accounts for one-third of cases. Phylogenetic analysis has identified two major clusters with NiV-M and NiV-B being the dominant clusters with an emerging Indian cluster designated as NiV-I. Only 34 studies used the One Health approach, but integration is limited because of institutional barriers, surveillance challenges, and resource limitations. NiV remains a geographically limited but epidemiologically relevant threat because of a complex transmission network. There is a pressing need to improve integrated surveillance, economically driven interventions in communities, and cross-sector response capacity to address the threat of future spillover.

HIGHLIGHTS

- NiV transmission occurs via multiple pathways: bat-to-human, pig amplification, horse spillover, and human-to-human
- Two major clades (NiV-M, NiV-B) and an emerging Indian variant (NiV-I) exist; NiV-B has higher CFR (77% vs. 40%) and greater human-to-human transmission.
- One Health integration remains limited; institutional fragmentation, surveillance gaps, and resource constraints require strengthened cross-sectoral collaboration.

Keywords: Nipah Virus, One Health, Spillover, bats

The emergence and re-emergence of zoonotic infections rank among the biggest global health risks to human health, animal health, and the health of the environment (Aditi and Shariff, 2019). Some of the deadliest pandemics in human history have been caused by pathogens that can jump the species barrier, highlighting the strong connections among human health, animal health, and the

health of the environment (Bruno *et al.*, 2023). Among the zoonotic infections that have been rising in recent

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years, the Nipah Virus (NiV) is one of the most alarming pathogens because it has a high case-fatality-rate, a wide host range, and strong epidemic/epizootic potential (Pillai *et al.*, 2020; Skowron *et al.*, 2022).

NiV emerged in 1999 in a large outbreak of respiratory and neurological illness among pig handlers in Malaysia and Singapore. Since then, Nipah has shown a striking ability to cross international and interspecies boundaries, contrary to the expectations that emerged from the 1999 outbreak (Weatherman *et al.*, 2018). The virus got its name from a village in Malaysia, known as Sungai Nipah, where it was first isolated from the cerebrospinal fluid of an infected patient (Kaliappan *et al.*, 2022).

Since the 1999 outbreak, Nipah has recurred in Bangladesh since 2001 and in India; West Bengal (2001 and 2007) and in Kerala (2018, 2019, 2021, 2023, and 2024) (Anish *et al.*, 2024; Chakraborty *et al.*, 2016; Veggalam *et al.*, 2025). Sporadic reports from the Philippines in 2014 further underscore the expanding geographical distribution of this highly pathogenic virus (Khadka, 2026).

The incubation period ranges from 4 to 14 days. Nipah infection in humans manifest primarily as acute fever with encephalitis and severe respiratory complications. The case-fatality rate varies from 40% to 94%. The survivors are left with neurological sequelae, a consequence of the infection (Ramphul *et al.*, 2018). The high case-fatality rate, absence of a licensed vaccine, and absence of a licensed treatment make Nipah a priority under the World Health Organization's Research and Development Blueprint, a list of priority pathogens for research and development (Faus-Cotino *et al.*, 2024; Mohapatra *et al.*, 2024; Kiran *et al.*, 2025).

The NiV epidemiology depends on the wildlife reservoir, which includes the Old World fruit bats of the *Pteropus* genus, or flying foxes. These bats maintain a silent or endemic level of the virus across a majority of their populations (Epstein *et al.*, 2020). There are a number of *Pteropus* species associated with NiV and its endemic range. These include *P. vampyrus*, *P. hypomelanus*, *P. lylei*, *P. giganteus*, and *P. medius* (Balasubramanian *et al.*, 2024; Epstein *et al.*, 2020). *Pteropus* bats are found across South and Southeast Asia, Oceania, and Africa. This means a large proportion of the global population lives in spillover risk zones (Mbu'u *et al.*, 2019; Sun *et al.*, 2024; Yu *et al.*, 2018). The spillover of NiV from bats to humans

has occurred via a number of routes. In Malaysia and Singapore, pigs functioned as an intermediary amplifier of the virus. Bats infect fruit, which is then ingested by pigs, resulting in a high mortality rate among pigs (McLean and Graham, 2019). In Bangladesh and India, outbreaks among humans have been attributed to consuming date palm sap that has been contaminated with saliva or urine of infected bats. This has been seen during winter outbreaks (Chakraborty *et al.*, 2016; Gurley *et al.*, 2017). Tari, a fermented form of date palm sap, has also been linked to spillover of NiV from bats to humans (Chakraborty *et al.*, 2016; Islam *et al.*, 2016). In the Philippines, spillover to humans have been attributed to contact with infected horses or consuming infected horses. There has been evidence of limited but significant transmission of NiV among humans, raising concerns of potential pandemics (Khadka, 2026). Nosocomial transmission and corpse-to-human transmission have also been seen. This emphasizes the need for strict infection control practices (Gurley *et al.*, 2017; Weatherman *et al.*, 2018). In the case of the Philippines, it is not just the case of the people contracting Nipah because of the bats; it is also because of the horses that the people eat and come into contact with, as has been proven in studies (Khadka, 2026). There is also evidence of the virus being transmitted from one human to another, which could lead to large-scale outbreaks (Gurley *et al.*, 2017; Weatherman *et al.*, 2018).

There are two different forms of the NiV, one of which is the NiV-M found in Malaysia, and the other is the NiV-B found in Bangladesh. These two forms of the virus have different genome sizes, virulence, and modes of transmission, as has been proven in studies (Branda *et al.*, 2025). The NiV-B form of the virus has been known to show higher levels of human-to-human transmission, higher virulence, and respiratory symptoms as opposed to the NiV-M form (Pillai *et al.*, 2020). The most recent form of the virus is the NiV-I, found in India in the state of Kerala (Singhai *et al.*, 2021).

Even after twenty years of research into the virus, many questions still remain unanswered, such as the reasons behind the spillover of the virus, which makes it hard to predict the outbreak of the virus (Gurley *et al.*, 2025). The role of the environment in the spread of the virus also needs to be taken into consideration, as has been proven in a few studies (McKee *et al.*, 2021; Bruno *et al.*, 2023; Lim and Min 2025). The evolution of the virus in the

host, specifically in the bats, also needs to be researched in depth to see the role of the immune system of the host in the resurgence of the virus (Epstein *et al.*, 2020). The differences in the behaviour of the different forms of the virus also need to be studied in depth (Branda *et al.*, 2025). The sporadic occurrence of NiV infections in resource-constrained situations has been a challenge to the collection of adequate data for thorough analysis of the phenomenon (Cortes *et al.*, 2018; McKee *et al.*, 2022).

In light of the above, the urgent need for a thorough, integrated, and comprehensive synthesis of the available evidence regarding NiV infections is urgently needed. This scoping review aims to systematically map and summarize the breadth of literature on NiV at the human-animal interface. The specific objectives are:

1. To collate and characterize the global evidence on the epidemiology of NiV, including its geographic distribution, incidence, and mortality
2. To characterize transmission dynamics across different hosts and settings
3. To examine the role of reservoir hosts and environmental drivers in spillover events
4. To critically evaluate the extent to which a One Health approach integrating human, animal, and environmental health perspectives has been applied in research and outbreak response.

By identifying where knowledge gaps and bringing together existing knowledge, this review seeks to provide a clear and comprehensive overview that will be useful in guiding research, informing evidence-based policy, and preparing the world for NiV, a zoonotic agent with significant human health implications.

METHODS

Protocol and reporting framework

This scoping review is conducted and reported in accordance with the Preferred Reporting Items for Systematic Reviews and Meta-Analyses extension for Scoping Reviews (PRISMA-ScR) guidelines (Tricco *et al.*, 2018) and is informed by a protocol that outlines how the review is conducted and how the results are reported.

Rationale for scoping review methodology

As such, a scoping review design was considered appropriate given the heterogeneity and dispersion of the evidence base on NiV, which spans multiple disciplines such as virology, epidemiology, veterinary science, ecology, and anthropology, and incorporates a range of study designs such as outbreak studies, longitudinal surveillance, case-control studies, phylogenetic studies, ethnographic studies, and pilot intervention studies. Moreover, a significant proportion of these studies are observational or descriptive in nature, as opposed to experimental designs. Finally, unlike systematic reviews, which are generally focused on a particular intervention and aim to synthesize homogeneous studies to conduct meta-analysis, a scoping review provides a broad overview of the whole range of literature on a particular topic or concept and explores different ideas and theories across multiple bodies of literature (Munn *et al.*, 2018). This is appropriate given our aim of providing a detailed overview of evidence on the interface of humans and animals, rather than providing a synthesis of results or assessing the certainty of particular interventions. Finally, as is common with scoping reviews, quality assessment of included studies was not undertaken (Tricco *et al.*, 2018).

Eligibility criteria

Studies were included or excluded on the basis of predefined criteria.

Inclusion criteria:

- ☐ Peer-reviewed articles and relevant grey literature on NiV infection in humans, animals, and the environment.
- ☐ Studies providing epidemiological, zoonotic, transmission, and prevention-related information on NiV.
- ☐ Original research articles on NiV infection.
- ☐ Systematic and narrative reviews were screened for primary sources but were not included as primary evidence in the final synthesis to avoid double-counting. Reviews cited for contextual background are clearly distinguished in the manuscript.



- ☐ Systematic reviews and narrative reviews that actually included primary data synthesis were included in the synthesis process for contextual purposes and for locating the original sources.
- ☐ The literature included was in English only, and the period was from 1998 to 2025 (from the first reported outbreak of NiV to the most recent year before the search).

Exclusion Criteria:

- ☐ Limited zoonotic and epidemiological relevance.
- ☐ Lack of primary focus on NiV.
- ☐ Inappropriate design for primary literature, such as editorials, commentaries, and conference abstracts.
- ☐ Lack of full-text accessibility after a reasonable attempt to procure the article through interlibrary loan.

Information sources

A wide literature search was conducted on PubMed, Google Scholar, and Semantic Scholar databases, with the final search conducted on February 16, 2026. The references of the included studies were also manually searched for additional relevant literature.

Search strategy

To conduct the literature search, keywords such as NiV, zoonosis, epidemiology, transmission, prevention, etc., associated with NiV, were used, and the search results were refined by combining the terms with AND/OR operators. The search results were restricted to the years 1998-2025.

PubMed search string used:

“Nipah Virus” OR “NiV” AND (zoonosis OR zoonotic OR epidemiology OR transmission OR outbreak OR reservoir OR bat OR “public health” OR prevention OR control OR “One Health” OR spillover)

Equivalent keyword combinations were adapted for Google Scholar but similar search yielded limited results on Semantic Scholar. As such the search string for

Semantic Scholar was “Nipah Virus” OR “NiV” in order to expand the search. For Google Scholar and Semantic Scholar, the first 200 results sorted by relevance were screened, as search functionality in these platforms does not allow for the same level of precision as PubMed.

Study selection

All the search results obtained on the databases mentioned above were imported into Rayyan, which is a software used for systematic review, for screening, (Ouzzani *et al.*, 2016). After which duplicates were removed, followed by title/abstract screening, and then full-text screening for potentially relevant studies for the review.

This resulted in a total of 988 articles. After removing duplicates, 790 articles were used for title and abstract screening. After this, 177 articles were used for full-text screening to determine eligibility. After full-text screening, 122 articles were excluded for reasons such as limited zoonotic or epidemiological evidence, inappropriate study design, articles not related to Nipah, and articles without full text after reasonable attempts to retrieve them. Finally, 55 articles were found to meet the eligibility criteria and were included for this scoping review. The selection of articles for this study has been represented in the PRISMA flow chart (Fig. 1).

RESULTS AND DISCUSSION

Study selection

A systematic search generated 988 articles from three different databases. In duplicate elimination, 198 duplicates were removed, leaving 790 articles for title/abstract screening. Of the 177 full texts reviewed, 55 articles met the inclusion criteria (37 being original research and 18 reviews). Figure 1 below shows the process of selection.

Characteristics of included studies

The 55 included articles showed heterogeneity in their characteristics. Table 1 provides an overview of the general characteristics of these studies.

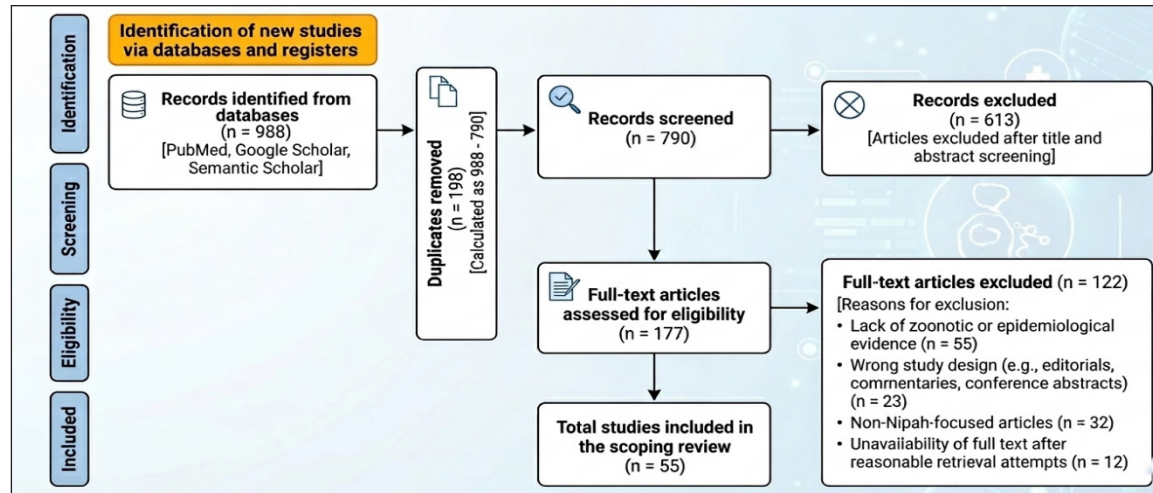


Fig. 1: PRISMA flow diagram

Table 1: Summary Characteristics of Included Studies (n=55)

Characteristic	Category	Number of Studies
Geographic Focus	Bangladesh	20
	India	12
	Malaysia	5
	Thailand	4
	Singapore	3
	Philippines	1
	Cambodia	2
	Indonesia	1
	China	1
	Australia	3
	Africa (multi-country)	1
	Other/Multi-region	2
Study Design	Outbreak Investigation	9
	Longitudinal	6
	Surveillance	
	Cross-sectional Survey	3
	Case-Control Study	2
	Spatial/Ecological	5
	Modeling	
	Phylogenetic/Molecular	6
	Analysis	
	Ethnographic/behavioural Study	3
	Pilot Intervention	3
	Comprehensive/Narrative Review	16
	Practical Clinical Review	2

Host Focus	Humans only	27
	Humans and Bats	15
	Humans and Pigs	8
	Humans and Horses	2
	Multi-host (≥ 3 species)	3
One Health Approach	Explicitly Mentioned	24
	Implied	12
	Not Mentioned	19
Publication Year	1998-2009	8
	2010-2019	24
	2020-2026	23

Most included studies were outbreak investigations and ecological surveillance studies, with fewer evaluating prevention or intervention outcomes. This predominance of observational research indicates that the evidence base on Nipah is largely reactive rather than preventive. Although a great deal is known regarding transmission and spillover patterns, few studies have assessed the effectiveness of long-term prevention strategies.

Geographic distribution

Research covered various geographic locations including South Asia (Bangladesh: 20 studies, India: 12 studies), Southeast Asia (Malaysia: 5, Singapore: 3, Thailand: 4, Cambodia: 2, Indonesia: 1, Philippines: 1, Timor-Leste: 1), East Asia (China: 1), Oceania (Australia: 3, Papua New Guinea: 1), and Africa (Cameroon, Ghana, Nigeria, Republic of Congo, Zambia, Madagascar: 1 multi-country



study). Bangladesh and India featured prominently, attributable to almost perennial outbreak events in the region. This geographic clustering reflects unique ecological and socio-cultural factors, including human-bat interfaces and widespread raw date palm sap consumption, that make the region a hotspot for Nipah spillover.

Study designs

The research included outbreak investigation reports (9), longitudinal surveillance studies (6), cross-sectional studies (3), case-control studies (2), spatial/ecological modelling studies (5), phylogenetic/molecular studies (6), ethnographic/behavioural studies (3), pilot intervention studies (3), and review studies (18).

Temporal distribution

Research spanned 1998-2026, with the majority conducted after 2010, likely due to increased research focus following perennial outbreaks in Bangladesh and India.

Host focus

Research covered humans (all 55 studies), bats (*Pteropus* spp., *Eidolon helvum*, other pteropodid bats) (28), pigs (12), horses (4), and other domestic animals including dogs, cats, cattle, and goats (6).

One Health approach

Of 55 studies, 34 clearly mentioned or implied the One Health approach. Despite this awareness, actual integration of human, animal, and environmental sectors remains limited. The 18-year surveillance program in Thailand successfully prevented spillover despite viral circulation, while Kerala's outbreak response from 2018-2023 demonstrated effective multisectoral integration, reducing case-fatality-rates.

Challenges to One Health implementation include fragmented institutional structure with divergent mandates and financing between the three sectors; lack of surveillance where animal information is not integrated with human surveillance; and financial constraints in low-resource endemic environments. Where multisectoral integration has been unsuccessful, effects have been

observed. For example, Malaysia had problems integrating the veterinary and public health sectors, which facilitated disease dissemination (Singhai *et al.*, 2021). In Africa, while there is serologic evidence that the henipavirus infection exists among bats, cattle, and bat butchers, there is no infrastructure to deal with any outbreaks (Mbu'u *et al.*, 2019).

Thematic synthesis of literature evidence

Research papers were organized based on their thematic importance to NiV, such as Reservoir Ecology, Transmission, and Prevention. Table 2 shows the allocation of studies according to these themes.

Attempts to find reservoirs and establish modes of transmission are the most prevalent findings in the literature. Evaluations on the effectiveness of prevention measures are rare. Again, fruit bats of the species *Pteropus* have continued to appear in literature as the natural reservoir for the disease. Spillover can occur through food products, intermediaries such as pigs and horses, and also through human-to-human infection.

Transmission depends on ecology, reservoir biology, and human-related issues. Deforestation, farming, and consumption of infected food products aid spillover; therefore, NiV has emerged as a re-emerging zoonotic virus.

Epidemiology

Geographical distribution

Distribution of NiV has increased significantly since its first appearance in Malaysia back in 1998. According to Sun *et al.* (2024), the disease was recorded in 749 human cases from five countries (Bangladesh, India, Malaysia, Singapore, Philippines) and 425 cases in bats from seven countries. The authors have developed a model for identifying risk zones with a total area of 185,312 km² in 13 countries, where 176.2 million people are potentially at risk. The population at risk includes 106.7 million people in Bangladesh, 36.4 million in India, 16.5 million in Thailand, and 10.2 million in Malaysia.

In Malaysia (1998-1999), the disease affected 283 people, causing 109 deaths (38.5% case-fatality-rate), mainly

Table 2: Thematic Summary of Evidence on NiV

Theme	Key Findings	No. of Primary Studies*	All Relevant Primary Studies
Bat reservoir evidence	Fruit bats (<i>Pteropus spp.</i>) consistently identified as the primary natural reservoir across multiple regions.	7	Epstein <i>et al.</i> , 2020; Balasubramanian <i>et al.</i> , 2024; McKee <i>et al.</i> , 2021; Wacharapluesadee <i>et al.</i> , 2021; Mbu’u <i>et al.</i> , 2019; Sun <i>et al.</i> , 2024; Kessler <i>et al.</i> , 2018
Pig amplification	Pigs acted as major amplifying hosts during the Malaysian and Singapore outbreaks, facilitating large-scale human infection.	3	Thanapongtharm <i>et al.</i> , 2019; Bruno <i>et al.</i> , 2023; McLean and Graham, 2019
Date palm sap spillover	Consumption of raw date palm sap was repeatedly linked to bat-to-human transmission in Bangladesh and India.	9	Gurley <i>et al.</i> , 2017; Chakraborty <i>et al.</i> , 2016; Islam <i>et al.</i> , 2016; Hossain <i>et al.</i> , 2025; Cortes <i>et al.</i> , 2018; McKee <i>et al.</i> , 2021; McKee <i>et al.</i> , 2022; Yeasmin <i>et al.</i> , 2025; Khan <i>et al.</i> , 2025
Human-to-human transmission	Secondary transmission occurred mainly through close caregiving contact and healthcare exposure.	4	Gurley <i>et al.</i> , 2017; Parveen <i>et al.</i> , 2016; Chakraborty <i>et al.</i> , 2016; Anish <i>et al.</i> , 2024
Healthcare transmission	Nosocomial clusters highlighted gaps in infection prevention and control during outbreaks.	2	Parveen <i>et al.</i> , 2016; Anish <i>et al.</i> , 2024
Prevention interventions	Physical barriers such as bamboo skirts showed effectiveness but variable community uptake.	5	Hossain <i>et al.</i> , 2025; Khan <i>et al.</i> , 2025; McKee <i>et al.</i> , 2022; Anish <i>et al.</i> , 2024; FAO, 2026
One Health approaches	Integrated human-animal-environment surveillance and response were repeatedly recommended.	12	Wacharapluesadee <i>et al.</i> , 2021; Anish <i>et al.</i> , 2024; Epstein <i>et al.</i> , 2020; McKee <i>et al.</i> , 2021; McKee <i>et al.</i> , 2022; Thanapongtharm <i>et al.</i> , 2019; Kessler <i>et al.</i> , 2018; Lim and Min, 2025; Gurley <i>et al.</i> , 2025; Parveen <i>et al.</i> , 2016; Gurley <i>et al.</i> , 2017; FAO, 2026

* Number of primary research studies only. Review articles are not included in the thematic counts to prevent duplication, as recommended in Section 2.5. In all, 37 primary research articles were included in the analysis, while 18 review articles are retained for background purposes only.

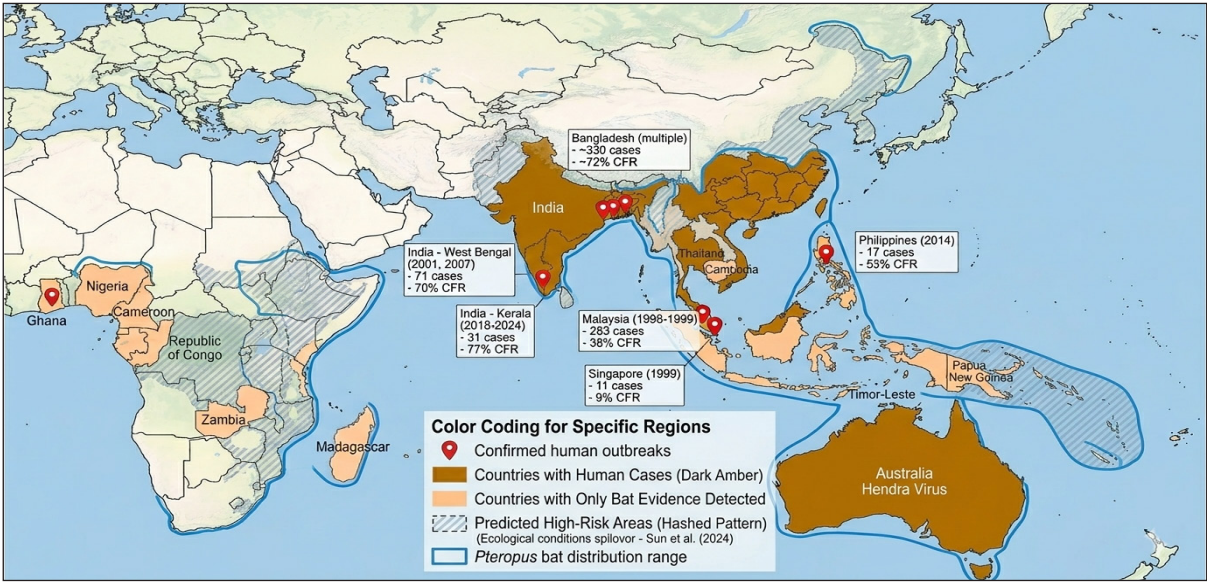


Fig. 2: Geographic Distribution of NiV Outbreaks and *Pteropus* Bat Range

among pig farmers. Singapore recorded 11 cases with 1 death in 1999 associated with Malaysian pigs.

Since 2001, there have been almost annual outbreaks in Bangladesh in the “Nipah belt” (Gurley *et al.*, 2017). For example, according to Siddique *et al.*, (2016), there were 67 cases with 50 deaths in 2004, 43 cases with 37 deaths in 2011, and 38 cases (16 deaths) in 2014. Bhowmik *et al.*, (2025) recorded 330 cases and 237 deaths in Bangladesh between 2001-2024.

India experienced outbreaks since 2001: West Bengal (2001: 66 cases, 45 deaths, 68% CFR), Nadia (2007: 5 cases, 5 deaths, 100% CFR), and Kerala (2018, 2019, 2021, 2023, 2024). In 2018 Kerala outbreak 23 cases were registered with 21 deaths (91% CFR); in 2023 6 cases (2 deaths; 33% CFR) (Anish *et al.*, 2024). Genotype “I-India” was discovered in south India (Singhai *et al.*, 2021).

Philippines (2014 outbreak) affected 17 individuals with 9 deaths (53% CFR); the virus was transmitted through horses as intermediate hosts. Of these ten patients had contact with infected horses or ate horse meat, 10 horses died with neurological symptoms. There were five instances of human-to-human transmission including medical staff (Khadka, 2026).

The continent of Africa has recently been pinpointed as an emerging focus area of infection. Evidence from serological

and molecular investigations in various countries include: in Ghana, 5% of pigs tested seropositive; in Nigeria, 15.5% of horses and 20% of pigs tested positive; in Cameroon, 48% of bats and 3-4% of people (bat butchers) were found to be seropositive; henipavirus RNA has been detected in bushmeat in Republic of Congo, while five new sequences have been discovered in Zambian bats. There are no recorded human clinical cases in Africa, although the presence of high seroprevalence among bat butchers suggests that spillover might be occurring. This could suggest low zoonotic potential due to strain variations, lack of surveillance, existing immunity, or genetic resistance.

China is known as a possible risk zone. According to Yu *et al.* (2018), risk factors here include fruit bats in southern provinces and free-range pig farming practices.

Phylogenetic diversity and viral strains

Sixty-six complete genome sequences were evaluated in Sun *et al.*, (2024), resulting in two distinct clades; first one was Malaysia clade (NiV-M), including samples from Malaysia (1999-2003), Thailand and Cambodia and estimated to emerge in 1960 (95% CI 1910-1991); second one -Bangladesh clade (NiV-B), including samples from Bangladesh, India and Thailand (2004-2023), estimated to emerge in 1971 (95% CI 1929-1996)

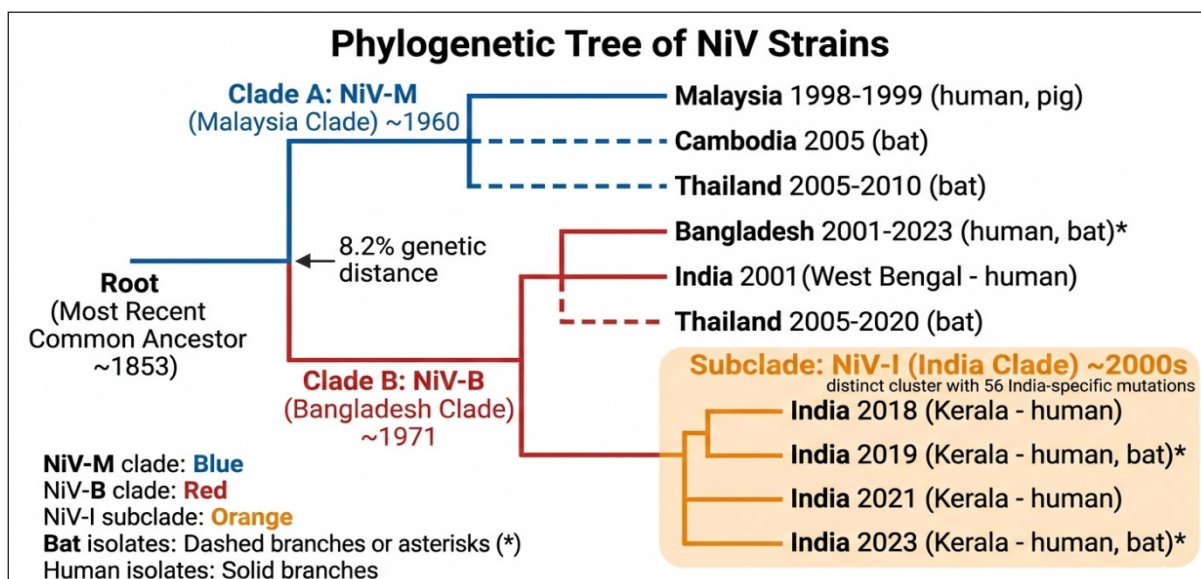


Fig. 3: Phylogenetic Strains of NiV

A common ancestor for all NiV isolates appeared in 1853 (95% CI 1687-1966), which means that NiV has been circulating among fruit bats much earlier than its discovery (Branda *et al.*, 2025).

The genome of NiV-B is made up of 18,252 nucleotides, six more than in the genome of NiV-M with 91.8% sequence identity (Pillai *et al.*, 2020). The NiV-B strain is associated with high mortality rates (70-100% against 40%), shorter incubation periods (1-14 vs. 4-18 days), sudden onset, respiratory symptoms (coughing: 62% vs. 27%; shortness of breath: 56% vs. 1%), and increased human-to-human transmission (33-75% vs. 8%).

Indian strains have 99% and 97% similarity with NiV-B. The Indian strain (NiV-I) detected in Kerala has undergone 746 mutations (560 synonymous and 187 non-synonymous mutations), including 56 mutations unique to India (Anish *et al.*, 2024; Singhai *et al.*, 2021).

Wacharapluesadee *et al.*, (2021) found that both strains infected Thai bats, but NiV-B dominated (35 out of 41 sequenced positives), exhibiting seasonality from April-June.

Temporal patterns and seasonality

Bangladesh outbreaks’ seasonal distribution occurs from December to May, during the period of date palm sap collection (Gurley *et al.*, 2017; Chakraborty *et al.*, 2016). According to Cortes *et al.* (2018), 40% of spillovers occur in January when temperature influences spillover variation at 36% each year (OR 2.11 per every 1 degree C drop). Distance to the hospitals for surveillance influenced 45% of spillover variance as spillover was 22% less probable for each additional 10 kilometers (OR 0.78). According to McKee *et al.* (2021), winter temperature influenced 53% of spillover variation each year from 2001 to 2018.

Spillover events occur in Kerala during May to June seasons that coincide with breeding seasons for bats (Singhai *et al.*, 2021; Anish *et al.*, 2024). From the six spillovers, four have occurred in El Nino years.

Outbreak patterns

Malaysia-Singapore pattern (1998-1999): Pigs as intermediate hosts with transmission from pigs to humans (McLean and Graham, 2019). It caused 283 cases with 106 deaths, which led to slaughter of one million pigs.

Bangladesh-India pattern (2001-onwards): Direct bat to human transmission through contaminated date palm juice with human-to-human transmission through close contacts (Gurley *et al.*, 2017). Transmission of disease through fermentation process of date palm juice (tari) has been described by Chakraborty *et al.* (2016) where all males, who were primary cases died (100% mortality) whereas all females, who were secondary cases survived. Half of the cases in Bangladesh are due to human-to-human transmission (Gurley *et al.*, 2017; Yeasmin *et al.*, 2025). In 2001 Siliguri outbreak, 75% of cases involved human to human transmission, out of 66 infected individuals, 25 were healthcare workers (Veggalam *et al.*, 2025). Parveen *et al.* (2016) documented corpse-to-human transmission through traditional funeral practices.

Philippines Pattern (2014): Novel use of horses as intermediate hosts. Ten out of 17 patients were in contact with the infected horses or consumed horse meat, which led to human-to-human transmission even involving healthcare personnel (Khadka, 2026). This shows that the virus can arise in novel environments with novel intermediate hosts while still retaining its human-to-human transmission ability.

Case-fatality-rates

According to Sun *et al.* (2024), adjusted CFR of 749 patients (1998-2021) was 71%, with country variations:

Country	CFR (95% CI)
India	78% (53-96)
Bangladesh	77% (68-84)
Philippines	53% (29-76)
Malaysia	40% (25-55)
Singapore	9% (0-35)

The CFR of NiV-B is estimated at around 77% (95% CI 69-84) as opposed to NiV-M at 37% (95% CI 24-52). Factors significantly related to the CFR include the viral clade ($p = 0.0021$), source country ($p = 0.016$), male sex proportion ($p = 0.036$), and travel distance to healthcare facilities ($p = 0.036$) (Sun *et al.*, 2024).

In a study done by Anish *et al.* (2024), it was noted that the CFR dropped from 91% in 2018 to 33% in 2023 in Kerala. In total, all 14 patients not on antiviral treatment died as compared to 12 out of 19 (63.2%) on antiviral treatment

dying ($p=0.013$). Nevertheless, sample size was very small (33 cases) and other factors like improved supportive care, early detection (mean 6 days in 2018 as compared to 3 days in 2023), healthcare staff training, and different strains might have been contributing. The finding of 100% survival (3/3) with Remdesivir versus 54.5% survival (6/11) with Ribavirin requires verification in controlled settings, though sporadic outbreaks make this challenging.

Reservoir hosts and transmission dynamics

Bat ecology and reservoir hosts

Multiple studies have established *Pteropus* fruit bats as the natural reservoir of NiV (Epstein et al., 2020). Eight bat species from four genera naturally host NiV (Table 4).

Table 4: Bat species with NiV detection

Species	Rate	Geographic Range
<i>Rousettus amplexicaudatus</i>	8% (95% CI 2-16)	Southeast Asia
<i>Pipistrellus pipistrellus</i>	3% (0-12)	South Asia, Europe
<i>Rousettus leschenaultia</i>	3% (0-10)	South Asia
<i>Pteropus lylei</i>	1% (1-2)	Thailand, Cambodia, Vietnam
<i>Pteropus hypomelanus</i>	1% (0-4)	Southeast Asia, Australia
<i>Pteropus medius</i>	<1% (0-1)	South Asia
<i>Pteropus vampyrus</i>	<1% (0-0)	Southeast Asia
<i>Hipposideros larvatus</i>	Detected	Southeast Asia

An 18-year study of Thailand (2002-2020) found the virus in bats without any spillover to humans and pigs, showing that the presence of viruses is not sufficient for spillover (Wacharapluesadee et al., 2021). A 2017 sample from bat urine in Thailand demonstrated 99.17% identity to a 2004 sample from a patient in Bangladesh and 97.82% identity to a 2018 sample from Kerala, which is evidence of regional virus connectivity.

Viral shedding depends on seasons and it peaks in May during the weaning of the pups (Wacharapluesadee et al., 2021). Shedding takes place April-June in Bangladesh; January-June and December in Malaysia.

Bat ecology is vital for the occurrence of spillover. McKee et al. (2021) reported that *Pteropus medius* lives in small groups in densely populated areas (the median of 996 people/km²) in 150 bats per roost (1-8,000 range). Date palms occur in 93% of roosts within 15 km of roosts. Roosts decrease due to hunting, harassment, and tree removal. Spillover villages have more unoccupied roosts.

Fragmentation of the forests is linked to greater bat roosts. Nipah belt villages have greater population density (1,311 versus 895 per km²; $p < 0.0001$) and greater forest fragmentation (0.50 versus 0.32 fragments/km²; $p < 0.0001$). Number of roosts is correlated with forest fragmentation ($r = 0.22$; $p=0.03$). Presence of silk cotton trees (*Bombax ceiba*) or Indian mast trees (*Polyalthia longifolia*) increases spillover risk by 10.8 times (95% CI 1.3-90.6; $p = 0.03$).

The prevalence rate in *P. medius* bats in Kerala increased to 20.9% from 9% in February to 28% in September 2023, according to Balasubramanian et al. (2024). It was detected in spleen, liver, and kidney, but not in oral and rectal swabs, showing that the virus has tissue tropism and eludes conventional detection.

Important ecological aspects: viral presence alone is not sufficient for spillover; changes in the landscape due to human activities have forced the bat colonies into the human population; tissue tropism complicates detection; and seasonally shedding peaks when human risk is highest (May during pup separation or winter during sap collection).

Pig amplification

Pigs played an important role as the host that amplified the disease during the Malaysian and Singaporean outbreaks, with 100% prevalence on pig farms (McLean and Graham, 2019). Sub-clinical infected pigs can excrete the virus, which makes diagnosis difficult (Weatherman et al., 2018). More than one million pigs were culled in order to contain the outbreak at a cost of RM280 million (US\$66.8 million), including feed industry losses worth RM67 million (US\$16 million) (Ochani et al., 2019).

Transmission through horses

Horses proved to be new intermediate hosts in the Philippines. Out of 17 infected persons, 10 individuals

were exposed to infected horses or ate horse meat, and 10 horses out of 12 died, with nine showing neurological symptoms (Khadka, 2026). It shows that NiV can transmit to new intermediate hosts while maintaining human-to-human transmission.

Human-to-human transmission

There is significant proof of transmission of the virus between humans in both Bangladesh and India. For example, Nikolay *et al.* (2019) report that about a third of infections are due to direct transmission (R0=0.33; 95% CI: 0.19-0.59). The probability of transmission is highest during close contact with infected persons, especially those with respiratory symptoms (Gurley *et al.*, 2017). Secondary infections affect family members caring for the sick (Chakraborty *et al.*, 2016). Health care professionals are also at moderate risk, especially when there are no infection control procedures (Anish *et al.*, 2024). Transmission through respiratory symptoms is more likely than in cases of encephalitis (Weatherman *et al.*, 2018). The five-generation transmission chain in Faridpur (2004) demonstrates sustained human-to-human spread is possible (Gurley *et al.*, 2017).

Risk factors include respiratory symptoms, illness severity, close contact, and lack of infection control measures. Nosocomial transmission is an important issue. In Siliguri, 25 out of 66 patients (38%) were nosocomial infections among healthcare workers (Anish *et al.*, 2024). Parveen *et al.* (2016) detected corpse-to-human transmission by traditional funeral rituals.

Spillover routes

Spillover routes differ geographically. In Bangladesh and India, consumption of fresh date palm sap with bat saliva/urine contamination is important. Gurley *et al.* (2017) reported that village case status was 6.39 times higher

for every 10% increase in household consumption of date palm sap, which grew to 26.97 times in comparison with distant controls. Behavior of people, not bats, is the most important factor.

Fermented date palm sap (tari) is another spillover route. Islam *et al.* (2016) observed three clusters (2011-2014), where primary cases usually drank tari; the virus withstands fermentation (5-8% alcohol) at 15-28 °C. Bat excreta were present in collectors’ vessels, and they were used several days without any cleaning.

In Malaysia, spillover involved ingestion of bat infected fruits by pigs through dual use of livestock farming (McKee *et al.*, 2021). In the Philippines, the horses ingested infected fruit and humans contracted infection through exposure or eating the meat of horses (Khadka, 2026). In Africa, spillover involves hunting, butchering and consumption of bats as bushmeat. Mbu’u *et al.* (2019) report 3-4% human seropositivity in Cameroon where infection is mostly among bat butchers.

Public health interventions and one health approaches

Surveillance and early detection

Surveillance has played an important role in early warning. Wacharapluesadee *et al.* (2021) describe 18 years of One Health surveillance in Thailand with no spillover even when virus circulated.

Outbreak investigations improve detection ability. McKee *et al.* (2022) note that investigation of bat roosts near reported cases improved viral detection rate from 0.48% to 4.9% (*p* < 0.001). From 39 NiV sequences in Bangladeshi bats, 72% were from urine near roosts, while 86% of cases were identified via investigations. In Joypurhat (2012), virus from bats and human cases had over 99.6% identity.

Table 5: Hierarchy of Human-to-Human Transmission Risk

Risk Level	Population	Key Drivers	Representative Studies
Highest	Family caregivers	Unprotected intimate contact, late-stage patient care	Chakraborty <i>et al.</i> , 2016; Parveen <i>et al.</i> , 2016
Intermediate	Healthcare workers	Inadequate PPE, aerosol-generating procedures	Anish <i>et al.</i> , 2024; Singhai <i>et al.</i> , 2021
Lower	Community contacts	Casual contact, shared spaces	Nikolay <i>et al.</i> , 2019

There are surveillance gaps. According to Cortes *et al.* (2018), 45% of variation in spillover detection was associated with distance to surveillance hospitals, where every 10 km decreased detection by 22% (OR 0.78), and there were estimates that half of the outbreaks go unnoticed. Media-based surveillance of ten newspapers and eight TV channels to monitor unusual deaths can help in detecting outbreaks in areas without surveillance hospitals (Gurley *et al.*, 2017).

Community interventions and behavior change

Skirt trials have been thoroughly analyzed. Studies confirm that physical barriers such as bamboo and jute skirts reliably block bat access to sap collection sites, improving sap quality (FAO, 2026). Despite their proven effectiveness, adoption remains limited. Sap collectors frequently report preferring non-conventional protective apparatuses such as jute bags, plastic bags, and polythene sheets due to time and resource constraints (Khan *et al.*, 2025). Only a few sap collectors are aware of Nipah virus; however, among those who are aware, the majority use protective measures (Khan *et al.*, 2025). Materials used for protection vary, with plastic bags being the most common choice, followed by polythene sheets and bamboo skirts (Khan *et al.*, 2025). Knowledge-behaviour gaps exist in the population. A nationwide survey found only 29.2% demonstrated good knowledge of NiV, yet over half (53.2%) reported consuming raw date palm sap. While 94.1% showed positive attitudes, only 33.0% practiced correct preventive measures (Hossain *et al.*, 2025). However, according to Khan *et al.*, (2025), while only 5 out of 31 tappers were knowledgeable about NiV, 80% of knowledgeable subjects engaged in protective behavior, indicating that awareness matters, but financial motivation is needed.

Social media use and sap trade create additional hazards. Khan *et al.* (2025) showed that raw sap trade is no longer confined to villages using Facebook, and involves districts lacking natural sap sources and Bangladeshi expatriates. The youth purchases sap for use in their social gatherings during the national holidays, thereby posing additional risks to individuals aged between 6-30 years. As many as 5 of 31 tappers were aware of NiV, but 80% of them practiced

precautionary measures. Expanding trade to younger and urban populations not reached by agricultural extension workers creates new risk communication opportunities.

Farm biosecurity and animal interventions

Biosecurity played an important role during the Malaysian NiV epidemic, which included culling more than one million pigs, movement control, decontamination, and disposal of animal carcasses by deep burial.

Thanapongtharm *et al.* (2019) determined the high-risk pig farms using spatial modelling techniques in Thailand. It is found that as much as 6.7% of the pig farms within 30 km distance from the bat colonies had high transmission suitability with key determinants such as distance from the bat colony, pig density, bat colony location, and orchard or forest location.

Preventive measures include livestock vaccines. Weatherman *et al.* (2018) report that the horse vaccine HeV-sG was licensed in Australia in 2012. Goswami *et al.* (2026) note that the HeV-sG-V Phase 1 trial (2025) generated dose-dependent neutralizing antibody response without any adverse effects.

One health in outbreak control

One Health approach is essential to successful outbreak control because it involves cooperation between the human health sector, the animal health sector, and the environmental sector. During an outbreak in Kerala (2018-2019), Singhai *et al.* (2021) utilized multidisciplinary teams including NCDC, AIIMS, NIV Pune (human health), NIHSAD Bhopal, State Animal Husbandry (animal health) and Forest Department, District Administration (environmental).

As a result of the application of One Health, the case-fatality-rate dropped from 91% in 2018 to 33% in 2023 owing to the use of early antivirals, contact tracing (2,084 contacts in 2018; 330 in 2019), point-of-care tests, intersectoral cooperation, and risk communication (Anish *et al.*, 2024). Gurley *et al.* (2025) outlined a roadmap for primary pandemic prevention through One Health spillover investigations.

Knowledge gaps identified

Surveillance gaps

Surveillance challenges include under-detection (50% of all outbreaks in Bangladesh are possibly under-detected due to distant location from hospitals and limited diagnostics), late detection (up to several weeks following symptom onset), unknown proportion of asymptomatic infections, poor detection of NiV RNA in bats (0.15-0.37%) in spite of the prevalence of seropositivity ranging from 31% to 82%, as well as tissue tropism problems (detected in spleen, liver, kidney but not in oral or rectal swabs) (Cortes *et al.*, 2018; Epstein *et al.*, 2020; Balasubramanian *et al.*, 2024).

Geographic challenges

Geographic gaps include possible hotspots in 13 countries with no reports of human cases (Thailand, Cambodia), China (fruit bats and pig rearing with no human cases), Africa (serological/molecular evidence but no isolations), and Indonesia/Papua New Guinea (poor surveillance).

Research limitations

Research limitations include uncertainty about the within-host dynamics of bats (acute versus chronic infection status; mechanism of recrudescence; impact of nutritional stress on virus shedding); strain variability (research focusing on NiV-M and NiV-B strains only, no information on phenotypic differences; relevance of NiV-I remains unclear); causes of spillover and spread in regions other than Bangladesh (cause of spillover in Kerala not known; importance of domesticated ruminants in transmission uncertain); pathogenesis in humans (lack of biological samples, poorly understood nature of immune response and reasons for clinical variability); impact of interventions (lack of any evidence that bamboo skirts prevent human infection, other protective equipment not tested; cost-effectiveness uncertain); vaccine and drug development (no vaccines or antiviral drugs despite decades of work); ecological causes (biodiversity and spillover link requires mechanistic studies, effect of habitat loss versus resource provisioning uncertain); and socio-economic causes (risky behavior driven by economic factors poorly understood; cost-effectiveness of prevention versus outbreak control unknown).

Recommendations and research agenda

Several recommendations arise based on the critical evaluation:

1. Leverage joint surveillance networks combining human encephalitis surveillance, animal surveillance (bats, pigs, horses), and environmental surveillance (date palm sap, water sources) to detect earlier spillover.
2. Leverage cross-sector rapid response teams based on the model of success seen in Kerala by pre-training these teams in high risk districts and not forming them when the time comes as Malaysia failed to do.
3. Leverage joint funding mechanisms which require joint applications for funding from human, animal, and environmental sectors to promote joint action instead of sectoral silos.
4. Implement community-based interventions motivated by economics. The interventions will generate economic incentives for safe behavior (such as “Nipah-safe” labelling of sap, prices incentives for skirt usage). Community social marketing will engage harvesters, traders, and youth. Social media campaigns will target new urban consumers.

Research agenda for Africa:

- ☐ Virus characterization (complete genome sequencing)
- ☐ Large-scale serosurveys in high-risk groups
- ☐ Enhanced clinical surveillance for encephalitis
- ☐ Longitudinal bat ecological studies
- ☐ Case-control studies on behavioural and environmental risk factors

Research agenda for South and Southeast Asia:

- ☐ Quantify underdetection through community-based seroprevalence studies
- ☐ Long-term bat cohort studies examining nutritional factors triggering shedding
- ☐ Assess intervention efficacy (cluster randomized trials, cost-effectiveness)

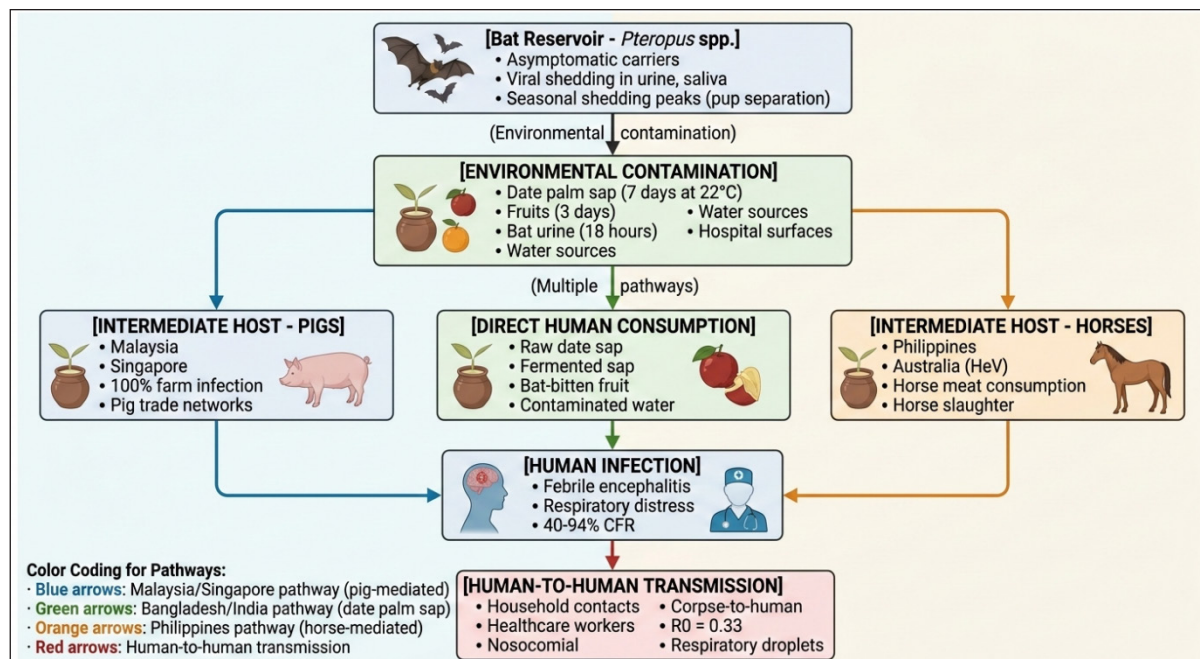


Fig. 4: Conceptual Diagram of Spillover Pathways (drawing on McLean and Graham, 2019; Khadka, 2026; Nikolay *et al.*, 2019)

- ☐ Investigate emerging hotspots (Kerala case-control studies, domestic ruminant role)
- ☐ Bridge knowledge and behaviour through ethnographic studies
- ☐ Strengthen health systems for inter-epidemic capacity
- ☐ Investigate virus strain variations (genomic surveys, phenotype comparisons)

Conceptual summary

The virus transfers from bats to humans through environmental contamination (date palm sap, fruit), intermediate hosts (pigs, horses), and human-to-human transmission. This multi-pathway transmission ecology confirms NiV as a lasting zoonotic threat with complex transmission dynamics and real outbreak potential. Future studies should integrate One Health surveillance, investigate long-term NiV maintenance in reservoir hosts, and rigorously evaluate prevention strategies.

CONCLUSION

This scoping review combines the latest information on the

epidemiology of NiV infections and zoonotic infections. The information illustrates that NiV is an ongoing, emerging infectious disease with complex modes of transmission. The evidence suggests that NiV infections have occurred mainly in South Asia and Southeast Asia. In these regions, the ecological determinants are stable, ensuring that the spillover of NiV from animals to humans continues. The ability of the virus to spread from human-to-human in multiple reported cases of NiV infections increases the likelihood of NiV outbreaks. The scoping review also identifies the progress that has been made in the identification of the natural reservoirs of NiV. However, gaps in the knowledge of NiV infections include long-term surveillance, geographic distribution, and the effectiveness of prevention strategies. Most of the studies on NiV infections have been conducted in response to reported cases of NiV infections. This implies that the knowledge of NiV infections is more reactive than preventive. The gaps in the knowledge of NiV infections need to be addressed to reduce the spillover risk of NiV infections in the future.

The high case-fatality rate of NiV infections, the zoonotic transmission of NiV infections, and the ability of NiV infections to spread from human-to-human make it an

important One Health issue. Reducing the spillover risk of NiV infections is an essential public health response that can reduce the public health impact of NiV infections.

GENERATIVE AI DECLARATION

The author(s) confirm that there was no use of artificial intelligence (AI)-assisted technology for assisting in the writing or editing of the manuscript, and no images were manipulated using AI. The authors developed and verified all scientific content, data analysis, interpretation of results, and conclusions. The authors take full responsibility for the accuracy, integrity, and originality of the work presented, and no AI tool was listed as an author.

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