



RESEARCH ARTICLE

Rodent-borne zoonotic diseases in Southeast Asia: A narrative review

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ARTICLE HISTORY

Received: 14 November 2024

Revised: 18 February 2025

Accepted: 19 February 2025

Published: 30 June 2025

ABSTRACT

Rodent-borne zoonotic diseases, including hantavirus pulmonary syndrome, leptospirosis, and rickettsiosis, significantly impact public health. However, there is a limited understanding of these diseases in Southeast Asia, a region emerging as a hotspot for zoonotic diseases. To address this, the authors reviewed the recent developments in prevalent rodent-borne diseases in Southeast Asia from 2000 to 2024. A comprehensive literature search was conducted in databases such as PubMed, Scopus, Web of Science, Google, and Google Scholar, using keywords like “rodent-borne diseases,” “prevalence,” “epidemiology,” “humans,” and “Southeast Asia”. Leptospirosis is widespread in several Southeast Asian countries. Malaysia and Thailand have established effective national surveillance systems, tracking annual cases and fatalities. For viral diseases, such as haemorrhagic fever with renal syndrome, most countries lack a structured reporting system. Vector-borne rodent diseases deal with similar underreporting, with diseases like bartonellosis and borreliosis noted only anecdotally, even in relatively-resourced countries like Thailand and Malaysia. This underreporting is concerning, as the causative pathogens are often detected in rodent reservoirs and their arthropod vectors around these regions during biosurveillance studies. Invasive rodents have long infiltrated into human environments and thrive as successful commensal species, facilitating the transmission of zoonotic pathogens to humans. Therefore, robust surveillance systems, often essential in disease control are urgently needed across the Southeast Asian region. Further scientific research and biosurveillance studies are crucial in understanding the impact of these diseases on human health, rodent populations, and the environment.

Keywords: Chigger; flea; hygiene; tick; tropical.

INTRODUCTION

Southeast Asia (SEA) is emerging as a hotspot for zoonotic diseases due to several factors, including biodiversity richness, population growth, increased migration (travel), land encroachment, agricultural expansion, bushmeat trade, and climate change (Villarroel *et al.*, 2023). Among mammals; rodents, bats, primates, and carnivores are the primary wildlife reservoirs, harbouring the majority of zoonotic viruses (Engel & Ziegler, 2020). Rodents and bats represent the largest wild mammal reservoirs for zoonotic emerging infectious diseases across SEA, East Asia, and Australasia. These mammals are 15 times more likely to inhabit human-modified environments (McFarlane *et al.*, 2012). The rapid reproductive cycle of some rodent species further amplifies their role as competent reservoirs for zoonotic pathogens (Han *et al.*, 2015). Rodent-borne diseases are classified based on their transmission routes. Direct transmission occurs via bites, contaminated food or water, and inhalation of aerosolized rodent excrement (Meerburg *et al.*, 2009). Indirect transmission involves rodents hosting infected arthropod

vectors such as ticks, fleas, lice, and mites, which then transmit the pathogens to humans (Ho *et al.*, 2021).

Globally, rodent-associated diseases of primary concern are hantavirus pulmonary syndrome (HPS), tick-borne encephalitis, Lassa fever, leptospirosis, scrub typhus, tularaemia, lymphocytic choriomeningitis, rickettsial diseases, Lyme disease (LD), and rat bite fever (Meerburg *et al.*, 2009; Low *et al.*, 2020b). Some of these diseases, such as leptospirosis and scrub typhus, are endemic to the Southeast Asian region. In this region, rodents inhabiting human-modified landscapes, particularly agricultural areas, exhibit higher species richness of pathogens, including *Leptospira* spp., *Bartonella* spp., *Orientia* spp., and hantaviruses (Bordes *et al.*, 2013). Consequently, infected rodents may carry higher pathogen loads, and the abundance of vector populations in these environments further promotes the disease transmission. Additionally, cultivated and frequently flooded lowland areas, such as rice fields, provide favourable conditions for pathogen transmission. To further complicate matters, several rodent-borne pathogens such as *Leptospira* spp., *Rickettsia* spp., and *Orientia*

tsutsugamushi are significant drivers of acute febrile illness (AFI) in SEA (Wangrangsimakul et al., 2018; Wangdi et al., 2019; Althaus et al., 2020). For instance, in endemic areas of Malaysia, rickettsial infections account for 14% of AFI cases, but they often remain underdiagnosed or neglected (Yuhana et al., 2022). AFI, also known as acute undifferentiated febrile illness (AUFI) is typically characterised by a fever of $\geq 38^{\circ}\text{C}$ occurring for less than two weeks (Tun et al., 2016; Wangdi et al., 2019). The incidence of AFI in regions where endemic tropical diseases are prevalent, complicates the differential diagnosis and accurate determination of aetiological agents (Bressan et al., 2023).

Despite the extensive distribution of rodents globally, particularly in SEA, there remains a significant lack of comprehensive studies on the epidemiology of endemic rodent-borne diseases. This has led to discrepancies in available data on the prevalence of these diseases in humans across the region. For example, many current reports on outbreaks are outdated and incomplete, and the full impact of these events on communities is poorly understood, creating a substantial knowledge gap. In light of this situation, this review aims to provide an overview of the epidemiology of key rodent-associated diseases in SEA, including leptospirosis, haemorrhagic fever with renal syndrome (HFRS), bartonellosis, borreliosis, scrub typhus, murine typhus, and spotted fever rickettsiosis (SFR). The review will focus on human cases and rodent reservoirs, drawing epidemiological data from available studies, and highlighting the existing knowledge gaps in the current literature.

METHODOLOGY

Literature Search

A comprehensive literature search was conducted using databases available in the public domain, such as PubMed, Scopus, and Web of Science, to compile this review article. In this review, the rodent-borne diseases were narrowed down to leptospirosis, HFRS, bartonellosis, borreliosis, scrub typhus, murine typhus, and SFR based on the frequencies and impact of these diseases in the Southeast Asian region. Articles on rodent-borne diseases in SEA from 2000 to 2024 were searched using keywords, such as “leptospirosis”, “hantavirus”, “bartonellosis”, “borreliosis”, “rickettsiosis”, “scrub typhus”, “murine typhus”, “spotted fever rickettsiosis”, “*Leptospira* spp.”, “*Bartonella* spp.”, “*Borrelia* spp.”, “*Orientia* spp.”, “*Rickettsia* spp.”, “rodents”, “humans”, “epidemiology”, “prevalence”, “Malaysia”, “Thailand”, “Indonesia”, “Philippines”, “Vietnam”, and “Southeast Asia”. The selected articles were organized and reviewed based on the epidemiology of these diseases in humans and rodent reservoirs. Additionally, search engines including Google and Google Scholar were utilized to identify relevant and significant articles. Only articles in English were included in the present study.

Rodent-borne zoonotic diseases

Leptospirosis

Approximately 1.03 million leptospirosis cases are reported annually, resulting in at least 58 900 deaths worldwide. A higher prevalence of disease and fatalities is observed in tropical regions of South Asia, SEA, Latin America, and East Sub-Saharan Africa (Abela-Ridder et al., 2010; Costa et al., 2015). This neglected zoonotic disease is caused by a gram-negative spirochete bacterium from the order Spirochaetales, family Leptospiraceae, and genus *Leptospira* (Mohammed et al., 2011). In SEA, this endemic disease is prevalent across various countries. The highest incidence rates are estimated to occur in Thailand and the Lao People's Democratic Republic (PDR), surpassing the overall expected incidence of 2.34 cases per 100 000 population in SEA (Douchet et al., 2022). According to Sakundarno et al. (2014), the elevated incidence of leptospirosis in tropical and subtropical areas is often related to temperate or humid climates and significant rainfall patterns in these regions.

Frequent contact with rodents, occupational exposure, recreational activities, lack of awareness, and natural disasters such as flash floods are common risks associated with the transmission of leptospirosis (Brown et al., 2011; Shafie et al., 2021; Senaka, 2022; Philip & Ahmed, 2023). Humans are typically infected via open wounds, ingestion of contaminated food or water, and contact with soil tainted by infected rodent urine (Haake & Levett, 2015). The clinical manifestations of leptospirosis range from mild to severe and life-threatening. Typical symptoms include fever, myalgia, headache, abdominal pain, nausea, vomiting, and diarrhoea (Chacko et al., 2021). A severe form of the disease is characterised by multiple organ failure, pulmonary haemorrhage, meningitis, or Weil's syndrome, which presents with jaundice and acute renal failure (Haake & Levett, 2015; Pothuri et al., 2016; Cardoso et al., 2022). The diagnosis of leptospirosis is often challenging due to co-infections or the presence of non-specific clinical signs, such as fever, myalgia, and headache, overlapping with other tropical diseases during the acute phase of illness (Kumar et al., 2012; Wijesinghe et al., 2015; Loong et al., 2022). Several studies have documented the co-infection of leptospirosis with febrile illnesses like dengue, malaria, and scrub typhus in tropical countries (Lindo et al., 2013; Philip et al., 2020). An early diagnosis is critical, as prompt antibiotic therapy involving drugs, such as doxycycline, azithromycin, and amoxicillin is effective in disease management (Kumar et al., 2012; Karpagam & Ganesh, 2020).

Non-native domestic animals, such as rats, dogs, pigs, and cattle serve as major reservoirs for *Leptospira* spp. in both urban and rural areas. Wildlife, including squirrels, shrews, and herpetofauna, are also implicated in the transmission and environmental maintenance of this pathogen (Bradley & Lockaby, 2023). Commensal rats, such as *Rattus rattus* and *Rattus norvegicus* are the principal carriers of this bacterium worldwide, especially in urban areas (Boey et al., 2019; Koizumi et al., 2019). However, a diverse species of infected rats has been reported across the urban, semi-urban, rural, and recreational areas in SEA (Blasdell et al., 2019a; Yusof et al., 2019; Shafie et al., 2022). In addition to *R. norvegicus* (Azhari et al., 2018; Kudo et al., 2018; Blasdell et al., 2019a; Koizumi et al., 2019) and *R. rattus* (Benacer et al., 2016; Noh et al., 2024), *Leptospira* spp. has been detected in *Rattus exulans* (Krairojananan et al., 2020), *Rattus tanezumi* (Widiastuti et al., 2016), *Bandicota bengalensis* (Sunaryo & Priyanto, 2022), *Mus cookii*, *Bandicota indica* (Cosson et al., 2014), *Berylmys bowersi*, *Bandicota savilei*, *Niviventer fulvescens*, and *Rattus nitidus* (Anh et al., 2021) in SEA (Table 1). In Malaysia, multiple studies have detected infected rodents around residential areas and commercial sites, like wet markets (Pui et al., 2017; Mohd-Taib et al., 2020; Wan et al., 2022). These anthropogenic sites are usually rodent breeding grounds that further amplify the risk of disease transmission to humans (Ikbal et al., 2019). Interestingly, rodents from industrial areas in Singapore were also heavily infested with *Leptospira* spp. (53.2%) (Griffiths et al., 2022). Recently, Anh et al. (2021) reported multiple infections of leptospiral agents with other bacteria, such as *Bartonella* spp. and *Rickettsia* spp. in several rodents including, *B. bowersi*, *B. savilei*, *N. fulvescens*, *R. rattus*, and *R. tanezumi* from Vietnam. The pervasive distribution of infected rodents in various landscapes of SEA has a larger implication for potential zoonotic transmission of leptospirosis. Thus, the continuous monitoring of reservoir animals is necessary in preventive management of the disease.

Past studies have shown that rats shed the highest concentration of leptospiral agents (5.7×10^6 cells/mL) in their urine compared to other reservoirs, such as deer, cattle, mice, and dogs (Barragan et al., 2017a). An infected animal may remain asymptomatic while continuously shedding the infectious agent in its urine for periods ranging from two weeks to several months, with rare cases of life-long persistence (Karpagam & Ganesh, 2020). Several studies found that, *R. norvegicus* had a higher leptospiral infection rate (Azhari et al., 2018; Mohd-Taib et al., 2020; Griffiths et al., 2022), possibly

due to an increased susceptibility towards the pathogen (Boey et al., 2019), and a wider spatial distribution (Wibowo et al., 2022). In contrast, other studies have found *R. rattus* to be more susceptible to leptospiral infections (Benacer et al., 2013, 2016). Thus far, host specificity has not been established for leptospiral agents carried by rodents (Ikbal et al., 2019). However, Benacer et al. (2013) implied a potential association between infection and the habitat of the carrier animals rather than the species of the carriers. Various factors, including host weight, urine volume, disease prevalence, and local host densities, influence the distribution of *Leptospira* spp. in soil and water (Barragan et al., 2017b). Despite these factors, rodents still pose a high infection and transmission risk to humans due to their ubiquitous presence in the environment (Barragan et al., 2017a, 2017b).

In the Philippines, leptospirosis has become a significant public health concern in recent years, with reported cases increasing from 182 in 2020 to 2,794 in 2022. Alarmingly, there was a 188% rise in cases within three months in 2023 compared to the same period in 2022 (Nazir et al., 2023). Over the years, numerous leptospirosis outbreaks in the Philippines have been linked to typhoons, heavy rainfall, and flooding (Amilasan et al., 2012; Nazir et al., 2023) (Figure 1). The incidence and case fatality rate (CFR) in Malaysia ranged from 8.63 to 17.2, and 0.6% to 2.4% per 100 000 population, respectively, based on data collected from 2011 to 2021. States such as Selangor, Kelantan, and Sarawak recorded some of the highest clinical cases in recent years (Philip & Ahmed, 2023). According to past research, multiple factors attributed to the elevated cases of leptospirosis in developed areas such as Selangor. This includes, improper waste management, increased rodent densities, rising temperatures, flooding events, and lack of awareness among the inhabitants (Lau et al., 2010; Abdullah et al., 2019). Furthermore, several outbreaks have occurred following flash floods in Kelantan and during a search operation at the Lubuk Yu waterfall in Pahang (Hin et al., 2012; Sapian et al., 2012; Mohd Radi et al., 2018) (Figure 1). The flash floods in Kelantan may justify the peak in clinical cases at the end of 2014 in Malaysia. Besides that, leptospiral antibodies have been detected in individuals across various socioeconomic backgrounds, including poor urban communities (12.6%), refugee students (24.7%), wet market workers (33.6%), rural residents (37.4%), urban sanitation workers (43.8%), and the Orang

Asli populations (60.7%), suggesting that the disease is widespread in Malaysia (Suut et al., 2016; Loong et al., 2018; Rahman et al., 2018; Sahimin et al., 2019; Jeffree et al., 2020; Mohd Hanapi et al., 2021).

In some endemic regions of Malaysia, such as Perak, high incidences of leptospirosis (12.5 per 100 000 population) and a CFR of 14.3% have been reported among hospitalized patients. However, nearly 79.5% of these cases are only diagnosed after the patient is discharged or has died, hampering effective disease management (Fann et al., 2020). Recently, Philip et al. (2020) detected a 56% infection prevalence among hospitalized individuals in Selangor and Perak, with pathogenic strains such as *Leptospira interrogans* and *Leptospira kirschneri* predominantly infecting the patients. *L. interrogans* have also been reported among patients with fever of unknown origin (FUO) that tested negative for dengue in Selangor (Loong et al., 2022). In East Malaysia, several studies employed the gold standard microscopic agglutination (MAT) test to further characterise *Leptospira* serovars by detecting specific antibody titres in serum samples. In Sabah, three serovars; Patoc, Sarawak, and Terengganu predominantly infected the urban sanitation workers, indicating potential occupational risks (Jeffree et al., 2020). Meanwhile, in Sarawak, antibodies against 20 local serovars were detected in 37.4% of seropositive samples, with pathogenic serovars like Djasiman and Shermani, previously implicated in alveolar haemorrhage and tubulonephritis, being prevalent (Suut et al., 2016). In contrast, fewer seroprevalence studies have been conducted in countries like the Philippines, despite the rising leptospirosis incidence reported recently. One prospective study confirmed leptospirosis in 7.4% of patients presenting with acute fever, using culture, serology, and molecular methods (Saiton et al., 2022), with much of the other information remaining obscure.

Thailand reports several thousand leptospirosis cases annually (Tanganakul et al., 2005). In 2008, the country ranked among the top ten globally for annual leptospirosis incidence (48.9 cases per 1 000 000 population) (Pappas et al., 2008). However, these figures came from passive surveillance based on suspected cases, without laboratory confirmation or details on serovar patterns (Hinjoy, 2014). More recently in 2023, an outbreak involving 2,700 cases was reported in the northern and southern regions of Thailand following heavy rainfall (The Nation, 2023) (Figure 1). Luenam & Puttannapong (2019) noted an increasing CFR for leptospirosis

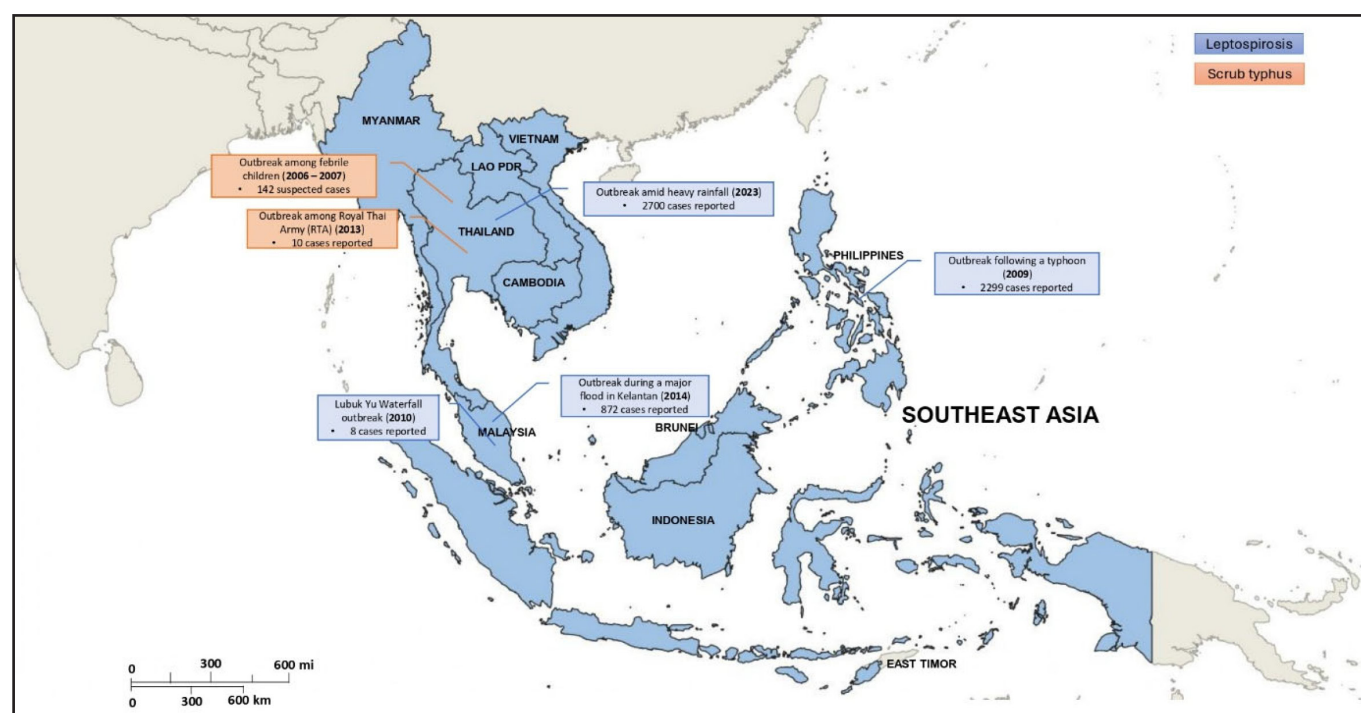


Figure 1. Map showing major leptospirosis and scrub typhus outbreaks in Southeast Asia.

nationwide from 2013 to 2015, despite a decline in the incidence. Severe complications, including multiple organ failure, pulmonary haemorrhage, and reliance on support (mechanical ventilator), were associated with higher mortality rates among patients with AUFI (Thipmontree *et al.*, 2014). A retrospective study found that 50% of confirmed leptospirosis cases in Songkhla required admission to the Medical Intensive Care Unit (MICU), with clinical presentations such as septic shock, acute respiratory failure, and neurologic dysfunction common among these patients (Ajijmarungsi *et al.*, 2020). Several studies reported leptospirosis seropositivity among healthy blood donors (1.7%), young Thai men (28%), and patients presenting typical leptospirosis clinical symptoms (23.8%) (Chadsuthi *et al.*, 2017; Gonwong *et al.*, 2017; Limothai *et al.*, 2023). Nevertheless, comprehensive nationwide seroprevalence data for the Thai general population remains lacking.

In Singapore, information available on leptospirosis is limited, with one case study from 1981 reporting the infection in a pregnant woman (Shaked *et al.*, 1993). In 2016, leptospirosis was gazetted as a notifiable disease in the country. Since then, the number of reported cases has been fluctuating (Ho *et al.*, 2019). In 2023, Singapore recorded the highest incidence in eight years, with 62 cases (Abdurrahman *et al.*, 2024). In Vietnam, children are also at risk of contracting leptospirosis with 12.8% testing positive for anti-*Leptospira* IgG antibodies, indicating a past exposure, primarily linked to activities in water bodies like swimming or wading (Thai *et al.*, 2006). In 2019, Tran *et al.* (2021) detected leptospiral antibodies in 9.5% (57 individuals) of healthy Vietnamese people indicating a past exposure, with farmers identified as being at high risk. However, between 2014 and 2017, fewer than 20 cases were reported nationwide in Vietnam (official data), and in 2018, the overall morbidity and mortality were reported as zero (Tokarevich & Blinova, 2022). These discrepancies indicate that the nationwide leptospirosis registry in Vietnam does not accurately reflect the true incidence or disease burden. Similar underreporting was observed in Lao PDR and Cambodia. In Cambodia, males aged between 15 and 19 showed the highest seropositivity for IgM leptospiral antibodies at 40.5% in both acute and convalescent samples (Hem *et al.*, 2016). Furthermore, in Lao PDR, 23.9% of healthy individuals in rural areas of the Khammouane Province were seropositive and had previously been exposed to the spirochete (Kawaguchi *et al.*, 2008).

In Indonesia, leptospirosis predominantly affects men aged between 31 and 40, and those over 45 years of age (Ristiyo *et al.*, 2018; Gasem *et al.*, 2020). The higher incidence in men is usually linked to occupational and recreational exposure, differences in physiological responses, disease severity in males, and underdiagnosis in women (Skufca & Arima, 2012). Additionally, between 2007 and 2017, Brunei reported only five clinical cases of leptospirosis, with much of the other information unavailable (Abdurrahman *et al.*, 2024). The current data on leptospirosis in SEA indicates potential underreporting, particularly in Brunei, Vietnam, Lao PDR, and Cambodia. These countries were previously confirmed as endemic regions based on seroprevalence data, despite the absence of official reporting (Pappas *et al.*, 2008). In contrast, Malaysia and Thailand have a more systematic national reporting system, likely due to leptospirosis being a notifiable disease in Malaysia. A more comprehensive and coordinated approach across the Southeast Asian countries is necessary to accurately track incidence, assess disease burden, and recognize risks, ensuring better disease management and mitigation of the impact on communities.

Haemorrhagic fever with renal syndrome (HFRS)

HFRS is a rodent-borne viral haemorrhagic fever widespread across Asia and Europe. The causative agent, orthohantaviruses (order: *Bunyavirales*, family: *Hantaviridae*, genus: *Orthohantavirus*), also causes HPS, a disease endemic to regions in America (Tariq & Kim, 2022). These viruses are divided into Old World and New World

strains based on the geographical distribution of their reservoir hosts, genetic relatedness, and disease manifestations in humans (Jonsson *et al.*, 2010; Lederer *et al.*, 2013). Old World hantaviruses, typically associated with rodents from the *Murinae* and *Arvicolinae* subfamilies, cause HFRS (Sehgal *et al.*, 2023). Globally, over 40 hantaviruses have been discovered, with at least 20 pathogenic genotypes (Watson *et al.*, 2014; Guterres & de Lemos, 2018). The close association between hantaviruses and their natural reservoirs has geographically confined the distribution of HFRS to European-Asian regions, and HPS to America (Krüger *et al.*, 2011). However, recent diagnostic advances have resulted in the detection of hantavirus antibodies in African patients (Witkowski *et al.*, 2014).

Rodents are the primary reservoirs for hantaviruses, although bats, moles, shrews, fish, and reptiles can also carry the virus (Avšič-Županc *et al.*, 2019; Laenen *et al.*, 2019). Hantaviruses are well-adapted to their reservoirs and coexist without requiring an intricate host-vector transmission cycle. Studies suggest that the coevolution between hantaviruses and their rodent reservoirs has resulted in infection persistence among hosts without deleterious effects (Meyer & Schmaljohn, 2000). Infected rodents usually remain asymptomatic while maintaining significant viral loads for transmission (Watson *et al.*, 2014). Rodent-to-rodent transmission is mainly facilitated by horizontal routes, such as biting or aggression, although aerosol transmission may also occur (Padula *et al.*, 2004). Humans, as dead-end hosts, contract the disease by inhaling aerosolized urine, faeces, or saliva from infected rodents (De Oliveira *et al.*, 2014).

Worldwide, an estimated 150 000 to 200 000 HFRS cases are reported annually, with China accounting for 70% to 90% of these cases (Bi *et al.*, 2008; Manigold & Vial, 2014; Zou & Sun, 2020). Clinically significant agents causing HFRS include Hantaan (HTNV), Dobrava (DOBV), Puumala (PUUV), Saaremaa (SAAV), and Seoul (SEOV) viruses (Schmaljohn & Hjelle, 1997). In Europe and Asia, the seroprevalence of infection ranges between 0.48% and 20%, and fatality rates vary from 0.4% to 10% (Vapalahti *et al.*, 2003; Bi *et al.*, 2008; Hjelle & Torres-Pérez, 2010). HFRS progresses through five clinical phases that are febrile, hypotensive, oliguric, diuretic, and convalescent (Jonsson *et al.*, 2010). Early diagnosis may be challenging due to the similarities of symptoms with other infectious diseases (Hamidon & Saadiah, 2003; Knust *et al.*, 2012; Jiang *et al.*, 2016). For example, two confirmed cases of SEOV infection in asymptomatic febrile patients from Indonesia clinically manifested as thrombocytopenia and elevated liver enzymes, that are usually associated with dengue fever. This could simply lead to a misdiagnosis of infection (Lie *et al.*, 2018).

In several Southeast Asian countries, such as Brunei and Cambodia, clinical cases of HFRS are rare or absent (Blasdell *et al.*, 2009). Hitherto, only three cases have been reported in Singapore (Chan *et al.*, 1996). In an earlier study, hantavirus exposure was observed among patients suspected of dengue haemorrhagic fever, hepatitis, leptospirosis, and acute nephritis when tested with immunofluorescence assay (IFA). However, the IFA titres were low, and the diagnostic specificity remained equivocal (Wong *et al.*, 1989). Serological evidence of hantavirus cases among chronic renal failure patients in Kelantan dates back to 2001 when 2.52% of the patients were seropositive for HNTV and Sin Nombre virus (SNV) (Lam *et al.*, 2001). Another seroprevalence study in Johor confirmed a past exposure in 23.3% of soldiers using IgM immunochromatographic rapid test (Arichandra *et al.*, 2006). The lower incidence or underestimation of hantavirus cases in these countries is often attributed to the lack of routine serological testing (Lam *et al.*, 2001).

In the Philippines, 6.1% of rural, urban, and urban-poor residents were seropositive for hantavirus antibodies (Quelapio *et al.*, 2000). Despite the prevalence being comparable to infection rates reported in other developing countries, no further follow-up studies have been conducted in the Philippines. Surveillance records

of hantavirus cases in Indonesia are sporadic and geographically limited. A recent retrospective serological study reported that 11.6% of patients with AFI in major cities such as Semarang, Denpasar, and Makassar, tested positive for past exposure, with the majority of cases found in adult males (Lukman *et al.*, 2019). The higher prevalence in men is usually associated with increased outdoor activities, occupational exposure, and lifelong contact with reservoir animals (Bi *et al.*, 2008; Kruger *et al.*, 2011). Another case study detected a SEOV-related strain in two patients from Surabaya and Jakarta (Lie *et al.*, 2018). Although neither patient had direct contact with rodents, they lived in densely populated areas close to open rubbish-filled gutters with abundant rodents, suggesting an accidental exposure.

In Thailand, hantavirus antibodies are widespread among rodents in various regions; however, only one clinical study has been published thus far. A serological study identified hantavirus antibodies in the serum of 15 FUO patients, with five individuals showing past exposure (IgG seropositive), eight indicating potential early infection (IgM seropositive), and one seropositive for both IgM and IgG antibodies (Suputthamongkol *et al.*, 2005). A study in Vietnam found that febrile patients had twice the rate of hantavirus infection compared to healthy individuals (Truong *et al.*, 2009). Another study in the Dong Thap farming community of Vietnam detected SEOV and DOBV seropositivity among 3.7% of the farmers (Cuong *et al.*, 2015). A surveillance study in Cambodia, conducted among hospitalized patients with acute fever between 2006 and 2009 confirmed past hantavirus exposure in 8.1% of the patients (Kasper *et al.*, 2012). Most human cases reported in SEA are geographically limited to certain regions, and many studies focused on individuals with acute febrile illnesses. Serological methods dominate these studies, while molecular methods for hantavirus detection in humans receive less attention. Hence, the true burden of hantavirus infection among the general population in SEA remains largely unknown.

Although reports on humans are limited, multiple studies have investigated the presence of hantaviruses among animal reservoirs across SEA. Various rodent species in this region have been exposed to the virus, which has been detected via serological or molecular assays (Ibrahim *et al.*, 1996; Reynes *et al.*, 2003; Hugot *et al.*, 2006; Plyusnina *et al.*, 2009; Blasdel *et al.*, 2011a) (Table 1). Hantavirus has been detected in *R. norvegicus* from Indonesia (Ibrahim *et al.*, 1996; Susanti *et al.*, 2022), Malaysia (Lam *et al.*, 2001), Singapore (Johansson *et al.*, 2010; Griffiths *et al.*, 2022), Vietnam (Luan *et al.*, 2012), and Cambodia (Blasdel *et al.*, 2011a). It has also been reported in *R. tanezumi* from Lao PDR (Blasdel *et al.*, 2011a), *R. rattus*, and *R. exulans* from Indonesia (Ibrahim *et al.*, 1996), *R. rattus* from Singapore (Griffiths *et al.*, 2022), and *Rattus argentiventer* from Vietnam (Cuong *et al.*, 2015). Thailand virus (THAIV) is commonly associated with *B. indica* (Hugot *et al.*, 2006), and recent studies suggest that *B. indica* may serve as a host for the Murinae-related phylogroup III hantavirus in Thailand (Wu *et al.*, 2021). Additionally, Serang virus (SERV) and Jurong virus were reported in *R. tanezumi* from Indonesia (Ibrahim *et al.*, 1996) and Singapore (Johansson *et al.*, 2010), respectively. Phylogenetic analyses further indicate that strains such as THAIV, SERV and Jurong virus, along with the Cambodian strains from *R. rattus*, form a distinct phylogroup, despite being carried by different rodent hosts (Johansson *et al.*, 2010).

Thus, the presence of genetically similar hantaviruses in diverse host species, along with the detection of hantaviruses in non-reservoirs, suggests possible host-switching or spillover events. Other rodent species, including, *B. savilei*, *Maxomys surifer*, *Mus caroli*, *M. cookii*, *Niviventer* spp., and *R. nitidus* from Thailand, Lao PDR, Vietnam, and Cambodia, have tested positive for hantavirus antibodies. However, the specific virus strains carried by these rodents remain unknown (Blasdel *et al.*, 2011a; Kikuchi *et al.*, 2021). Kikuchi *et al.* (2021) reported that some of these strains were closely

related to the HTNV Da Bie Shan (DBS) from Yunnan province, China. Notably, hantavirus-infected rodents are commonly found in human habitations, including urban cities, ports (industrial areas), and rural, forested or agricultural areas within this region (Johansson *et al.*, 2010; Blasdel *et al.*, 2011b; Cuong *et al.*, 2015; Griffiths *et al.*, 2022). Despite the potential risk of pathogen transmission to humans, recent scientific and clinical reports on hantavirus that are crucial for advocating specific prevention and cure for the community in SEA are limited. This highlights the need for more surveillance studies on hantavirus infection, diversity, distribution, and reservoirs in this region.

Rodent-borne zoonotic diseases transmitted by vectors

Bartonellosis

Bartonellosis is an umbrella term describing the zoonotic disease caused by *Bartonella* spp. Infectious agents from the *Bartonella* genus cause clinical diseases such as cat-scratch disease (CSD), trench fever, and Carrion's disease (Lins *et al.*, 2019). A wide range of arthropod vectors, including fleas (Ashtiani *et al.*, 2024), lice (Boodman *et al.*, 2024), sandflies (Minnick *et al.*, 2023), mites, and ticks (Tsai *et al.*, 2011), mediate the transmission of this pathogen to natural and accidental hosts. An asymptomatic intraerythrocytic persistence is the hallmark of *Bartonella* infections among natural reservoirs, while bacteremia is rare in healthy incidental hosts (Dehio, 2004; Hong *et al.*, 2016). However, recent reports indicate that bacteremia is common within asymptomatic patients, challenging the earlier notion (Vayssier-Taussat *et al.*, 2016). In immunocompromised individuals, the disease manifestations are often severe, characterized by bacillary angiomatosis, hepatic peliosis, endocarditis, and osteomyelitis (Mosepele *et al.*, 2012). The CFR of Carrion's disease in humans during the Oroya phase varies from 40% to 80% (Minnick *et al.*, 2014; Gomes *et al.*, 2016).

In addition to *Bartonella bacilliformis*, *Bartonella henselae*, and *Bartonella quintana*, at least 15 *Bartonella* spp. are pathogenic to humans and have been implicated with severe diseases (Breitschwerdt, 2017). However, currently, humans are the primary reservoirs of only two species, *B. bacilliformis* and *B. quintana*. In other cases, humans serve as accidental or incidental hosts, succumbing to opportunistic infections. Besides humans, a diverse group of mammals, including rodents, cats, dogs, macaques, rabbits, sheep, and horses, serve as the primary reservoirs of specific *Bartonella* spp. (Cheslock & Embers, 2019). Recently, two novel species, *Bartonella kosoyi* sp. nov. and *Bartonella krasnovii* sp. nov., were isolated from *R. rattus* rats and *Synosternus cleopatrae* fleas, respectively (Gutiérrez *et al.*, 2020). Another strain, closely related to *Bartonella elizabethae*; *Bartonella mastomydis* sp. nov., was detected in *Mastomys erythroleucus* rodents from Senegal (Dahmani *et al.*, 2018). Currently, insufficient information is known about the zoonotic potential of these novel strains.

A diverse species of rodents (approximately 90) is linked with more than 20 *Bartonella* spp. (Gutiérrez *et al.*, 2015; Yao *et al.*, 2022). At least 10 rodent-borne *Bartonella*, including *Bartonella doshiae*, *B. elizabethae*, *Bartonella grahamii*, *Bartonella rattimassiliensis*, *Bartonella rochalimae*, *Bartonella tribocorum*, *Bartonella washoensis*, and *Bartonella vinsonii*, are pathogenic to humans (Buffet *et al.*, 2013; Krügel *et al.*, 2022). The role of rodents in maintaining *Bartonella tamiae* remains unclear, even though the bacterium was initially isolated from three febrile patients in Thailand, who reported trapping or killing rodents around their home (Kosoy *et al.*, 2008). Strains genetically similar to *B. tamiae* from Thai patients were subsequently detected in ticks and chigger mites collected from rodents in Thailand (Kabeya *et al.*, 2010). This study suggested that chiggers may serve as the natural reservoirs of *B. tamiae* due to their single-host feeding habit during the larval stage. There have been increasing reports of *Bartonella* spp. detected from ectoparasites, such as fleas in Cambodia and

Xenopsylla cheopis in Thailand (Panthawong et al., 2020; Mullins et al., 2023). Despite the increasing prevalence of *Bartonella* reported in rodents and their ectoparasites in SEA, clinical cases remain sporadic and anecdotal (Inoue et al., 2008; Kr gel et al., 2022). Limited incidences have also been reported in humans from France, Mexico, the United States, Finland, the Netherlands, and Thailand (O'Halloran et al., 1988; Kerkhoff et al., 1999; Fenollar et al., 2005; Kosoy et al., 2010; Oksi et al., 2013; Corral et al., 2019).

Common symptoms exhibited by patients exposed to rodent-borne *Bartonella* strains include fever, headache, lethargy, arthralgia, and malaise (Bai et al., 2012). Rare symptoms, such as endocarditis and neuroretinitis, have been detected in cases associated with *B. elizabethae*, *B. grahamii*, and *B. vinsonii* subsp. *arupensis* (Daly et al., 1993; Kerkhoff et al., 1999; Fenollar et al., 2005). Another common theme observed among infected patients is their frequent association with rat exposures and tick bites (Bai et al., 2012; Vayssier-Taussat et al., 2016). To our knowledge, the overall seroprevalence data on rodent-borne bartonellosis in SEA is limited. For instance, Kosoy et al. (2010) reported infection in 7.7% of febrile patients from Thailand, with 71% recalling an exposure to rats a fortnight before the onset of disease. *B. elizabethae*, *B. tribocorum*, *B. rattimassiliensis*, *B. vinsonii* subsp. *arupensis*, and *B. vinsonii* subsp. *vinsonii* predominantly infected these patients. These pathogenic strains had previously been detected in rodents from Asia, Europe, and America (Saisongkorh et al., 2009a). Another study provided serological evidence of past exposure to *Bartonella* spp. in 28.9% of febrile and afebrile patients from rural Thailand (Bhengri et al., 2011). Most of the seropositivity cases (9.8%) were associated with *B. elizabethae*. These are pioneering studies conducted in Thailand that involved large sample sizes, ranging between 200 and 500 individuals. The scarcity of biosurveillance studies suggests a potential underdiagnosis of bartonellosis in these regions. According to past research, clinical cases may be overlooked due to the lack of proper diagnostic tools or the ability of the pathogen to remain asymptomatic in immunocompetent hosts (Oksi et al., 2013; Kim et al., 2016).

In SEA, several bacterial cultures and molecular studies have determined the prevalence of *Bartonella* in rodent reservoirs (Table 1). Studies in Thailand detected diverse strains, including *Bartonella coopersplainsensis*, *Bartonella phoceensis*, *Bartonella queenslandensis*, *B. elizabethae*, *B. grahamii*, *B. rattimassiliensis*, *B. rochalimae*, and *B. tribocorum* from murine species (Pangjai et al., 2014). The infection prevalence in Thai rodents ranged from 8.5% to 61% (Saisongkorh et al., 2009b; Kim et al., 2016). Recently, several novel species, including *Bartonella chanthaburi* spp. nov., *Bartonella satun* spp. nov., and *Candidatus Bartonella thailandensis* were detected in *R. rattus*, *R. tanezumi*, and *Rattus surifer* using molecular techniques (Saisongkorh et al., 2009b; Pangjai et al., 2022). However, information regarding their potential vectors and pathogenicity to humans remain obscure.

Interestingly, *B. henselae*, the primary causative agent of CSD, was isolated from *R. norvegicus* and *R. rattus* in Ranong, Thailand through conventional PCR amplification (Pangjai et al., 2022). This was the first study in SEA to report *B. henselae* DNA in rodents. Similar observations were previously made in three other countries; New Zealand, Denmark, and Italy (Engbaek & Lawson, 2004; Nesaraj et al., 2018). It was therefore hypothesized that rodents might play a larger role in the ecological epidemiology of CSD (Divari et al., 2020). In Sri Lanka, *B. henselae* was detected in *Suncus murinus*, leading the author to suggest that these small mammals could serve as potential carriers, transmitting the pathogen to humans due to frequent contact (Böge et al., 2021). Oksi et al. (2013) reported a peculiar case of CSD in an immunocompromised patient, caused by *B. grahamii*. The patient's history of cat scratches led the authors to suggest that cats might carry *B. grahamii*-infected blood or tissues in their claws following contact with infected rodents. Therefore, it implies that cats could increase the risk of *Bartonella* transmission from rodents to humans, either by acting as mechanical flea vectors

or through contaminated claws following an interaction with rodents (Castle et al., 2004; Oksi et al., 2013). However, the role of rodents in transmitting cat-borne *Bartonella* strains to humans has not been fully established. Further studies are warranted to corroborate the existence of a cat-rodent-human transmission cycle of *Bartonella*.

In Thailand, several studies found that *B. indica* and *R. rattus* were predominantly infected with *Bartonella* spp. (Castle et al., 2004; Bai et al., 2009; Klangthong et al., 2015; Panthawong et al., 2020). Other rodents from the Muridae family, including *R. norvegicus*, *R. exulans*, *R. surifer*, *R. tanezumi*, *Rattus losea*, *R. argentiventer*, *B. savilei*, and *Mus cervicolor* irregularly harboured *Bartonella*. According to Panthawong et al. (2020), 34.9% of rodents from the Nakhon Ratchasima province were bacteremic with *B. queenslandensis*. Subsequently, five pools of *X. cheopis* fleas collected from the infected *R. losea* also harboured *B. queenslandensis*. An unknown *Bartonella* genotype, previously isolated from a febrile patient in Thailand, shared more than 95% nucleotide homogeneity with the rodent-borne *B. queenslandensis* strain (Frank et al., 2018). This implied a potential rodent-human transmission cycle involving the particular genotype, which has not been discovered in humans outside Thailand. However, currently, there are yet to be any studies investigating the pathogenicity of *B. queenslandensis* in humans.

In urban (Bangkok) and suburban (Nakhon Sawan) regions of Thailand, 38.57% of rats tested positive for several *Bartonella* spp., including *B. phoceensis*, *B. tribocorum*, *B. grahamii*, and *B. rattimassiliensis* (Saengsawang et al., 2021). Additionally, the study discovered a high prevalence (26.67%) of a unique strain, *B. kosoyi* in the blood of *R. exulans*. A high nucleotide homogeneity between the bacterium and *B. tribocorum* was noted, leading the author to refer to it as the *B. kosoyi* - *B. tribocorum* complex. The initial discovery of *B. kosoyi* dates back to 2009, when it was first detected in *R. rattus* and provisionally termed the Tel Aviv isolates (Harrus et al., 2009). However, it was not until 2020 that the strain was morphologically characterized and officially named *B. kosoyi* sp. nov. (Gutiérrez et al., 2020). Remarkably, the zoonotic potential of *B. kosoyi* (then known as the Tel Aviv strain) was suggested following its presence in a patient presenting CSD-like symptoms, including lymphadenopathy and fever, in Tbilisi, Georgia (Kandelaki et al., 2016). Nevertheless, experimental studies are essential to confirm the pathogenicity and zoonotic potential of *B. kosoyi*.

Another study detected a significantly higher prevalence (19.4%) of *Bartonella* spp. in ectoparasites of infected rodents compared to non-infected ones by amplifying the *gltA* and *nuoG* genes (Klangthong et al., 2015). Ectoparasite infestations are thought to enhance the horizontal transmission of *Bartonella* between arthropod vectors and their rodent reservoirs, especially while feeding or biting. Similarly, in Malaysia, a positive association was observed between *Bartonella* infection in rodents and infestations by lice or ticks (Blasdell et al., 2019b). This study substantiated the existence of a complex vector-reservoir cycle in maintaining *Bartonella* in the environment. Moreover, *B. phoceensis* DNA was identified in *Dermacentor auratus* and *Haemaphysalis hystricis* ticks, along with their host, *R. tiomanicus*, in a mangrove forest in Malaysia (Asyikha et al., 2020). The authors believe transmission could have occurred during a blood meal session.

In Malaysia, *Bartonella* has been detected in rodents across various environments, including urban, developing, rural, forests, and plantation areas (Asyikha et al., 2020; Low et al., 2020a; Mohd-Azami et al., 2023). However, only one study is available for each of these landscapes. The overall prevalence in rats ranged between 4.9% and 57.3% in previous studies. *B. phoceensis* was commonly detected among the *Rattus* rats in Malaysia across all landscapes. Interestingly, a native rodent, *Sundamys muelleri* was more frequently infected with *Bartonella* compared to *Rattus* spp. in Sarawak, Malaysia (Blasdell et al., 2019b). This finding differs from the common reports of *Bartonella* in *Rattus* spp. or *Bandicota* spp. around Malaysia and Thailand. The authors attributed this

occurrence to the restriction of *S. muelleri* in green patches around Sarawak, where intraspecies contact increases and results in higher pathogen transmission. This warrants for more studies to be conducted for better insights on the host range of rodent-borne *Bartonella* in SEA.

In urban areas of Malaysia, a wide range of *Bartonella* species, including *B. queenslandensis*, *B. elizabethae*, *B. tribocorum*, *B. cooperspainsensis*, and *B. rattimassiliensis*, were prevalent among the *Rattus* rats (Tay et al., 2014b). The authors performed a subsequent genome analysis on the *B. elizabethae* (BeUM) strain recovered from *Rattus diardii* in Kuala Lumpur. The virulence profiling revealed that BeUM is more closely related to human strains (*B. elizabethae* ATCC49927 and *B. elizabethae* F9251) and possesses six putative virulence genes that are absent in other *B. elizabethae* (Tay et al., 2016). This finding further substantiates a potential rodent-human transmission cycle in urban landscapes. In neighbouring countries like Indonesia and Singapore, information on *Bartonella* detection is scarce. Winoto et al. (2005) detected *Bartonella* in 6% of rats and shrews using blood-smearing techniques followed by molecular procedures in Jakarta, Indonesia. In Singapore, 20.8% of rats and shrews were positive for *Bartonella* DNA (Neves et al., 2018). Phylogenetic analysis revealed that these strains were related to *B. elizabethae* and *B. queenslandensis*. In both countries, infection was more common among commensal species such as *R. tanezumi*, *R. norvegicus*, and *S. murinus*, given that the studies were mainly conducted in urban areas.

In Northern Vietnam, 31.6% of rodents were primarily infected with *Bartonella* spp. during a multiple pathogen detection study (Anh et al., 2021). Additionally, dual infection of *Bartonella* spp. with *Leptospira* spp. or *Rickettsia* spp. was present in approximately 40% of the rodents. Meanwhile, Loan et al. (2015) reported an overall infection rate of 14.9% in rodents around Southern Vietnam. These rodents were predominantly infected with zoonotic strains such as *B. rattimassiliensis*, *B. tribocorum*, and *B. elizabethae*. According to the authors, the contrast in prevalence between the two regions was presumptively due to climate and natural conditions. Another study detected *Bartonella* DNA in 10.7% of rodents from regions in Lao PDR, Cambodia, and Thailand, providing dawning evidence of *Bartonella* spp. in rodents such as *N. fulvescens*, *M. cookii*, and *Rattus andamanensis* for the first time around SEA (Jiyipong et al., 2012). In addition, a high prevalence of *Bartonella* (25.5%) was found in rodents from Lao PDR. The study identified additional putative species like *Bartonella* sp. Lao/Nh1 and *Bartonella* sp. Lao/Nh2 using the *gltA*, *rpoB*, and *ITS* genes (Angelakis et al., 2009). Currently, minimal data is available on the pathogenicity, reservoir hosts, and potential vectors of these putative strains.

The detection of pathogenic *Bartonella* spp. in rodents, especially in urban and agricultural areas of Thailand and Malaysia, heightens the potential for zoonotic spillover into human populations (Blasdel et al., 2019b; Panthawong et al., 2020). Therefore, monitoring *Bartonella* prevalence in rodents is crucial for assessing, managing, and mitigating the risk of disease transmission to humans, pets, and livestock, especially in densely populated areas. Currently, there is a paucity of clinical data on *Bartonella* infections in most Southeast Asian countries, suggesting a serious underdiagnosis issue. Hence, enhanced surveillance is essential for accurately determining the true disease burden in SEA, identifying the principal reservoirs in the region, and evaluating the zoonotic risks towards the community. Further studies on ectoparasites are also important in establishing the pathogen maintenance and transmission cycle in endemic regions.

Borreliosis

The genus *Borrelia* is typically classified into Lyme borreliosis (LB)-inducing pathogens and relapsing fever (RF)-inducing pathogens (Margos et al., 2020). Both diseases are distinct in terms of ecological, clinical, and epidemiological features. Recent studies suggest the existence of a novel echidna-reptile-related monophyletic cluster

consisting of *Borrelia mahuryensis*, *Borrelia tachyglossi*, *Borrelia turcica*, and several unclassified strains. It is unclear whether these species can induce human infections (Trevisan et al., 2021a). LB is the most common hard tick-borne (*Ixodes* spp.) zoonotic disease, widespread across the Northern Hemisphere and Europe (Radolf et al., 2021). Pathogenic species such as *Borrelia afzelii*, *Borrelia burgdorferi sensu stricto*, *Borrelia garinii*, and *Borrelia mayonii*, within the *sensu lato* complex, are commonly associated with LB (Tay et al., 2002; Strle et al., 2006; Khor et al., 2019; Madison-Antenucci et al., 2020). Strains such as *B. afzelii* and *B. garinii* are known to cause neuroborreliosis (Strle et al., 2006). Other spirochetes associated with human disease include *Borrelia bavariensis*, *Borrelia lusitaniae*, and *Borrelia spielmanii* (Marques et al., 2021). RF is predominantly transmitted via soft ticks (argasid), although *Borrelia miyamotoi* and *Borrelia recurrentis* are spread by hard ticks and lice, respectively. Notably, *B. recurrentis* is the only RF agent without an animal reservoir, as it is transmitted solely by the human body louse, *Pediculus humanus corporis*. RF is therefore classified into soft tick-borne RF, hard tick-borne RF, and louse-borne RF based on its arthropod vectors. These diseases predominantly occur in the Americas, Africa, Asia, and Europe (Trevisan et al., 2021b).

The enzootic transmission cycle of *Borrelia* spp. is complex. The spirochete bacterium requires both competent reservoirs and tick vectors for its ecological maintenance. Infected reservoirs play a key role in transmitting the bacterium to naive arthropod vectors (Lopez et al., 2021). As dead-end hosts, humans acquire the pathogen from tick saliva during a blood meal. Infected nymphs and adult ticks are more likely to bite humans, leading to clinical disease, although ticks of all life stages can transmit the pathogen (Eisen et al., 2017; Strnad et al., 2023). While rodents are the primary reservoirs for LB-associated *B. burgdorferi sensu lato* (Bbsl) complex, other animals such as rabbits, bank voles, shrews, carnivores, birds, and lizards can also carry the spirochete bacterium (Margos et al., 2019). Some ungulates, such as deer, are incompetent reservoirs of *Borrelia*, but are essential in tick reproduction and population maintenance of the bacteria (Jaenson & Talleklint, 1992).

Over the past two decades, LB has accounted for 82% of all tick-borne diseases in the United States (Rosenberg et al., 2018). Its annual incidence is reaching endemic levels in Europe, especially in Western European countries (Sykes & Makiello, 2017). In the United States, clinical cases are mainly caused by *B. burgdorferi sensu stricto*, although newer cases related to *B. mayonii* have been reported in this region (Pritt et al., 2016; Marques et al., 2021). In Europe, infections are associated with genospecies like *B. afzelii* and *B. garinii* (Marques et al., 2021). In Asia, LB has been reported in China (Wu et al., 2013), Japan, Korea (Im et al., 2019), and Taiwan. Recently, LB was detected in Nepal for the first time in a patient presenting with arthralgia, headache, and fatigue (Pun et al., 2018). In South Korea, LB was gazetted as a notifiable disease in 2010, with rising incidences since then (Acharya & Park, 2021).

Contrastingly, information on the epidemiology of LB in SEA is scarce. Hitherto, cases have only been reported in Malaysia and Indonesia. The first seroprevalence study in Malaysia detected antibodies against *B. afzelii* in a blood donor. In addition, IgM (19.8%) and IgG (4.1%) antibodies against *Borrelia* were detected using Western blot assay in patients suspected of febrile illnesses such as leptospirosis and melioidosis (Tay et al., 2002). Almost two decades later, using the IgG ELISA method, Khor et al. (2019) detected antibodies against *B. burgdorferi* in 8.1% of the Orang Asli community in Peninsular Malaysia. In Indonesia, 7.32% of patients with a history of tick bites were exposed to LB (Rotan et al., 2018). In Singapore, attempts to detect LB in patients with annular erythema were futile (Goh et al., 1996). Furthermore, a patient with neuroretinitis was suspected of having LB, but no conclusive diagnosis was made (Lam & Sanjay, 2012). Recently in Thailand, 17.9% of human sera tested positive for *B. miyamotoi*, the causative agent of RF (Takhampanya et al., 2023). However, LB has not been

detected in this region so far, and RF has not been detected in any Southeast Asian countries except for Thailand.

Similar to clinical cases, the distribution of borrelial agents in rodents is underexplored in SEA, with studies largely restricted to Malaysia and Thailand (Table 1). Recently, Mohd-Azami *et al.* (2023) detected both LB and RF-associated *Borrelia* spp. in 5.9% of rodents from an oil palm plantation. RF agents were found in several rodents, including, *R. tanezumi* R3 mitotype, *R. tiomanicus*, and *Tupaia glis*, while LB strains genetically similar to *B. burgdorferi sensu stricto* and *Borrelia yangtzensis* were limited to the *Rattus tanezumi* R3 mitotype. Notably, one of the rodents infected with the *B. burgdorferi* strain was captured in Kampung Tumbuh Hangat, Perak, an oil palm plantation bordering human settlements. Khor *et al.* (2019) previously reported that the indigenous population (Orang Asli) from Kampung Tumbuh Hangat are 1.65 times more likely to be seropositive for anti-*B. burgdorferi* antibodies. However, the zoonotic spillover of *B. burgdorferi* has not been established in this region, despite findings showing similar strains in both humans and rodents. More surveillance studies are required to establish the maintenance cycle of *B. burgdorferi* and its transmission route to humans in this region.

Recently, the first clinical infection of *B. yangtzensis* was reported in a Korean individual who travelled to the Taean Peninsula (Kim *et al.*, 2021). In China and Japan, *B. yangtzensis* is maintained in rodent reservoirs such as *N. fulvescens*, *R. rattus*, and *M. caroli*, and transmitted by the *Ixodes* ticks (Margos *et al.*, 2015). In Sarawak, Lau *et al.* (2020) detected borrelial pathogens in 8.9% of rodents and 43.8% of *Ixodes granulatus* ticks. LD agents such as *B. yangtzensis* and *B. valasiana*-related genospecies were isolated from *Rattus* rats, while *B. miyamotoi* was detected in *S. muelleri*. The circulation of *B. yangtzensis* in both *Ixodes* ticks and rodents suggests the existence of a pathogen maintenance cycle in the environment, where rodents and ticks may play the roles of natural reservoirs and vectors, respectively. A separate study in Malaysia, detected a high prevalence (46.2%) of *B. yangtzensis* in *I. granulatus* ticks, but the presence of borrelial agents in the respective rodent hosts was not investigated (Khoo *et al.*, 2018). An increasing detection of *B. yangtzensis* in tick vectors suggests an impending risk of pathogen transmission to humans in the environment. This postulation is supported by the recent incident of *B. yangtzensis* infection following a tick bite in a Korean woman (Kim *et al.*, 2021).

I. granulatus is one of the most widespread and commonly encountered ticks from the *Ixodes* genus in SEA (Petney *et al.*, 2019). Despite its wide distribution and tendency to infest humans, relatively little is known about the frequency of human bites and subsequent infections. The vector competence of various human-biting ticks from the *Ixodes*, *Amblyomma*, and *Dermacentor* genera for the Bbsl complex has been investigated experimentally; however, a formal demonstration for *I. granulatus* is lacking (Eisen, 2020). In Malaysia and Thailand, *I. granulatus* ticks, which occasionally bite humans, have been associated with carrying LD agents, indicating the potential for this species to serve as competent vectors (Khoo *et al.*, 2018; Lau *et al.*, 2020; Takhampunya *et al.*, 2021). These field evidences justify an experimental demonstration for the vector competence of *I. granulatus* ticks. Experimental studies could shed a light on the roles of the ticks in the ecological maintenance of borrelial spirochetes. Although humans are typically the incidental hosts for tick species, further evaluation is necessary to understand the pathogenicity of borrelial diseases in humans and the transmission cycle of Bbsl complex in SEA.

In Thailand, studies have reported a low prevalence of borrelial agents in rodents, ranging from 1.2% to 3.2% (Takhampunya *et al.*, 2019, 2021, 2023). In contrast, 14% to 22% of the infesting ticks were infected with borrelial spirochetes. Some of these spirochetes including, *B. miyamotoi* and *B. yangtzensis*, are pathogenic to humans (Kim *et al.*, 2021; Takhampunya *et al.*, 2023). Despite the presence of a pathogen maintenance cycle in the environment, data on clinical cases of borreliosis in Thailand are scarce. It is currently

unknown whether the paucity of information stems from a lack of surveillance and monitoring. Overall, insufficient information is available on the competence of rodents and their arthropod vectors in maintaining borrelial agents in SEA. Even though the prevalence in Southeast Asian rodents is relatively low, it cannot be dismissed that they pose a threat to humans, as recent studies show increasing infection rates in humans. Moreover, an expanding detection of pathogenic *Borrelia* spp. in tick pools insinuates the existence of a maintenance cycle in the environment. Thus, continuous surveillances are essential in corroborating these postulations. Currently, the lower prevalence of clinical cases in SEA could be attributed to inadequate disease regulation systems. Hence, continuous monitoring and experimental studies are crucial in identifying the competent reservoirs and vectors of LB and RF in SEA.

Rickettsiosis

There is an increasing body of knowledge on the prevalence of rickettsioses, including scrub typhus, murine typhus, and spotted fever in SEA [reviewed in (Low *et al.*, 2020b)]. Findings from serological studies have attributed rickettsial infections as the cause of many AUFI cases in Southeast Asian countries (Tay *et al.*, 2000; Wangrangsamakul *et al.*, 2018; Luvira *et al.*, 2019; Lokida *et al.*, 2020). *Orientia tsutsugamushi*, the causative agent of scrub typhus, and various *Rickettsia* spp. are transmitted via the bites of arthropods such as chiggers, fleas, and ticks. The role of rodents in the ecology of rickettsial diseases is well-established for scrub typhus and murine typhus, as rodents are the primary animal hosts for the arthropod vectors of the causative agents. However, the role of rodents in the transmission of spotted fever is less clear.

Scrub typhus - *Orientia tsutsugamushi*

Previously confined to the Tsutsugamushi Triangle, scrub typhus and its etiological agent are now found in a wider geographical area, including Chile, Africa, and the United Arab Emirates as reviewed by Xu *et al.* (2017) and Richards & Jiang. (2020). *O. tsutsugamushi* is the causative agent of scrub typhus in SEA, while the newly reported species, *Orientia chuto* causes scrub typhus in other parts of the world (Richards & Jiang, 2020). The ecological roles of rodents and their chigger vectors in the transmission of scrub typhus have been widely investigated since the disease was first described in Japan in the 1800s [reviewed in (Elliott *et al.*, 2019; Richards & Jiang, 2020)]. Epidemiological investigations of recent outbreaks continue to associate the presence of rodents and chiggers with the disease upsurge (Tilak *et al.*, 2011; Rodkvamtook *et al.*, 2018) (Figure 1). For example, during a recent scrub typhus outbreak among training soldiers in Chonburi, Thailand, follow-up studies detected a high prevalence of *O. tsutsugamushi* infections in rodents and chiggers nearby the training site (Rodkvamtook *et al.*, 2018). Another outbreak among febrile children in Chiang Mai was linked to infected rodent reservoirs (65.5%) in the surrounding areas (Rodkvamtook *et al.*, 2013). Several factors may influence the acquisition of scrub typhus, including direct contact with household floors, households with poor sanitation, high-risk occupational environments, frequent rodent exposures, and low awareness of personal protective equipment usage (Tran *et al.*, 2021).

Common *O. tsutsugamushi* strains circulating in SEA include Karp, TA763, Kato, Gilliam, UT176, TA678, TA686, TA716, TA763, JG-v, and TH1817. Moreover, most of these strains are based on data collected in Thailand, where the Thai strains closely resembled Japanese and Taiwanese strains (Elisberg *et al.*, 1968; Shirai *et al.*, 1981; Blacksell *et al.*, 2008; Duong *et al.*, 2013a, 2013b; Wongprompitak *et al.*, 2013; Mohd-Azami *et al.*, 2023). Recently, efforts have been made to develop a sensitive tool that detects the recent *O. tsutsugamushi* strains, alongside studying the disease model of scrub typhus to enable vaccine development (Elliott *et al.*, 2021b; Linsuwanon *et al.*, 2021b; Chankate *et al.*, 2022; Indrawattana *et al.*, 2022; Inthawong *et al.*, 2023). However, more studies are

necessary to evaluate the pathogenicity of these strains in humans and the roles of synanthropic small mammals in maintaining the scrub typhus transmission cycle.

The transmission of *O. tsutsugamushi* is facilitated by the larvae of *Trombiculidae* mites, commonly known as chiggers. The pathogenicity of *O. tsutsugamushi* has been demonstrated in rhesus macaques, with chiggers requiring only a minimum of an hour of feeding to transmit the pathogen (Linsuwanon et al., 2021b). The primary vectors for *O. tsutsugamushi* are chiggers from the *Leptotrombidium* genus, including *Leptotrombidium pallidum*, *Leptotrombidium deliense*, *Leptotrombidium scutellare*, *Leptotrombidium fletcheri*, and *Leptotrombidium chiangraiensis* (Lerdthusnee et al., 2003; Elliott et al., 2019). Several chigger species have been associated with specific habitats: *Ascoschoengastia indica*, *Eutrombicula wichmanni*, *Leptotrombidium arenicola*, *L. deliense*, *Trombiculindus paniculatum*, *Walchia disparunguis pingue*, *Walchia kritochaeta*, and *Walchiella oudemansi* are associated with human-modified habitats, whereas three chiggers (*Gahrlepiea rutila*, *Walchia ewingi ewingi*, and *Walchia rustica*) are predominantly found within forested areas (Alkathiry et al., 2022).

In Thailand, a few species of chiggers tested positive for *O. tsutsugamushi* infection, including *L. deliense*, *Leptotrombidium imphalum*, and *W. kritochaeta* (Elliott et al., 2021a). In contrast, in Malaysia, only *L. deliense* collected from *R. rattus* and *Tupaia* spp. has tested positive for the Karp prototype strain thus far (Ernieenor et al., 2021). In Lao PDR, a low detection rate was reported, with only a single pool of chiggers testing positive for *O. tsutsugamushi* and no positive detections in small mammals (Elliott et al., 2022). An outbreak investigation in India suggested *Schoengastiella ligula* as a potential vector for scrub typhus (Tilak et al., 2011). Chiggers that are not the primary vectors may also contribute to the maintenance of scrub typhus agents in rodent hosts. In addition to Muridae infestations, chiggers have also been reported infesting Tupaiidae and Sciuridae hosts (Paramasvaran et al., 2009; Adrus et al., 2021). Chiggers are successful vectors because they can maintain the transmission cycle of *O. tsutsugamushi* via transovarial and transstadial routes, as well as by co-feeding on animal hosts (Phasomkusolsil et al., 2009).

Rodents are the well-established primary hosts for chiggers, playing a key role in the dispersal of scrub typhus vectors. They may also be infected with *O. tsutsugamushi*, potentially serving as reservoirs of the pathogen (Rodkvamtook et al., 2018). However, a recent study suggests that rodents may be the dead-end host of *O. tsutsugamushi*, with the increase in rodent populations contributing to the growth of chigger populations (Linsuwanon et al., 2021a). A survey in rural Thailand found that approximately 42% of rodents, including *R. rattus*, *R. exulans*, *R. losea*, *R. norvegicus*, and *B. indica*, were infected with *O. tsutsugamushi* (Lerdthusnee et al., 2008) (Table 1). In Indonesia, a recent study reported the prevalence of *O. tsutsugamushi* in *R. norvegicus*, raising concerns as the pathogen is no longer restricted to rural landscapes (Susanti et al., 2022). Data from Thailand indicates that the host, *R. tanezumi* and vector, *Leptotrombidium* spp. are habitat generalists (Elliott et al., 2021a). The study also found that *R. tanezumi* and *B. indica* were heavily infested with chiggers, and their chigger pools tested positive for *O. tsutsugamushi*.

In Northern Thailand, approximately 25% of rodents including *R. tanezumi*, *R. andamanensis*, *R. exulans*, *B. indica*, *M. cookii*, *Berylmys berdmorei*, and *R. nitidus* were infected with *O. tsutsugamushi* (Elliott et al., 2021a). Previous exposure was confirmed in 42.6% of rodents trapped in Chiang Rai, Thailand (Linsuwanon et al., 2021a). Lerdthusnee et al. (2008) suggest that the dry season is associated with higher risks of scrub typhus due to increased rodent populations and chigger densities. The dry season also aligned with greater species richness of chiggers, with a high infestation rate of 94%, compared to 55% during the wet season (Alkathiry et al., 2022). Linsuwanon et al. (2021a) further

supported this, by detecting the highest infection rate in rodents during December, the dry-cool season. Moreover, Elliott et al. (2021a), observed higher *O. tsutsugamushi* infections during season transition. In contrast, a clinical study found that scrub typhus cases were higher during the wet season in Lao PDR (Roberts et al., 2021). More studies are warranted across SEA to gather comprehensive data on the epidemiology of scrub typhus in relation to seasonal patterns.

O. tsutsugamushi-infected rodents are more commonly found in forested and lowland habitats (Chaisiri et al., 2017; Elliott et al., 2021a). A recent ecological study presented evidence of a positive correlation between chigger species richness and latitude, with the incidence of scrub typhus in Thailand (Chaisiri et al., 2019). Chigger abundance decreases with increasing distance from forests, thus reducing humans contact (Linsuwanon et al., 2021a). The study also suggests that anthropogenic activities may reduce chigger populations. These findings highlight the need for further research into the ecology of scrub typhus. Other Southeast Asian countries, including Indonesia (Richards et al., 1997), Malaysia (Hanifah, 2013; Mohd-Azami et al., 2023), and the Philippines (Van Peenen et al., 1977), have also reported *O. tsutsugamushi* in rodents. Commonly infected rodents within the Muridae family include *Apodemus agrarius*, *R. rattus*, *R. norvegicus*, *R. tiomanicus*, and *B. indica* as reviewed by Elliott et al. (2019). In addition, *R. exulans*, *R. tiomanicus*, *M. cookii*, *R. nitidus*, *R. argentiventer*, *R. bowersi*, *Rattus mackenziei*, *Leopoldamys sabanus*, *T. glis*, and *B. berdmorei* have also carried *O. tsutsugamushi* (Elliott et al., 2021a; Linsuwanon et al., 2021a; Mohd-Azami et al., 2023). Since most recent ecological studies on scrub typhus are based in Thailand, further research from other Southeast Asian countries is necessary to account for differences in rural and agricultural landscapes.

Murine typhus – *Rickettsia typhi*

Members of the typhus group *Rickettsia* spp., including *Rickettsia typhi* and *Rickettsia prowazekii*, cause murine typhus (endemic typhus) and louse-borne typhus (epidemic typhus), respectively (Rauch et al., 2018). Murine typhus is the only type endemic in SEA (Barbara et al., 2010; Vallée et al., 2010). Globally, around 60% of patients have been infected by *R. typhi* (Vaca et al., 2022). The illness is generally mild but can be fatal if not diagnosed and treated promptly (Osterloh et al., 2016). In SEA, murine typhus is a common cause of undifferentiated fevers, especially in urban areas [reviewed in (Low et al., 2020b)]. In Thailand, approximately 3.5% of patients in Chiang Rai and 5% in Bangkok tested positive for murine typhus (Wangrangsamakul et al., 2018; Luvira et al., 2019).

In Lao PDR, a patient diagnosed with meningoencephalitis was positive for anti-*R. typhi* IgM antibodies (Uy et al., 2022). The diagnosis of murine typhus is challenging due to symptoms overlapping with other endemic tropical diseases, leading to some patients receiving ineffective antibiotics. Seroprevalence studies indicate that murine typhus is prevalent in both rural and urban areas (Strickman et al., 1994; Vallée et al., 2010; Trung et al., 2017; Tappe et al., 2018; Chaisiri et al., 2022). The pathogen is transmitted via the oriental rat fleas, *X. cheopis*, from rodents (Barbara et al., 2010). Common rodents in SEA including *R. tanezumi* (Widjaja et al., 2016; Pramestuti et al., 2018), *R. rattus* (Ibrahim et al., 1999; Griffiths et al., 2022), *R. exulans*, *R. norvegicus* (Ibrahim et al., 1999; Griffiths et al., 2022), and *Mus musculus* (Chareonviriyaphap et al. 2014), have been reported to be infected with *R. typhi*. These rodents are likely the reservoirs for murine typhus agent in SEA.

In Singapore, rodents captured in schools had the highest seropositivity for *R. typhi*, with 60% of 1,143 individuals testing positive (Griffiths et al., 2022) (Table 1). In Indonesia, *R. norvegicus* had significant infection compared to other rodent species, with most positive cases occurring in Jakarta (Ibrahim et al., 1999). Similar findings were reported in other studies from Indonesia (Richards et al., 2002), Singapore (Griffiths et al., 2022), and

Table 1. The summary of peridomestic rodents/shrews and their associated pathogens reported in SEA

Country	Prevalence (%)	Host	Pathogen	Specimen	Method	Reference
Malaysia	34.7	<i>R. rattus</i>	<i>L. interrogans</i> Malaya, IMR LEP 75, <i>L. interrogans</i> Bataviae, <i>L. interrogans</i> Gurungi, <i>L. interrogans</i> Hardjo, <i>L. interrogans</i> Copenhageni	Blood, kidney	Serology, molecular	Noh et al., 2024
Malaysia	20.0	<i>R. tiomanicus</i> , <i>T. glis</i> , <i>M. rajah</i> , <i>M. whiteheadi</i> , <i>S. muelleri</i>	<i>L. interrogans</i>	Kidney	Molecular	Shafie et al., 2022
Malaysia	36.7	Rats	<i>L. interrogans</i> , <i>L. borgpetersenii</i>	Kidney	Molecular	Wan et al., 2022
Malaysia	15.7	<i>R. norvegicus</i> , <i>R. rattus</i> , <i>T. glis</i> , <i>S. murinus</i>	Pathogenic <i>Leptospira</i> spp.	Kidney	Molecular	Mohd-Taib et al., 2020
Malaysia	31.6	<i>R. rattus</i> R3, <i>R. tanezumii</i> , <i>R. tiomanicus</i> , <i>S. muelleri</i> , <i>M. ochraceiventris</i> , <i>M. whiteheadi</i> , <i>N. cremoriventer</i>	<i>L. interrogans</i> , <i>L. borgpetersenii</i>	Kidney	Molecular	Blasdel et al., 2019a
Malaysia	39.2	<i>R. rattus</i>	<i>L. borgpetersenii</i> , <i>L. interrogans</i>	Kidney, liver	Molecular	Ikbal et al., 2019
Malaysia	14.9	<i>R. norvegicus</i> , <i>R. rattus</i> , <i>M. whiteheadi</i> , <i>S. muelleri</i> , <i>R. tiomanicus</i> , <i>T. glis</i> , <i>S. murinus</i>	Pathogenic <i>Leptospira</i> spp.	Kidney	Molecular	Yusof et al., 2019
Malaysia	14.3	<i>R. norvegicus</i> , <i>R. rattus</i> , <i>M. whiteheadi</i> , <i>S. muelleri</i> , <i>R. tiomanicus</i> , <i>T. glis</i> , <i>S. murinus</i>	<i>L. interrogans</i> , <i>L. kirschneri</i> , <i>L. borgpetersenii</i> , <i>L. weilii</i>	Kidney	Culture, molecular	Azhari et al., 2018
Malaysia	15.9	Rats	<i>L. interrogans</i> Icterohaemorrhagiae, <i>L. noguchii</i> , <i>L. meyeri</i>	Kidney, liver	Culture, molecular	Pui et al., 2017
Malaysia	11.0	<i>R. rattus</i> , <i>R. norvegicus</i> , <i>R. exulans</i>	<i>L. interrogans</i> Bataviae, <i>L. borgpetersenii</i> Javanica	Urine, kidney, blood	Culture, molecular, serology	Benacer et al., 2016
Malaysia	6.7	<i>R. rattus</i> , <i>R. norvegicus</i>	<i>L. borgpetersenii</i> Javanica, <i>L. interrogans</i> Bataviae	Urine, kidney	Culture, molecular, serology	Benacer et al., 2013
Thailand	3.6	<i>R. exulans</i> , <i>R. rattus</i> , <i>B. indica</i>	<i>L. interrogans</i> , <i>L. borgpetersenii</i>	Kidney	Molecular	Krairojananan et al., 2020
Indonesia	8.0	<i>R. tanezumii</i> , <i>R. norvegicus</i> , <i>B. indica</i> , <i>B. bengalensis</i>	<i>Leptospira</i> spp.	Kidney	Molecular	Sunaryo & Priyanto, 2022
Indonesia	6.6	<i>R. tanezumii</i> , <i>R. argentiventer</i> , <i>S. murinus</i>	<i>L. borgpetersenii</i> Seirae	Kidney	Molecular	Widiastuti et al., 2016
Vietnam	18.0	<i>R. tanezumii</i> , <i>Rattus</i> cf. <i>rattus</i> , <i>B. bowersi</i> , <i>Callosciurus erythraeus</i> , <i>B. savilei</i> , <i>N. fulvescens</i> , <i>R. nitidus</i>	<i>Leptospira</i> spp.	Kidney, liver	Molecular	Anh et al., 2021
Vietnam	Culture: 12.6 Molecular: 28.4	<i>R. norvegicus</i>	<i>L. interrogans</i> Bataviae, <i>L. interrogans</i> Pomona	Kidney	Culture, molecular	Koizumi et al., 2019
Cambodia	12.3	<i>R. norvegicus</i> , <i>R. argentiventer</i> , <i>Rattus</i> spp.	<i>L. interrogans</i> , <i>L. noguchii</i>	Kidney, bladder	Molecular	Kudo et al., 2018
Lao PDR-Cambodia-Thailand	7.1	<i>M. cookii</i> , <i>R. tanezumii</i> , <i>M. cervicolor</i> , <i>R. losea</i> , <i>M. caroli</i> , <i>R. argentiventer</i> , <i>M. surifer</i> , <i>B. berdmorei</i> , <i>B. indica</i> , <i>B. savilei</i> , <i>R. exulans</i>	<i>L. borgpetersenii</i> , <i>L. interrogans</i> , <i>L. kirschneri</i> , <i>L. weilii</i>	Kidney	Molecular	Cosson et al., 2014
Singapore	46.8	<i>R. norvegicus</i> , <i>R. rattus</i>	<i>Leptospira</i> spp.	Kidney	Molecular	Griffiths et al., 2022
Malaysia	13.7	<i>R. norvegicus</i>	HNTV, PUUV, SNV, SEOV	Sera	Serology	Lam et al., 2001

Thailand	6.6	<i>B. indica</i>	THAIV	Lungs, liver	Serology, molecular	Hugot et al., 2006
Indonesia	N/A	<i>R. tanezumii</i>	SERV	Sera, lungs	Serology, molecular	Plyusnina et al., 2009
Indonesia	4.0	<i>R. norvegicus</i> , <i>R. exulans</i> , <i>R. rattus</i>	SEOV	Sera	Serology	Ibrahim et al., 1996
Vietnam	1.6	<i>Niviventer cf. confucianus</i>	HTNV	Lungs	Molecular	Kikuchi et al., 2021
Vietnam	6.9	<i>B. indica</i> , <i>R. argentiventer</i> , <i>R. norvegicus</i> , <i>R. tanezumii</i>	DOBV, SEOV	Sera, blood	Serology	Cuong et al., 2015
Vietnam	0.4	<i>R. argentiventer</i>	SEOV	Lungs	Molecular	
Vietnam	2.8	<i>R. norvegicus</i>	HTNV strain 76-118, SEOV strain SR-11	Sera	Serology	Luan et al., 2012
Vietnam	13.11	<i>S. murinus</i>	Thottapalayam virus	Sera	Serology	
Cambodia	8.2	<i>R. norvegicus</i> , <i>R. rattus</i> , <i>Rattus</i> spp.	HTNV	Sera	Serology	Reynes et al., 2003
	87.0	<i>R. norvegicus</i> , <i>R. rattus</i> , <i>Rattus</i> spp.	SEOV	Liver, kidney, lungs	Molecular	
Laos-Cambodia-Thailand	3.0	<i>B. indica</i> , <i>B. savilei</i> , <i>M. surifer</i> , <i>R. exulans</i> , <i>R. nitidus</i> , <i>R. norvegicus</i> , <i>R. tanezumii</i> , <i>M. caroli</i> , <i>M. cookii</i>	Hantavirus	Sera	Serology	Blasdel et al., 2011a
Laos-Cambodia-Thailand	1.9	<i>B. indica</i> , <i>R. tanezumii</i> , <i>R. norvegicus</i>	THAIV, SEOV	Lungs	Molecular	
Singapore	35.5	<i>R. norvegicus</i> , <i>R. rattus</i>	SEOV	Sera	Serology	Griffiths et al., 2022
Singapore	34.0	<i>R. norvegicus</i> , <i>R. tanezumii</i>	Hantavirus	Sera	Serology	Johansson et al., 2010
Singapore	2.4	<i>R. norvegicus</i> , <i>R. tanezumii</i>	Seoul Singapore virus, Jorong TIK/06 virus	Lungs, kidney	Molecular	
Malaysia	4.9	<i>R. tanezumii</i> R3 mitotype	<i>B. phoceensis</i>	Spleen	Molecular	Mohd-Azami et al., 2023
Malaysia	N/A	<i>R. tiomanicus</i>	<i>B. phoceensis</i>	N/A	Molecular	Asyikha et al., 2020
Malaysia	3.7	<i>R. rattus diardii</i> , <i>R. norvegicus</i> , <i>R. argentiventer</i> , <i>R. tiomanicus</i> , <i>R. exulans</i>	<i>B. phoceensis</i>	Blood	Molecular	Low et al., 2020a
Malaysia	57.3	<i>S. muelleri</i> , <i>R. rattus</i> super group <i>M. whiteheadi</i> , <i>N. cremoriventer</i>	<i>B. phoceensis</i> , <i>B. rattimassiliensis</i> , <i>B. queenslandensis</i> , <i>B. tribocorum</i> , <i>B. elizabethae</i> , <i>undescribed clade</i>	Spleen	Molecular	Blasdel et al., 2019b
Malaysia	13.7	<i>Rattus diardii</i> , <i>R. norvegicus</i>	<i>B. queenslandensis</i> , <i>B. elizabethae</i> , <i>B. tribocorum</i> , <i>B. rattimassiliensis</i> , <i>B. coopersplainsensis</i>	Spleen, kidney	Culture, molecular	Tay et al., 2014b
Thailand	11.5	<i>R. rattus</i> , <i>R. norvegicus</i> , <i>R. exulans</i> , <i>M. musculus</i> , <i>B. indica</i> , <i>S. murinus</i> , <i>R. tanezumii</i>	<i>B. tribocorum</i> , <i>B. elizabethae</i> , <i>B. coopersplainsensis</i> , <i>Bartonella ranong</i> spp. nov., <i>B. henselae</i>	Blood	Culture, molecular	Pangjai et al., 2022
Thailand	34.9	<i>R. rattus</i> , <i>B. indica</i> , <i>R. argentiventer</i> , <i>B. savilei</i> , <i>R. losea</i> , <i>R. exulans</i> , <i>R. norvegicus</i>	<i>B. queenslandensis</i>	Blood	Molecular	Panthawong et al., 2020
Thailand	38.5	<i>R. tanezumii</i> , <i>R. exulans</i>	<i>B. phoceensis</i> , <i>B. kosoyi</i> - <i>B. tribocorum</i> complex, <i>Bartonella</i> spp., <i>B. tribocorum</i> , <i>B. grahamii</i> , <i>B. rattimassiliensis</i>	Blood	Molecular	Saengsawang et al., 2021
Thailand	61.0	<i>R. rattus</i> , <i>R. exulans</i>	<i>B. queenslandensis</i> , <i>B. rattimassiliensis</i> , <i>B. tribocorum</i> , <i>B. elizabethae</i> , <i>B. phoceensis</i>	Blood	Culture, molecular	Kim et al., 2016
Thailand	17.6	<i>R. rattus</i> , <i>B. indica</i> , <i>R. norvegicus</i> , <i>B. savilei</i> , <i>R. exulans</i> , <i>R. sabanus</i>	<i>B. rattimassiliensis</i> , <i>B. coopersplainsensis</i> , <i>B. tribocorum</i>	Liver, blood	Molecular, culture	Klangthong et al., 2015
Thailand	15.5	<i>R. norvegicus</i> , <i>R. rattus</i> , <i>R. tanezumii</i> , <i>R. exulans</i> , <i>B. indica</i> , <i>R. muelleri</i> , <i>R. nitidus</i> , <i>R. bukit bukit</i>	<i>B. tribocorum</i> , <i>B. rattimassiliensis</i> , <i>B. elizabethae</i> , <i>B. queenslandensis</i>	Blood	Culture, molecular	Pangjai et al., 2014

Thailand	41.5	<i>R. rattus</i> , <i>R. norvegicus</i> , <i>B. indica</i> , <i>B. savilei</i> , <i>R. exulans</i> , <i>M. cervicolor</i> , <i>R. argentiventer</i> , <i>R. nitidus</i> , <i>R. rematus</i> , <i>B. berdmorei</i>	<i>B. rattimassiliensis</i> , <i>B. tribocorum</i> , <i>B. phoceensis</i> , <i>B. coopersplainsensis</i> , <i>B. elizabethae</i> , unknown genogroup	Blood	Culture, molecular	Bai et al., 2009
Thailand	8.5	<i>R. surifer</i> , <i>B. berdmorei</i> , <i>R. rattus</i> , <i>B. savilei</i> , <i>M. cervicolor</i> , <i>R. exulans</i>	<i>B. coopersplainsensis</i> , <i>B. queenslandensis</i> , <i>B. phoceensis</i> , <i>Candidatus Bartonella thailandensis</i> , <i>B. rochalimae</i> , <i>Bartonella</i> sp. RN24BJ	Blood	Molecular	Saisongkroh et al., 2009b
Thailand	8.7	<i>B. indica</i> , <i>R. rattus</i> , <i>R. losea</i>	<i>B. elizabethae</i> , <i>B. grahamii</i>	Blood	Culture, molecular	Castle et al., 2004
Indonesia	6.0	<i>R. tanezumii</i> , <i>S. murinus</i> , <i>R. norvegicus</i>	<i>B. phoceensis</i> , <i>B. rattimassiliensis</i> , <i>B. elizabethae</i>	Blood, spleen	Microscopy, molecular	Winoto et al., 2005
Vietnam	31.6	<i>R. tanezumii</i> , <i>N. fulvescens</i> , <i>R. cf. rattus</i> , <i>B. savilei</i> , <i>R. norvegicus</i> , <i>R. nitidus</i> , <i>N. mekongis</i> , <i>N. lotipes</i> , <i>B. bowersi</i> , <i>C. inornatus</i> , <i>R. andamanensis</i> , <i>N. confucianus</i> , <i>L. edwardsi</i>	<i>Bartonella</i> spp.	Liver, kidney	Molecular	Anh et al., 2021
Vietnam	14.9	<i>R. argentiventer</i> , <i>B. indica</i> , <i>R. tanezumii</i> , <i>R. norvegicus</i>	<i>B. rattimassiliensis</i> , <i>B. tribocorum</i> , <i>B. elizabethae</i> , <i>B. coopersplainsensis</i> , <i>B. queenslandensis</i>	Blood	Culture, molecular	Loan et al., 2015
Lao PDR-Cambodia-Thailand	8.7	<i>Bandicota</i> spp., <i>Mus</i> spp., <i>Rattus</i> spp., <i>Berylmys</i> spp., <i>Maxomys</i> spp., <i>Niviventer</i> spp.	<i>B. queenslandensis</i> , <i>B. rattimassiliensis</i> , <i>B. tribocorum</i> , <i>B. elizabethae</i> , <i>B. coopersplainsensis</i> , <i>B. phoceensis</i>	Blood	Culture, molecular	Jiyipong et al., 2012
Lao PDR	25.5	<i>R. exulans</i> , <i>R. rattus</i> , <i>M. cervicolor</i> , <i>M. caroli</i> , <i>C. badius</i>	<i>B. phoceensis</i> , <i>B. elizabethae</i> , <i>B. tribocorum</i> , <i>Bartonella</i> sp. Lao/Nh2, <i>Bartonella</i> sp. Lao/Nh1	Spleen, liver	Molecular	Angelakis et al., 2009
Singapore	20.8	<i>R. tanezumii</i> , <i>S. murinus</i> , <i>R. norvegicus</i> , <i>T. glis</i> , <i>M. castaneus</i>	<i>B. queenslandensis</i> , <i>B. elizabethae</i> , <i>Bartonella</i> spp.	Spleen	Molecular	Neves et al., 2018
Malaysia	5.9	<i>R. tanezumii</i> R3 mitotype <i>R. tanezumii</i> R3 mitotype, <i>R. tiomanicus</i> , <i>T. glis</i>	<i>B. burgdorferi</i> s.s., <i>B. yangtzensis</i> Relapsing fever <i>Borrelia</i> spp.	Spleen	Molecular	Mohd-Azami et al., 2023
Malaysia	8.9	<i>Rattus</i> spp. <i>S. muelleri</i>	<i>B. yangtzensis</i> , <i>B. valisiana</i> -related genospecies <i>B. miyamotai</i>	Spleen	Molecular	Lau et al., 2020
Thailand	2.3	<i>B. berdmorei</i> , <i>B. indica</i> , <i>M. caroli</i> , <i>M. parahi</i> , <i>B. bowersi</i>	<i>B. yangtzensis</i>	Spleen, kidney	Molecular	Takhampunya et al., 2023
Thailand	9.0	<i>B. indica</i> , <i>Mus</i> spp., <i>M. caroli</i> , <i>L. sabanus</i> <i>B. indica</i> , <i>R. exulans</i> , <i>M. caroli</i> , <i>R. tanezumii</i> , <i>B. berdmorei</i> , <i>M. cookii</i> , <i>B. mackenziei</i> , <i>M. pahari</i>	<i>B. miyamotai</i> , <i>B. theileri</i> <i>B. miyamotai</i>	Blood	Serology	
Thailand	1.2	<i>R. rattus</i> , <i>B. indica</i> , <i>L. sabanus</i> , <i>C. fuliginosa</i> , <i>M. cookii</i> , <i>N. tenaster</i> , <i>M. caroli</i>	<i>B. theileri</i> / <i>B. lonestari</i> , <i>B. miyamotai</i>	Spleen	Molecular	Takhampunya et al., 2021
Thailand	3.2	<i>R. rattus</i> <i>Niviventer tenaster</i>	<i>B. yangtzensis</i> <i>B. miyamotai</i>	Spleen, kidney	Molecular	Takhampunya et al., 2019
Malaysia	12.3	<i>R. tanezumii</i> R3 mitotype, <i>R. exulans</i> , <i>R. argentiventer</i> , <i>T. glis</i> , <i>R. tiomanicus</i>	<i>O. tsutsugamushi</i> strain UT176, <i>O. tsutsugamushi</i> strain TA763, <i>O. tsutsugamushi</i> Karp, <i>O. tsutsugamushi</i> strain Wuj/2014	Spleen	Molecular	Mohd-Azami et al., 2023
Malaysia	11.7	<i>R. tanezumii</i> R3 mitotype, <i>R. exulans</i> , <i>R. argentiventer</i> , <i>T. glis</i> , <i>R. tiomanicus</i>	<i>O. tsutsugamushi</i>	Spleen	Molecular	Alkathiry et al., 2022
Malaysia	1.14	<i>L. sabanus</i>	<i>O. tsutsugamushi</i> /Gilliam	Blood	Molecular	Hanifah, 2013
Thailand	25	<i>R. tanezumii</i> , <i>R. andamanensis</i> , <i>B. indica</i> , <i>R. exulans</i> , <i>M. cookii</i> , <i>R. nitidus</i> , <i>B. bowersi</i> , <i>Rattus</i> spp., <i>B. berdmorei</i>	<i>O. tsutsugamushi</i>	Spleen, lungs, liver	Molecular	Elliott et al., 2021a

Thailand	5.5	<i>R. tanezumi</i> , <i>T. glis</i> , <i>B. berdmorei</i>	<i>O. tsutsugamushi</i> Karp, <i>O. tsutsugamushi</i> TA	Spleen, lungs, liver	Molecular	Linsuwanon et al., 2021a
Thailand	42.6	<i>R. tanezumi</i> , <i>R. bowersi</i> , <i>B. berdmorei</i> , <i>R. mackenziei</i> , <i>L. sabanus</i>	<i>O. tsutsugamushi</i>	Serum	Serology	
Thailand	71.1	<i>R. rattus</i> , <i>B. indica</i> , <i>R. exulans</i>	N/A	Blood	Serology	Rodkvamtook et al., 2018
Thailand	22.2	<i>R. rattus</i> , <i>R. exulans</i> , <i>B. savilei</i> , <i>Menetes berdmorei</i>	<i>O. tsutsugamushi</i> Karp, <i>O. tsutsugamushi</i> Gilliam	Spleen, liver	Molecular	
Thailand	2.3	<i>Rattus</i> sp. clade 3, <i>R. tanezumi</i> , <i>B. savilei</i> , <i>B. bowersi</i> , <i>L. edwardsi</i> , <i>R. exulans</i>	<i>O. tsutsugamushi</i>	Spleen	Molecular	Chaisiri et al., 2017
Thailand	18.3	<i>R. norvegicus</i> , <i>R. rattus</i> , <i>B. indica</i>	<i>O. tsutsugamushi</i>	Sera	Serology	Chareonviriyaphap et al. 2014
Thailand	42.0	Small mammals	<i>Orientia</i> spp.	N/A	Molecular, serology	Lerdthusnee et al., 2008
Indonesia	0 - 25	<i>R. tanezumi</i> , <i>R. tiomanicus</i> , <i>R. norvegicus</i> , <i>R. exulans</i> , <i>R. sabanus</i> , <i>R. whiteheadi</i> , <i>Maxomys</i> spp.	<i>O. tsutsugamushi</i>	Sera	Serology	Widjaja et al., 2016
Indonesia	2.6	<i>Maxomys</i> spp., <i>R. exulans</i> , <i>R. whiteheadi</i>	<i>O. tsutsugamushi</i>	Spleen, kidney	Molecular	
Indonesia	11.3	<i>R. norvegicus</i>	<i>O. tsutsugamushi</i>	N/A	Serology	Susanti et al., 2022
Indonesia	12.5	<i>Rattus</i> spp.	<i>O. tsutsugamushi</i>	Sera	Serology	Richards et al., 2002
Indonesia	5.1	<i>R. tiomanicus</i> , <i>R. rattus</i> , <i>C. glorioides</i>	<i>O. tsutsugamushi</i>	Blood	Serology	Richards et al., 1997
Philippines	12.5	<i>R. exulans</i> , <i>R. mindanensis</i> , <i>R. everetti</i>	<i>O. tsutsugamushi</i>	Spleen, kidney	Molecular	
Philippines	84.0	<i>R. rattus</i> , <i>R. everetti</i> , <i>R. panglima</i> , <i>R. exulans</i> , <i>R. mindanensis</i>	<i>O. tsutsugamushi</i>	Ocular sinuses, heart puncture	Serology	Van Peenen et al., 1977
Thailand	23.7	<i>R. norvegicus</i> , <i>R. exulans</i> , <i>M. mucusus</i> , <i>C. murina</i>	<i>R. typhi</i>	Sera	Serology	Chareonviriyaphap et al. 2014
Thailand	5.0	<i>R. norvegicus</i> , <i>R. rattus</i> , <i>R. exulans</i> , <i>M. musculus</i>	<i>R. typhi</i>	N/A	Serology	Siritantikorn et al., 2003
Indonesia	0 - 78	<i>R. tanezumi</i> , <i>R. norvegicus</i>	<i>R. typhi</i>	Sera	Serology	
Indonesia	2.6	<i>R. tanezumi</i>	<i>R. typhi</i>	Spleen, kidney	Molecular	Widjaja et al., 2016
Indonesia	14.7	<i>R. norvegicus</i> , <i>R. rattus</i> , <i>R. exulans</i>	<i>R. typhi</i> Wilmington	Sera	Serology	Ibrahim et al., 1999
Singapore	32.2	<i>R. norvegicus</i> , <i>R. rattus</i>	<i>R. typhi</i> Wilmington	Blood	Serology	Griffiths et al., 2022
Malaysia	13.7	<i>R. diardii</i> , <i>R. norvegicus</i>	<i>R. honei</i> , <i>R. conorii</i> , <i>R. raoultii</i>	Spleen, kidney, heart, liver	Molecular	Tay et al., 2014a
Thailand	66.2	<i>B. indica</i> , <i>R. argentiventer</i>	<i>R. honei</i> Wilmington, <i>R. japonica</i> YH	Sera	Serology	Okabayashi et al., 1996
Indonesia	9 – 73	<i>R. tanezumi</i> , <i>R. tiomanicus</i> , <i>R. norvegicus</i> , <i>R. exulans</i> , <i>R. sabanus</i> , <i>Maxomys</i> spp.	<i>R. rickettsii</i>	Sera	Serology	Widjaja et al., 2016
Indonesia	39.1	<i>R. norvegicus</i> , <i>R. exulans</i> , <i>R. rattus</i> , <i>R. tiomanicus</i>	<i>R. conorii</i> Moroccan	Sera	Serology	
Indonesia	40.0	<i>R. norvegicus</i> , <i>R. exulans</i> , <i>R. rattus</i> , <i>R. tiomanicus</i>	<i>R. honei</i>	Sera	Serology	Ibrahim et al., 1999
Philippines	12.2	<i>R. rattus</i>	<i>R. japonica</i>	Sera	Serology	Camer et al., 2000

Thailand (Siritantikorn et al., 2003; Chareonviriyaphap et al., 2014), highlighting a higher prevalence of *R. typhi* in *R. norvegicus* from urban vicinities. However, the overall molecular studies on the prevalence of *R. typhi* in rodents are limited. An attempt by Mohd-Azami et al. (2023) to detect *R. typhi* from rodents was unsuccessful and this was likely due to the difference in rodent habitats, since the authors sampled rodents away from urban areas.

Spotted fever rickettsiosis (SFR)

The spotted fever group of *Rickettsiae* (SFGR) includes at least 30 species globally, with 21 classified as pathogenic strains (Satjanadumrong et al., 2019). In SEA, the seroprevalence of SFR has been reported in most countries [reviewed in (Low et al., 2020b)]. However, most serological assays are based on antigens from SFGR species not endemic to this region, leaving the exact pathogens causing human infections largely unknown. Molecular assays have detected *Rickettsia felis*, *Rickettsia* sp. RF2125 or *Rickettsia assembonensis*, *Rickettsia raoultii*, *Rickettsia honei* TT-118, and *Rickettsia japonica* in humans (Jiang et al., 2005; Gaywee et al., 2007; Kho et al., 2016). Seroprevalence studies suggest a higher risk of SFR in upland forested areas compared to lowland urban areas, indicating frequent host-vector interactions in rural regions (Chaisiri et al., 2022). SFGR are primarily transmitted by the Ixodid ticks, which commonly infest rodents in forested or agricultural areas. For example, *Rickettsia* sp. closely related to *R. honei* was reported in *I. granulatus* collected from *R. rattus* across three provinces of Thailand (Kollars et al., 2001). In Malaysia, ticks like *Haemaphysalis* spp., *Dermacentor atrosignatus*, and *Amblyomma helvolum*, collected from rodents like *Maxomys rajah* and *L. sabanus*, harboured *Rickettsia* spp. closely related to *R. raoultii*, *Rickettsia heilongjiangensis*, and *Rickettsia* sp. RF2125 (Kho et al., 2019).

Domestic animals, including rodents, dogs, cattle, buffalo, cats, and ferret-badgers are potential carriers of SFGR (Singh et al., 2011; Kuo et al., 2017; Ishak et al., 2018; Ehlers et al., 2020; Khoo et al., 2021; Chaisiri et al., 2022; Hirunkanokpun et al., 2022). In Indonesia, serological studies revealed that *R. tanezumi*, *R. norvegicus*, *R. exulans*, *R. tiomanicus*, and *Maxomys* spp. were exposed to SFGR pathogens (Widjaja et al., 2016). Additionally, *R. honei* TT-118 and *R. japonica* were detected in *B. indica* and *R. argentiventer* from Thailand (Okabayashi et al., 1996). In the Philippines, 12.2% of rats captured in selected areas showed past exposures to SFGR based on IFA with *R. japonica* antigens (Camer et al., 2000) (Table 1). Ibrahim et al. (1999) found that 40% of rats from Indonesian ports and 39.1% of rats from inland areas had antibodies against *R. honei* TT-118 and *Rickettsia conorii*, respectively. In Malaysia, molecular studies identified SFGR related to *R. honei*, *R. conorii*, *R. raoultii*, and *Rickettsia* sp. TCM1 in wild rodents from markets in Kuala Lumpur and Penang (Tay et al., 2014a). In contrast, no rickettsial agents were found in rodents from rural areas in Johor and Perak, suggesting a lower risk in these regions (Mohd-Azami et al., 2023). Further molecular studies are required to detect SFGR agents circulating in Southeast Asian rodents, and assess their roles in pathogen transmission to humans and pathogen maintenance in tick vectors.

CONCLUSIONS

This review attempted to provide an overview of the available epidemiological data on significant rodent-borne diseases around SEA. First, there is a notable lack of comprehensive clinical surveillance data for several rodent-borne diseases in this region. Diseases such as bartonellosis and borreliosis remain understudied, despite the growing anecdotal evidence of their occurrence. Serological studies also indicate sporadic cases across SEA, but annual national records for many of these diseases are completely lacking. For instance, clinical records of hantavirus infections are outdated, with the most recent reports from over two decades ago, except for sporadic acute incidences reported in Indonesia. Thus, implementing multi-

centre screening studies in endemic regions where these diseases are prevalent, may improve the disease management across SEA. Furthermore, limited knowledge is available on the pathogenicity, competent reservoirs, and transmission routes of several endemic strains, such as *B. tamiae*, *B. chanthaburi* spp. nov., *B. satun* spp. nov., *Ca. B. thailandensis*, THAIV, SERV, and Jurong virus, detected in rodents from Thailand, Indonesia, and Singapore, respectively. Additionally, most surveillance studies in humans and rodents have relied on serological methods such as ELISA, MAT, and IFA, which may delay pathogen detection, especially when symptoms such as fever and myalgia are common. Serological detection is essential in determining past exposures and provides fundamental information on the infecting strains or serovars. However, many rodent-borne diseases manifest as AFI; hence, additional molecular methods are essential for differential diagnosis. Thus, combining both serological and molecular diagnosis is crucial for the timely and accurate detection of endemic rodent-borne diseases in SEA. Finally, a deeper understanding of the infectious agents causing rodent-borne diseases in SEA is essential in curbing the diseases. More research is warranted to identify rodent reservoirs, arthropod vectors, and their roles in maintaining and transmitting these diseases to humans. Experimental studies are deemed necessary to determine the competence of rodent reservoirs and their vectors in spreading diseases in SEA. Therefore, conducting such studies on pathogenic or novel endemic strains may widen our perspective on the particular disease ecology in SEA.

Conflict of interest disclosure statement

The authors declare that they have no known competing interests that could constitute a conflict of interest or to have influenced the work reported in this paper.

ACKNOWLEDGEMENTS

This study was supported in parts by the Ministry of Higher Education, Malaysia under the Higher Institution Centre of Excellence (HiCoE) program (Grant nos. MO002-2019 and TIDREC-2023), the Dana Langganan Sukuk Pakej Rangsangan Ekonomi Prihatin Rakyat (SUKUK PRIHATIN)—Fasa 2 (Grant no. MO002-2021), and the French National Research Institute for Sustainable Development (Grant nos. IF028-2022 and IF027-2022).

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