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Aedes aegypti and *Aedes albopictus* (Diptera: Culicidae) ecology, biology, behaviour, and implications on arbovirus transmission in Thailand: Review

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ABSTRACT

Aedes aegypti and *Aedes albopictus* (*Aedes*) transmit highly pathogenic viruses such as dengue, chikungunya, yellow fever, and Zika which can cause life-threatening diseases in humans. They are the most important vectors of arboviruses in Thailand. Their vectorial capacity (VC) is highly complex mainly due to the interplay between biotic and abiotic factors that vary in time and space. A literature survey was conducted to collate and discuss recent research regarding the influence of *Aedes* vector biology, behaviour, and ecology on arbovirus transmission in Thailand. The survey followed guidelines of preferred reporting items of systematic reviews and meta-analyses (PRISMA). All fields, keyword search was conducted in the Web of Science database for the period of 2000–2021. The search yielded 821 records on *Ae. aegypti* and 293 records on *Aedes albopictus,* of which 77 were selected for discussion. Genomic studies showed that there is a high genetic variation in *Aedes albopictus* whereas *Ae. aegypti* generally shows low genetic variation. Along with genetically unstable arboviruses, the interaction between *Aedes* and arboviruses is largely regulated by genomic events such as genetic mutations and immune response protein factors. Temperature and precipitation are the major climatic events driving arbovirus transmission. Human exposure risk factors are mainly due to multiple feeding patterns, including endophagy by *Aedes albopictus* and zoophagic behaviour of *Ae. aegypti* as well as diverse human-associated breeding sites. Integration of the One Health approach in control interventions is a priority with a rigorous focus on *Aedes*-arbovirus surveillance as a complementary strategy.

1. Introduction

Aedes aegypti (L.) and *Aedes albopictus* (Skuse) (Subgenus: *Stegomyia*; Diptera: Culicidae) are medically important vectors found in over 129 countries worldwide [1]. They are the two vital vectors of arboviruses in Thailand, transmitting three viruses of major public health concern and economic burden, *i.e.*, dengue virus (DENV), chikungunya virus (CHIKV) and Zika virus (ZIKV) [2].

Dengue remains the most important arbovirus disease in Thailand manifesting with symptoms of dengue fever, followed by the deadly dengue hemorrhagic fever and/or dengue shock syndrome. It is caused by an endemic RNA virus of four serotypes (DENV–1, DENV–2, DENV–3 and DENV–4) which are genetically and antigenically different, and can co-infect humans [3]. The first recognized outbreak of dengue in Thailand occurred in 1958 [5]. Although research on dengue and its vectors began in 1960s, with support from World Health Organization (WHO) collaborating with Thai Ministry of Public Health (MoPH) [4,5], irregular but pronounced annual dengue outbreaks have continuously been reported to-date [2]. Over the last two decades, the country's arbovirus disease burden has been exacerbated by the emergence and re-emergence of CHIKV in three separate outbreaks. The two chikungunya fever outbreaks of 2008–2009 and 2018–2019 infected some 32,000 and 15,000 people, respectively, mainly in the southern provinces [6] while cases from the 2013 outbreak in the north eastern region were still being reported in 2020 [7]. Meanwhile the cases of ZIKV were first reported in a retrospective study from 2012 to 2014, and by the end of 2017, the number cases had risen to 1612 [8,9]. However, it was reported to have been circulating since 2002, an indicator of a low but sustained circulation [10]. Serological surveillance is complicated by the asymptomatic cases especially DENV for which MoPH has observed that >80% do not

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show symptoms [11]. Robust entomological surveillance along with other control options, will be necessary to reducing the rising number of dengue and other arbovirus diseases.

The gaps in the surveillance of arboviruses in *Aedes*, particularly for dengue, have been previously identified. Questions such as what constitutes an acceptable level of dengue risk, what mosquito densities are necessary to achieve that goal, and what is the most effective method of measuring entomological risk [12], remain largely unanswered despite the growing threat of dengue and other arboviruses. One major limiting factor in *Aedes*-borne arbovirus surveillance is the low infection rates in *Aedes* vectors *versus* the expensive surveillance technologies such as reverse-transcription polymerase chain reaction (RT-PCR) and limited manpower. More frustratingly, entomological thresholds that precisely correlate with disease incidence have not been established [13]. These limitations underscore the importance of identifying places where mosquito-human contact occurs, and understanding of environment effects [12,14]. This will give timely and less costly intervention to prevent epidemics. Prerequisites to such surveillance studies include adequate understanding of vectorial capacity (VC) of the vector population. However, VC is affected by several factors such as mosquito population size, feeding habits, virus replication and dissemination within mosquitoes, mosquito lifespan, and other factors. It is described as the number of infectious bites produced by a population of mosquitoes that bite a single fully infectious person on a single day, and is expressed as:

$$\mathrm{VC} = ma^2bp^n/(-\log_e p)$$

where m = number of female mosquitoes per host, a = daily feeding rate, b = transmission rate among exposed mosquitoes, p = probability of daily survival and n = extrinsic incubation period (EIP: the time a mosquito being studied will take to transmit the virus after the first infectious bite). The transmission rate (b) can otherwise be referred to as vector competence (the ability of a given vector to acquire and subsequently transmit the pathogen), which links the often interchangeably used terminologies in the entomological arbovirus transmission complex [15]. Identifying those events that modulate the VC of *Aedes* vectors in the transmission complex is crucial in mitigating the transmission of *Aedes*-borne arboviruses.

While the influences of vector-to-virus interaction, vector-to-human exposure risk, and the vector-to-environment factors on arbovirus transmission have been studied on global and regional levels [16,17], the uniqueness of foci and localities in arbovirus outbreaks requires a fine scale analysis. Thailand being endemic to both *Aedes* vectors and home to all four serotypes (at least four genotypes each) of DENV, as well as different clades of CHIKV and ZIKV make this review timely not only locally but also in other places where *Aedes*-borne arboviruses are a burden. By adopting the One Health concept as a policy in 2013 [84], Thailand faced the challenge of tackling complex arbovirus transmission. One Health involves "a collaborative effort of multiple disciplines working locally, nationally, and globally to attain optimal health for people and animals, and a healthy environment" [107]. Evidence-based studies in arbovirus and vector surveillance are required for successful prevention and control strategies. Therefore, the objective of this review paper was to aggregate and discuss entomological factors that influence VC of *Ae. aegypti* and *Aedes albopictus* in Thailand. In this aspect, we explored the virus-to-vector interaction, vector-to-human exposure risk and vector-to-environment interaction factors. The goal is to determine whether these factors can serve as a benchmark for designing sustainable entomology-based strategies to control arbovirus transmission.

2. Materials and methods

The protocol followed guidelines of the preferred reporting items of systematic reviews and meta-analyses (PRISMA) guidelines [18]. "Only original article" publications were searched for in the Web of Knowledge database (Science Citation Index Expanded). Search was filtered to 'All fields', with a date range of 01/01/2000–31/12/2021, and used the key words "*Aedes aegypti* Thailand" and "*Aedes albopictus* Thailand" in two separate searches. The search was filtered to "All fields", which retrieves all records with the search terms not necessarily limited to the "Front page" (title, abstract or keywords) [19] but mentioned in materials and methods. The search yielded 821 records on *Ae. aegypti* and 293 records on *Aedes albopictus* were retrieved from the search. To understand the national statistics of diseases transmitted by these mosquitoes, information was sourced from the online database of the Department of Disease Control, MoPH, Thailand where countrywide disease cases are reported weekly. Backward citation as well as citation of key terminologies was done using Google Scholar, PubMed and Google. Three authors were involved in the screening and reviewing of the searched articles at different stages. The reviewers reached consensus on inclusion of articles and on other important resources to include such as reports, systematic reviews, short communications and mathematical models. A total of 77 eligible studies were selected for discussion (Fig. 1).

3. Results

3.1. Virus-to-vector interaction and arbovirus transmission

After the vector acquires an infectious blood meal, arboviruses must overcome several barriers in the mosquito to effect transmission [15]. These virus-to-vector interactions are governed by the individual biology of the infecting virus and the infected mosquito. They are endogenous events, mostly genetically driven, that involve virus genetic variation [20], vector genetic variation [21], endogenous elements [22] and vector microbiome.

3.1.1. Vector genetic variations

Genetic variation has been observed in *Ae. aegypti* [23–27] and *Aedes albopictus* [28–30] across different habitats and landscapes of Thailand. While *Ae. aegypti* populations generally show low genetic variation, *Aedes albopictus* exhibit a high occurrence of genetic polymorphism. This genetic variation affects genotype-by-genotype (G-x-G) interactions between the virus and *Aedes,* which modulates infection of the mosquito mid-gut and dissemination of the virus to other tissues [31]. For instance, Mousson et al. [32] reported that *Ae. aegypti* samples with significantly high polymorphism ($P < 0.05$) showed heterogeneous susceptibilities to DENV–2. In a marker-based genetic mapping study of *Ae. aegypti* from Kamphaeng Phet Province, Fansiri et al. [33] demonstrated that there were virus isolate-specific and serotype-specific interactions between DENV–1 and DENV–3, and mosquito genome. Moreover, phenotypic polymorphism associated with markers (16.5% to 22% variations by each marker), that showed different virus-vector interactions, affected virus dissemination from mid gut and final viremia quantities in the head [33]. A significant virus isolate-specific G-x-G interaction (likelihood ratio: $X^2 = 5.75$, d.f. = 1, $P = 0.0165$) was reported earlier the same year by Lambrechts et al. [34] who studied the specificity of resistance to DENV–1 by the *Ae. aegypti* antiviral gene *Dicer-2*. In the same study, a significant *Ae. aegypti* isofemale family-by-DENV–1 isolate interaction was reported with no significant G-x-G interaction (likelihood ratio: $X^2 = 2.29$, d.f. = 4, $P = 0.6825$) [34]. Detailed genotyping using RADseq reported that *Ae. aegypti* and DENV from Kamphaeng Phet Province showed significant genetic variations working together to overcome the virus-vector endogenous barriers [35].

On the other hand, endogenous protein factors may be produced in response to viral infection in the mid-gut [36] or salivary glands [37] or released in saliva during blood meal acquisition [38] which influence the binding of arboviruses to the mosquito cells. Surasombatpattana et al. [38] reported that saliva of *Ae. aegypti* possessed a prominent

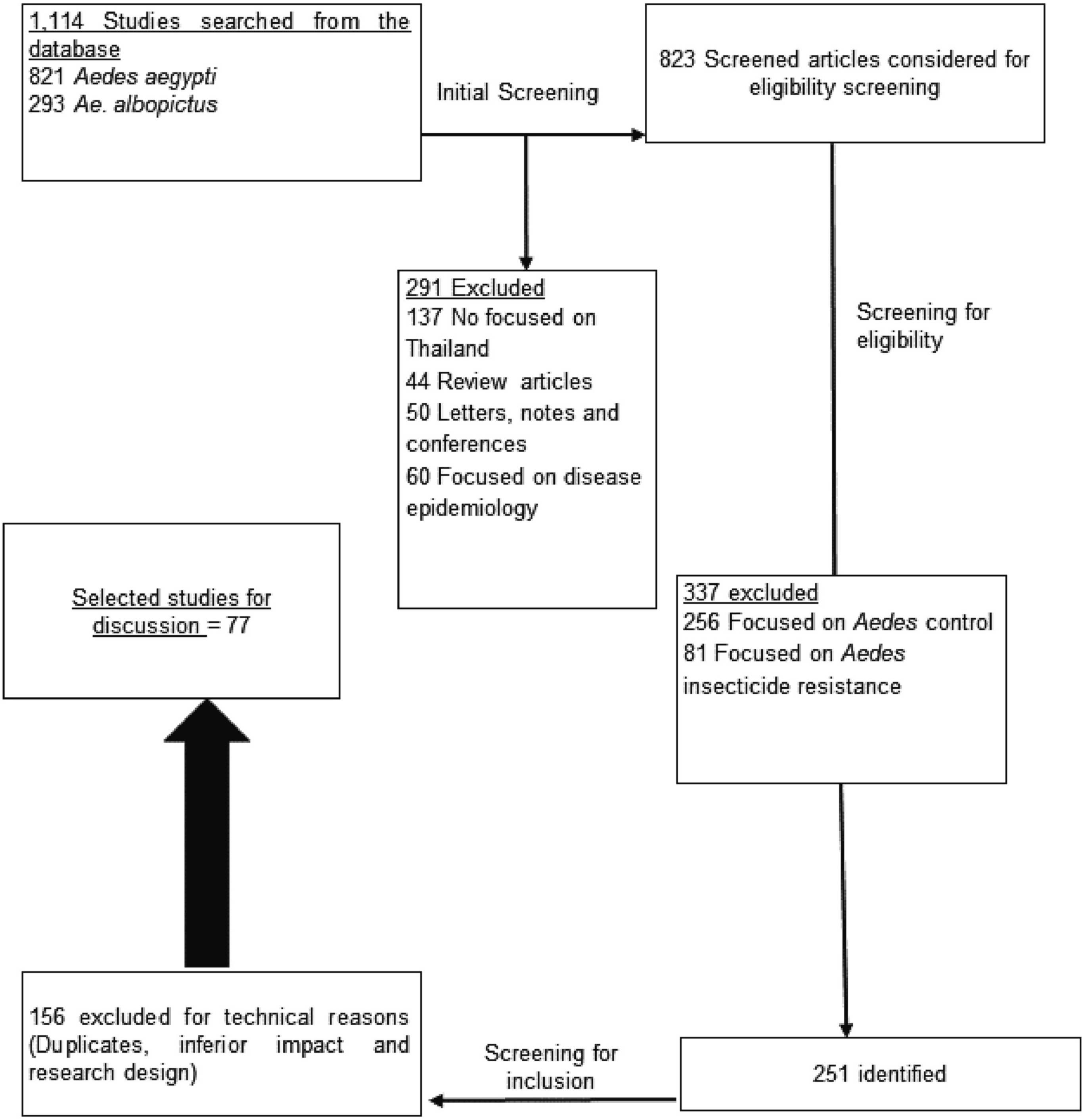

Fig. 1. Summary of literature survey showing the search criteria, included and excluded studies. The key words "*Aedes aegypti* Thailand" and "*Aedes albopictus* Thailand" were used in two separate searches within a search range of 01/01/2000–31/12/2021 (PRISMA 2021).

putative 34-kDa family secreting salivary protein that enhanced infection and multiplication of DENV in human keratinocytes. The mid-gut protein, 35 kDa prohibitin, was reported as a receptor of DENV–2 in *Ae. aegypti* cells [39]. Prohibitin has been targeted for *Ae. aegypti* control using *Bacillus thuringiensis* toxins such as Cry4B [40] which gives much hope in control of disease transmission. In a laboratory experiment, C3/36 cell line extracted from *Aedes albopictus* larvae and treated with an antibody of a 36/37-kDa high-affinity laminin receptor or soluble laminin were infected with the four serotypes of DENV. Only DENV–3 and –4 showed significant inhibition, which shows a facilitated internalization of the two serotypes [41]. In the same study, 50-kDa heparin sulfate was demonstrated to significantly contribute to the binding of DENV–1, and less of the other serotypes, to the mosquito cells [41]. Tudor-SN protein translated by C3/36 and Aag2 cell lines of *Aedes albopictus* and *Ae. aegypti*, respectively, enhanced replication of DENV–1 and DENV–3 in the gut of wild-type *Ae. aegypti* from Kamphaeng Phet Province in central Thailand [42]. Transcriptome analysis using RNAi-mediated gene knockdown confirmed that the sterol regulatory element-binding protein was a promoter of DENV–1 replication in the mid-gut of *Ae. aegypti* [43]. However, when the salivary glands of *Ae. aegypti* were infected with DENV–1, the production of anti-DENV peptides was observed [37]. A similar immune response was reported to be evaded by

Table 1
Arbovirus surveillance in *Ae. aegypti* and *Aedes albopictus* of Thailand detected using different methods within 2000–2021. The specimens were collected from various provinces.

Virus (Strain)	Location (Province)	Vector infection rate (%)	Species (n)	Detection method	Reference
CHIK (ECSA)	Uthai Thani	~26.9%	*Aedes albopictus*	RT-PCR	[94]
CHIKV (ECSA)	Chiang Rai (7.1%), Chiang Mai (5.4%), Nan (4.5%), Nong Khai (2.7%), Ubon Ratchathani (23.8%), Bangkok (15.7%), Nakhon Sawan (5.7%), Parachuap Khiri Khan (34.4%), Songkhla (2.6%), Krabi (3.7%)	*4.1%	*Ae. aegypti*	RT-PCR	[54]
CHIKV (IOC)	Bangkok	Males (10.71%) Females (39.29%)	*Ae. aegypti*	Nested-RT-PCR	[50]
CHIKV	Khon Khaen, Roi Et, Maha Sarakham and Kalasin	*2.9%	*Ae. aegypti*	Real-time qRT-PCR	[7]
CHIKV (IOC)	Rayong	3.8% (Females) 2.6% (Larvae)	*Ae. aegypti*	mrt-RT-PCR, hn-RT-PCR	[95]
CHIKV (IOC)	Songkla	16% 53%	*Ae. aegypti* *Aedes albopictus*	RT-PCR	[96]
DENV (1, 2, 3 and 4)	Nakhon Pathom (34.5%), Nonthaburi (75.5%), Ratchaburi (13.3%), Samut Sakhon (34.1%)	*37.4%	*Ae. aegypti*	RT-PCR	[70]
DENV	Khon Khaen, Roi Et, Maha Sarakham and Kalasin	*8.0%	*Ae. aegypti*	RT-PCR	[13]
DENV (1 and 4)	Kamphaeng Phet	2.8%	*Ae. aegypti*	RT-PCR	[96]
DENV	Chiangmai & Lampang	0%	*Ae. aegypti* (9825), *Aedes albopictus* (150)	NASBA	[97]
DENV	Kamphaeng Phet	0.8%	*Ae. aegypti*	RT-PCR	[98]
DENV	Ratchaburi	18.3% (by ELISA), 15% (by RT-PCR), and 28.9% (by IFA)	*Ae. aegypti*	ELISA, RT-PCR and IFA	[99]
DENV (1–4)	Ratchaburi	18.3%	*Ae. aegypti*	ELISA	[100]
DENV (2)	Si Sa Ket	0.52% (*Ae. aegypti*) 0% (*Aedes albopictus*)	*Ae. aegypti* (1583) *Aedes albopictus* (69)	RT-PCR	[101]
DENV (2, 3, and 4)	Phang-Nga, Surat Thani, Phuket, Krabi	*11.3% (Females), *4.7% (Males) 36.2%	*Ae. aegypti* (469) *Aedes albopictus* (58)	RT-PCR	[102]
DENV (1, 2 and 3)	Kamphaeng Phet	1.8%	*Ae. aegypti*	RT-PCR	[103]
DENV (1–4)	Bangkok	~42%	*Ae. aegypti*	RT-PCR, n-PCR	[104]
DENV (1–4)	Bangkok	43%	*Ae. aegypti*	RT-PCR, n-PCR	[105]
DENV (3)	Bangkok, Songkhla, Lop Buri, Nonthaburi		*Ae. aegypti*	n-PCR	[106]
ZIKV	Kamphaeng Phet	1.4%	*Ae. aegypti*	RT-PCR	[96]
ZIKV (Asian and American clades).	15 provinces	*2.24% (Females), *1.27% (Males) & *0.19% (Larvae)	*Ae. aegypti*	hn-RT-PCR	[55]
ZIKV (Asian clade)	Rayong	7.7% (Females), 2.56% (Males)	*Ae. aegypti* and *Ar. subalbatus*	hn-RT-PCR	[95]

* = Average infection rate from the provinces surveyed; ** = Average infection rate for both *Ae. aegypti* and *Aedes albopictus;* n = number of specimen that were tested. IOC = Indian Ocean clade.
RT-PCR = Reverse transcription polymerase chain reaction; hn-RT-PCR = heminested RT-PCR; n-PCR = nested PCR; mrt-RT-PCR = Multiplex real-time RT-PCR; qRT-PCR = quantitative RT-PCR, ELISA = Enzyme linked immunosorbent assay; IFA = Indirect Fluorescent Antibody Assay; NASBA = Nucleic acid sequence based amplification assay.

DENV–2 in *Ae. aegypti* through flavivirus nonstructural protein 1 (NS1) binding of a neutralizing protein mannose-binding lectin [22]. There is a demonstration of variation in the receptors of different serotypes of DENV and various protein factors influencing arbovirus transmission by *Aedes*. However, the major paradox lies in a clear understanding of virus-to-vector adaptation which largely depends on the genetically diverse arboviruses and the environment.

3.1.2. Arbovirus genetic variations

Thai *Aedes* mosquitoes transmit three arboviruses of major public health concern (Table 1). The two *Flaviviruses* (DENV and ZIKV; Family: Flaviviridae) encode three structural [Caspid (C), precursor membrane (prM) and envelope (E)] and three non-structural (NS1, NS2A, NS2B, NS3, NS4A, NS4B and NS5) proteins [44]. Chikungunya virus (CHIKV) is an *Alphavirus* in the family Togaviridae and encodes four non-structural proteins (nsP1–4) and six structural proteins–C, E3, E2, E1, 6 K and transframe (TF). Structural and non-structural proteins play special roles in modulating infection and dissemination of the virus in the vector. Phylogenetically, DENV, ZIKV and CHIKV are single-stranded positive-sense ribonucleic acid viruses with varying degrees of genetic variations.

Epidemiological studies have shown that Thailand is characteristic with serotype-specific DENV prevalence [45,46] which makes DENV genetic variations a very important consideration in arbovirus transmission and disease epidemics. At least four DENV genotypes, for each serotype, have been identified [44]. Pittaksajakul et al. [47] analysed amino acid and nucleotide sequences in the *E*-gene of DENV–2 from human and *Ae. aegypti* mosquitoes using Clustwal and Bioedit programs. The study confirmed the circulation of quasispecies, steady-state distribution of error copies, of a self-replicating DENV–2 in Bangkok. Mean nucleotide and amino acid sequence diversity was 1.52% and 0.53%, respectively. More interesting is that the nucleotide sequences of DENV–2 in humans and mosquitoes were different, which elaborates the complexity of genetic plasticity in dengue transmission and the burden for its diagnosis [47]. Such variation which may be in response to DENV infection consequently affects the interaction in different ways according to both the virus and the *Aedes* vector. A three-year study assessed the relationship of DENV infection between humans and *Ae. aegypti*. Genetic variation genotype one of DENV–1 and DENV–4, and cocirculation of the cosmopolitan and Asian one genotypes of DENV–2 were identified and resulted in 81% mismatch in serotypic infection [46]. Although, genetic variations were not implicated in variability of infection in the study, this can only be ruled out cautiously. Lambrechts et al. [48] assessed the potential of wild-type *Ae. aegypti*, from Kamphaeng Phet Province, to transmit DENV–1 isolates of different ages (isolated between 1985 and 2009). The study observed that there was a clade replacement that occurred in the mid-1990s—a new clade replaced the old clade—which enhanced mosquito transmission of the virus [48]. Fansiri et al. [49] showed that DENV–1 infection and dissemination in wild-type *Ae. aegypti* from Kamphaeng Phet was significantly clade-specific ($p < 0.0001$). However, with sympatric and allopatric pairings, adaptation of the virus to the local *Ae. aegypti* was not pronounced, which contradicts with the hypothesis of virus local adaptation [49].

CHIKV is genetically classified into three genotypes–East/Central/South African (ECSA), West African and Asian. Even though only the Indian Ocean clade and East/South African clade of the ECSA genotype have been reported in the recent outbreaks, they have crucial mutations that aid their adaptation to *Aedes* [50]. The naturally circulating ECSA in the three recent outbreaks was characterized by E1:A226V amino acid substitution that enhances virus infectivity, dissemination, and transmission by *Aedes albopictus* [51]. This mutation was reported in the two outbreaks of 2008–2009 and 2013 [52]. The E1: K211E and E2: V264A residue changes that enhances fitness for virus transmission by *Ae. aegypti* [53] were reported from the 2018 outbreak in Bangkok. Recently, complete genome analysis revealed nsP3-N495S, capsid-K73R, E1:K211E, E2:V264A and E1:K245R amino acid mutations in CHIKV (ECSA: Indian ocean clade) isolated from wild-type *Ae. aegypti* [50]. In contrast, E1:A226V mutation, which negatively affects CHIKV inefectivity and dissemination in *Ae. aegypti* was reported occuring together with E1: K211E in samples where *Aedes albopictus* was not infected [54]. Such co-occurrences require detailed molecular studies that reveal if potential antagonisms or synergisms exist in the fast evolving CHIKV.

The re-emerging ZIKV identified in the recent outbreaks was clustered into the Asian and American clades. ZIKV isolates from *Ae. aegypti* and other mosquitoes, but not *Aedes albopictus*, from 15 provinces across Thailand, showed genetic variations of 1–6% between the two clades [55]. However, their influence in ZIKV adaptation to *Aedes* mosquitoes has been understudied and our survey did not find any relevant publications. Elsewhere, isoleucine-to-valine mutation (I39V) in the NS2B proteins enhanced ZIKV infectivity in *Ae. aegypti* [56].

In a nutshell, genetic plasticity shows pronounced effects on virus-to-vector interactions. Arbovirus-*Aedes* interaction evolution studies are crucial to the development of sustainable and tailored disease control measures, for example, in vaccine development where RNAi pathways have been targeted [57]. Consequently, achieving success will require North-South and sustained collaborations among different experts such as vaccinologists, entomologists, molecular biologists, geneticists, and medical epidemiologists. Given that One Health vaccinology requires evidence-based vaccine studies, the identification and characterization of novel salivary proteins from distinct mosquito species will advance the development of safe mosquito saliva-based vaccines.

3.1.3. Insect-specific viruses

In the past two decades, there has been growing research interest in insect-specific viruses (ISVs)—viruses that are able to infect mosquitoes and replicate in mosquito cells but do not infect and/or replicate in humans and other vertebrates [58]. Thailand is home to a number of ISV families circulating naturally in mosquitoes. Densoviruses with notable genetic variations have been isolated from both *Ae. aegypti* and *Aedes albopictus* [59–61]. *Aedes* densovirus was demonstrated to modulate progressive survival, an important factor of vectorial capacity, of *Ae. aegypti* from 15% to 58% until fourth generation under laboratory conditions [62]. In a multi-country study, over 20 ISVs were sequenced from wild-type *Ae. aegypti* from Bangkok and Cairns, Australia. Phasi Charoen-like virus (PCLV) [Family: Phenuviridae; Genus: Phasivirus], Cell-fusing agent virus (CFAV) [Family: Flaviviridae; genus: Flavivirus], and Humaita-Tubiacanga (Unclassified) were dominant [63]. Baidaliuk et al. [64] demonstrated that a naturally circulating strain of CFAV inhibited DENV-1 and ZIKV replication *in vitro* (in *Aedes albopictus* C6/36 cell line), and interfered with virus dissemination and viremia quantities *in vivo* (in *Ae. aegypti*). Elsewhere, CFAV and PCLV were reported to induce a 90% reduction of DENV and ZIKV infection in *Aedes albopictus* and *Ae. aegypti* cell lines [65]. As it is for arboviruses, there is a selective compatibility of ISVs in *Aedes* which may be due to genetic influence or crucially, the environment. To this extent, a research gap exists as it does with intra-interactions between ISVs, arbovirus and the *Aedes* vectors.

3.2. Vector-to-human exposure risks and arbovirus transmission

3.2.1. Biting patterns of Aedes mosquitoes

The vectorial capacity of *Aedes* mosquitoes relies on their ability to successfully acquire an infectious blood meal. Multiple blood feeding supports their survival and reproduction through stimulation of multiple physiological activities such as oogenesis, immunity and cell regeneration in the mid-gut [66], and acquisition of infectious viremia [67]. Biting frequencies of up to nine times by *Ae. aegypti* in some hosts have been reported in Mae Sot district, Tak Province. The authors estimated that 43–46% of engorged mosquitoes bit more than one person. The study also found out that people aged 25 years and below were less bitten than those older. Interestingly, most blood meals were from people who transiently passed through the area. This could be the reason why no biting differences were observed between low and high dengue season [66]. In Ko Samui Island, Surat Thanee Province, southern Thailand, the indoor and outdoor biting rate was 1.5 to 8.1 and 5–78 mosquitoes/man-hour, respectively. The indoor biting activity was mostly (and nearly uniform) by *Ae. aegypti* (75.4%; and 24.6% by *Aedes albopictus*) whereas the outdoor biting was almost exclusively (and heterogeneous by season) due to *Aedes albopictus* (99%) [68]. Although this was expected, a 24.6% endophagy of *Aedes albopictus* is an indicator of evolving change from exophapic feeding hence an increased risk of exposure to bites in humans who stay indoors such as children and the elderly. In tandem with biting frequency, is the peak biting time. The peak biting time of *Aedes albopictus* was reported to vary between rubber plantations and orchards [69]. Longer biting hours (6:00 to 11:00 h) were observed in rubber plantation compared to orchards (6:00–8:00 h). A sizeable land area in southern and eastern Thailand is under rubber plantation where local and immigrant workers—characterized with high inter-provincial mobility—are employed, hence, a higher risk of arbovirus transmission. Chompoosri et al. [70] reported that the peak biting activity to *Ae. aegypti* from Bang Bua Thong District, Nonthaburi Province, was between 14:00–15:00 h during the summer season, and 8:00–11:00 h during the rainy and winter seasons. The researchers also reported that summer seasons had the longest biting activity which started from 6:00 to 20:00 h [70]. Data collected during the rainy season (July 1996), in the study of Ko Samui island showed similar results with peak biting time of 8:00–12:00 h during July (rainy season).

Aedes-borne arboviruses in Thailand are transmitted through two main epidemiological cycles, that is, sylvatic (*Aedes*–non-human primates (NHP)/wild vertebrates) and urban (*Aedes*–human and/or domestic vertebrates) [71]. Three urban/rural study sites from which 20.5% of captive monkeys ($n = 38$) were tested reported dengue seropositivity and outbreaks of 8968 cases during 2008–2009 in north western Thailand [108]. Two studies showed that both *Aedes* vectors feed preferably on humans (70–99%) but supplement their feeding needs with blood from domestic and non-domestic bovines, pets, monkeys, chicken and rats [72,73]. The sylvatic cycle involving NHPs and domestic vertebrates suggests potential enzootic transmission in nature and spillover to humans may be inescapable. The above results indicate that in the science of health and disease, the difference between humans and animals should not be considered. Collaborative efforts different disciplines, particularly, veterinary, medicine and entomology are required. It is necessary that developing a One Health arbovirus vaccine (for animals and humans) is made a priority or at least be considered.

3.2.2. Breeding sites

Females of *Aedes* oviposit in domestic as well as natural water-holding containers and spread their eggs over two or more sites in a practice known as “skip oviposition”. Container capacity, utility, water temperature, source of water, spectral reflectance from water surfaces and container location influenced *Aedes* vectors distribution across potential larval development sites [74–76]. In Samut Prakan Province, central Thailand, Waewwab et al. [74] reported that the water chemical properties, particularly pH, had a significant effect on the presence of *Aedes* immatures. Socio-economic factors affect container characteristics and distribution as well as land use patterns. Low level of education, overcrowded households, poor households, unemployed-, student- and retired-headed households, households living in two-floor houses, lack of window screens on houses, and poor knowledge of climate and dengue were reportedly associated with significantly high abundance of *Ae. aegypti* in northeastern Thailand [13,77,78]. Land use influences the expansion of *Aedes* across different landscapes including urban, suburban, rural, forests and agricultural areas. Thai people are now at a risk of being bitten by both *Aedes* irrespective of which geographical landscape one is at [77,79–81]. Container attributes, human activities and social structure demonstrate how much risk there is in exposing humans to arboviruses through mosquito bites. The number of mosquitoes per person is an essential element of vectorial capacity.

However, the most pressing issue is associating the vector exposure risks to disease incidence. In a cohort study of 1811 students from 10 schools in rural, semi-rural and semi-urban Kampahaeng Phet Province, dengue infections were positively correlated to breeding sites and *Ae. aegypti* abundance [82]. Whereas a three-year study in northern region showed that land use was positively correlated to dengue transmission by modulating human exposure to bites of infected vectors. The researchers predicted that increase of orchards (breeding sites of *Aedes albopictus*) lead to an increase of dengue transmission by *Aedes albopictus* [81]. However, in hospital-based case-control study in north eastern Thailand, container index was negatively associated with DENV incidence [13]. Similary, in a three-year comprehensive study that involved collection of *Aedes* immatures in about one million households from >900 districts did not find clear correlation between house index and dengue hemorrhagic fever incidence [83]. In summary, the correlation between vector indices and disease incidence remains elusive. Vector control interventions that allow interaction of factors such as socio-economics, landscape, knowledge, attitudes and practices have the potential for optimizing vector control strategies, future mosquito suppression, prediction and prevention of epidemics. However, such multidisciplinary factors require multisectoral approach involving the government, community and other stakeholders.

3.3. Climate and arbovirus transmission

Thailand is a tropical country with a tropical climate–a conducive habitat to many tropical pests and diseases. Campbell et al. [84] profiled weather dynamics and dengue transmission cycles over a period of 18 years in 76 provinces of Thailand. Eighty percent of 1.2 million severe dengue cases had occurred at a mean temperature of 27–29.5 °C and mean humidity >75%. These results imply that there is a very high sensitivity of dengue dynamics to specific yet small variations in weather conditions [84]. There are field and laboratory studies that have reported a relationship between weather factors and vectorial capacity elements of *Aedes* mosquitoes [85–87]. Under laboratory conditions, it was observed that a large diurnal temperature range (DTR) of 20 °C decreased the probability of mid-gut infection by DENV–1 and DENV–2, and survival, of *Ae. aegypti* which may have reduced virus extrinsic incubation period [70,88,89]. In addition, serotyping and detection assays of *Ae. aegypti* collected between March 2007 and February 2008 from Nakhon Pathom, Nonthaburi, Ratchaburi and Samut Sakhon provinces showed that mosquitoes were significantly infected with DENV, and presented the highest biting activity during the summer season compared to winter or rainy seasons. These findings were analogous to another reported influence of hot temperature (34 °C) on *Ae. aegypti* outbreaks in Chachoengsao Province where the authors predicted that there was a reduction in larval survival ability [90,91]. In Tak Province more engorged females were sampled during the rainy season (78%) than the dry season [92]. Overall, *Aedes* vectors are abundant during the rainy season, obviously due to available moisture for oviposition and egg hatching, and perhaps due to the ability of their immatures to withstand flushing effects of rainfall. But most importantly is the fact that temperature is the primary weather element influencing VC elements by reducing the EIP as well as survival. In some areas temperature varies just slightly between rainy and summer seasons. Therefore, the link between DTR, temperature and *Aedes* vectorial capacity is important. The influence of climate change across different spheres of life is fast approaching. Entomological studies that evaluate the impact of climatic factors on the VC of *Aedes* under natural realities are necessary.

4. Conclusions and summary

This review highlights the interconnectedness of genetic variations, insect specific viruses, feeding patterns, breeding sites and climate in influencing *Aedes* vectorial capacity. With improved tools, it is imperative that virus surveillance in *Aedes* vectors takes centre stage in the planning of control programs. Community education and government intervention needs strengthening, continuously, especially on container management in order to interfere with both the growth fitness and survival of *Aedes* as well as avoiding contact with adult biting females. Perhaps formulation of by-laws that foster social behavioural change such as water storage behaviour and extension of piped water to homesteads will improve people’s attitudes towards arbovirus diseases. Thus, a transdisciplinary approach, with a One Health focus aimed at integrating different fields of knowledge, will improve the understanding of the important social, educational, vector and agro-environmental obstacles faced by control services, especially in the complex urban and rural areas of Thailand. The dialogue with other forms of knowledge will allow the definition of more viable strategies according to different political, social, environmental, and wildlife realities.

- Low genetic variation in *Aedes aegypti* in Thailand conform with global estimates but the same cannot be said for *Aedes albopictus* that generally shows high genetic variation. Despite this, lack of standard uniformity in the sampling methods and genetic markers used by different researchers make it hard to make concrete conclusions.
- The relationship between arbovirus incidence and vector abundance remains elusive overall. Fine scale surveillance studies show positive, but weak, correlation between disease and vector abundance. The present review agrees with existing literature that criticizes the reliance on *Aedes* indices in predicting arbovirus outbreaks [14]. Referring to the sharp decline in the dengue (>150%) cases during the COVID-19 pandemic [93], without a significant decline in vector indices emphasizes these criticisms further.
- The exposure of Thai people to mosquito bites is an interplay among several factors such as mosquito feeding patterns, breeding sites, socioeconomic factors, human movements and climate in a complex manner. These are events that change over time and space.

Author summary

- The compatibility of *Aedes* mosquitoes with DENV and CHIK is strongly influenced by genotype-to-genotype interaction.
- *Aedes albopictus* shows high genetic polymorphism whereas *Ae. aegypti* exhibits low genetic variation.
- Temperature and precipitation are the most pronounced climatic factors.
- *Aedes aegypti* is adapting to zoophagic feeding while *Aedes albopictus* is becoming endophagic.
- Association of vector abundance with arbovirus disease epidemics remains a puzzle to solve.
- *Aedes aegypti* exhibits a stronger feeding activity during hot season while *Aedes albopictus* is an all-round biter.

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Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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