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Temperature and transmission of chikungunya, dengue, and Zika viruses: A systematic review of experimental studies on *Aedes aegypti* and *Aedes albopictus*

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ABSTRACT

Mosquito-borne viruses are leading causes of morbidity and mortality in many parts of the world. In recent years, modelling studies have shown that climate change strongly influences vector-borne disease transmission, particularly rising temperatures. As a result, the risk of epidemics has increased, posing a significant public health risk. This review aims to summarize all published laboratory experimental studies carried out over the years to determine the impact of temperature on the transmission of arboviruses by the mosquito vector. Given their high public health importance, we focus on dengue, chikungunya, and Zika viruses, which are transmitted by the mosquitoes *Aedes aegypti* and *Aedes albopictus*. Following PRISMA guidelines, 34 papers were included in this systematic review. Most studies found that increasing temperatures result in higher rates of infection, dissemination, and transmission of these viruses in mosquitoes, although several studies had differing findings. Overall, the studies reviewed here suggest that rising temperatures due to climate change would alter the vector competence of mosquitoes to increase epidemic risk, but that some critical research gaps remain.

1. Introduction

Arthropod-borne viruses (arboviruses) such as dengue virus (DENV), Zika virus (ZIKV), and chikungunya virus (CHIKV) have caused numerous epidemics in several regions of the globe. DENV is the most important mosquito-borne virus, infecting an estimated 390 million people per year with a total of 40 million symptomatic infections (Bhatt et al., 2013; Shepard et al., 2016). An individual infected with DENV may either be asymptomatic or develop symptoms such as fever, muscle aches, and headaches lasting up to three weeks (Harapan et al., 2020). A vast range of symptoms can be reported, from asymptomatic infection to mild febrile illness through to severe dengue, where the infected person can develop multiple haemorrhages sometimes leading to fatality (Gubler, 1998; Kularatne and Dalugama, 2022). DENV is widespread in tropical and subtropical areas, with most outbreaks and epidemics occurring in South America, Southeast Asia, and the Western Pacific Region (Bhatt et al., 2013; Guo et al., 2017).

ZIKV had caused sporadic cases in several locations prior to 2007, when the first large outbreak occurred, in Micronesia (Duffy et al., 2009). ZIKV re-emerged in 2013 and rapidly spread throughout the New World in 2015 (Depoux et al., 2018). Following this epidemic, ZIKV was declared a Public Health Emergency by the World Health Organization (Weaver et al., 2016). Several thousands of cases of congenital Zika syndrome with microcephaly and Guillain-Barré syndrome were reported in 2015, as well as other neurological complications associated with ZIKV infection (Cao-Lormeau et al., 2016).

Multiple outbreaks of CHIKV were reported in Asia during the 1950s and 1970s, and then CHIKV re-emerged in the 2000s in Africa and

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spread to the islands of the Indian Ocean (Burt et al., 2012). The last recent outbreaks of CHIKV occurred in 2014 and 2017 in Europe, including in France and Italy (Silva and Dermody, 2017; Vairo et al., 2019). There are numerous symptoms associated with CHIKV, including fever, headache, myalgia, rash, and polyarthralgia. In some cases, the symptoms can persist for months after infection (Manimunda et al., 2010; Burt et al., 2012). There are no effective treatments for these diseases (Pielnaa et al., 2020; Huang et al., 2021). However, two vaccines against DENV are currently marketed: Dengvaxia developed by Sanofi Pasteur with limited effectiveness and use - only people who have already had dengue fever are eligible for vaccination (Huang et al., 2021; WHO, 2019); and the recently licensed Qdenga developed by Takeda (Thomas and Yoon, 2019; Rivera et al., 2022).

CHIKV, DENV and ZIKV are transmitted by mosquitoes of the genus *Aedes*, mainly *Aedes aegypti* and *Aedes albopictus*. Historically, *Ae. aegypti* was geographically restricted to the African continent but is now widespread in all tropical and subtropical regions and is considered to be the major vector of DENV (Paupy et al., 2009; Lwande et al., 2020). While *Ae. albopictus* was mainly found in Southeast Asia, this species has been expanding in geographical range for several years, in tropical to subtropical regions and temperate areas, invading new areas and causing major epidemics of arboviruses (Kraemer et al., 2019).

Climate change is an important global issue of recent years, impacting all aspects of human life, including health. Vector-borne diseases (e.g. arboviral diseases, malaria) may be particularly impacted by climate change (Semenza et al., 2022; Wu and Huang, 2022), exacerbating their already considerable global health burden (Franklinos et al., 2019; Huang et al., 2019). This concern has led to significant research efforts investigating the impact of climate change, and rising average temperatures, on vector-borne disease circulation. Climate change is altering the distribution of vectors and, in turn, the pathogens they transmit. It has been shown that *Ae. aegypti* and *Ae. albopictus* distribution may expand in some world regions in the long-term horizon under temperature increases in response to climate change. The geographical distributions of *Ae. aegypti* and *Ae. albopictus* are expanding, exposing more people to the viruses they transmit (Paupy et al., 2009; Weaver et al., 2016; Kraemer et al., 2019). Africa, South America, Asia, and the Pacific are areas frequently affected by arbovirus epidemics, making it a necessity to anticipate future risks to public health (Tjaden et al., 2017; Caminade et al., 2019; Franklinos et al., 2019; Huang et al., 2019; Harapan et al., 2020; Semenza et al., 2022; Wu and Huang, 2022).

Most studies have used epidemiological and climate data to demonstrate a link between climate and vector-borne diseases (Tjaden et al., 2017) in order to predict disease incidence based on climate projections for future years, along with projections of future epidemic risks (Kraemer et al., 2015; Tjaden et al., 2017; Caminade et al., 2019; Messina et al., 2019). Other studies aimed to show how climate parameters affect the vector and the viruses it transmits. Hopp and Foley (2003) developed a numerical mosquito model to simulate the response of *Ae. aegypti* to observed climatic variations and how the modelled vector population is related to dengue cases. Other modelling studies predict an intensification in the future circulation of arboviruses (Mordecai et al., 2017; Tjaden et al., 2017; Colón-González et al., 2021; Ochida et al., 2022). However, several important gaps limit our ability to understand the effect of temperature on mosquito-borne disease. Studies so far have described an increase in the transmission of the virus by mosquito vectors due to increased temperatures (Parham et al., 2015; Rocklöv and Dubrow, 2020; Semenza et al., 2022), but empirical data are scarce, thus impacting the quality of the modelling studies. In fact, most modelling studies demonstrate that the impact of rising temperature increases the epidemic risks, e.g. epidemics of DENV in the Pacific Islands (Teurlai et al., 2015; Ochida et al., 2022), but do not describe how rising temperatures affect virus transmission by mosquitoes. In this review, we aim to synthesize scientific knowledge regarding the role of temperature in arbovirus transmission by the mosquito vector at a mechanistic level. To address this, we focused on literature using experimental studies to analyze how temperature impacts the transmission of CHIKV, DENV and ZIKV by *Ae. aegypti* and *Ae. albopictus*.

2. Materials and methods

Our study follows the recommendations of the Preferred Reporting Items for Systematic Review and Meta-analysis (PRISMA) guideline and statement of 2020 for reporting systematic reviews (Page et al., 2021) (Supplementary file S1: PRISMA checklist).

2.1. Search strategy

An exhaustive search of the literature was conducted using two databases: PubMed (https://pubmed.ncbi.nlm.nih.gov/) and Web of Science (https://www.webofscience.com/wos/woscc/basic-search), with records imported into EndNote™ 20. The following terms were selected to optimize the search: [(Chikungunya) OR (Zika) OR (Dengue)] AND [(*Aedes albopictus*) OR (*Aedes aegypti*)] AND [(Temperature)]. The abstracts of all the articles obtained contain at least one of these terms. We did not limit the publication period but stopped the search on December 31, 2022.

2.2. Study selection

The selection was conducted by first screening titles and abstracts to confirm the eligibility of the work. From the sorted abstracts, a second person checked the selection of articles. Then, the full text of selected articles was read to ensure that the articles complied with the eligibility criteria.

2.3. Eligibility criteria

Articles had to meet four eligibility criteria for inclusion. For criterion one, studies must include either a laboratory or an experimental component as part of the study, otherwise, the article was excluded. To meet the second and third criteria, all selected articles must at least deal with one of the three viruses (CHIKV, DENV, ZIKV) and one of the two vectors (*Ae. albopictus*, *Ae. aegypti*), respectively. Finally, the work must include the exposure of virus-infected mosquitoes to different ambient temperatures. If an article did not meet these four criteria, then it was not included in our review. We excluded all studies modelling the effect of climate change or meteorological parameters on arboviruses and arboviruses incidence and studies focusing only on the impact of meteorological parameters on arboviruses incidence.

2.4. Data extraction and analysis

Study characteristics were extracted from the eligible studies into a database. For each article, the following information was recorded: the mosquito vector species, the virus tested and its genotype, the infectious titer of the blood meal, larval rearing temperature, and adult rearing temperature post-infection (Supplementary Table S1). The results of each study, such as infection rates, dissemination rates, transmission rates, and transmission efficiency, are provided in Supplementary Tables S2–S6. Infection rate (IR) corresponds to the proportion of mosquitoes with virus-positive bodies among analyzed mosquitoes. Dissemination rate (DR) refers to the proportion of mosquitoes with virus-positive legs and heads among infected mosquitoes. Transmission rate (TR) is defined as the proportion of mosquitoes with virus-positive saliva among mosquitoes with disseminated infection. Transmission efficiency (TE) refers to the proportion of mosquitoes with virus-positive saliva among the total of blood-fed mosquitoes (Richards et al., 2007, 2012; Anderson et al., 2010; Chouin-Carneiro et al., 2020).

3. Results

3.1. Identification of studies

With the previously mentioned terms defined in the strategy, we obtained 821 and 3410 articles from the PubMed, Web of Science Core Collection and Web of Science SCI databases, respectively. By applying our eligibility criteria, we were able to eliminate 182 articles out of the 229 pre-selected. Among the 44 eligible articles, 10 were further excluded, because one study was on modelling, two studies did not apply different temperatures on infected mosquitoes, one was a review, and the content of the others was not relevant. After the removal of duplicates, screening, and application of the eligibility criteria, a total of 34 articles were included for analysis (Fig. 1).

3.2. Characteristics of included studies

The final selection included 34 articles meeting all of the eligibility criteria (Supplementary Table S1). These studies were carried out with the aim of anticipating the risk of climate change, particularly changing temperatures, on the capacity for transmission of arboviruses by *Ae. aegypti* and *Ae. albopictus*. To carry out a thorough analysis of the effects of temperature on the transmission of the three viruses of interest, the included articles had to compare at least two different temperature regimes for virus-infected mosquitoes. Most studies applied 28 °C as the reference temperature. Most of the included studies placed infected mosquitoes at constant temperatures; however, we also included studies that placed vectors under fluctuating temperature regimes. The number of articles where mosquitoes were kept at temperatures above or below 28 °C, fluctuating temperature regimes included, are shown in Fig. 2A. These different temperatures were applied to two vectors *Ae. aegypti* and *Ae. albopictus* (Fig. 2B) infected with either CHIKV, DENV, or ZIKV (Fig. 2C). As shown in Fig. 2, most studies have been conducted on *Ae. aegypti* using DENV.

3.3. Impact of temperature on viral transmission

Following the inclusion of the 34 articles corresponding to the four criteria, most of the studies (n = 26) demonstrated that higher temperatures have an impact on the infection, dissemination, or transmission rates of the three viruses (Fig. 3, Table 1). Of these 26 articles, 3 articles were based on studies placing infected vectors under fluctuating temperatures. Two studies showed that high temperatures decrease the vectorial competence of both vectors for CHIKV and ZIKV. Three papers showed no difference in the infection, dissemination, and transmission rates of the three viruses in mosquitoes placed at low or high temperatures. Finally, three studies attempted to analyze virus transmission in mosquitoes exposed to different temperatures during the larval stages (Table 1). Below, we discuss the studies in these categories of impact in greater detail.

3.4. Viral transmission increases at higher temperatures

McLean et al. (1974) followed by Watts et al. (1987), carried out perhaps the earliest studies to explore the effect of elevated temperatures on DENV transmission, demonstrating that high temperatures increase the transmission potential of mosquito vectors. As climate change has increasingly become recognized as a major threat for infectious disease resurgence, additional studies on how temperature influences arbovirus transmission have been performed over the last few decades. Most studies tend to show that increased temperatures raise the potential DENV transmission by vectors (Table 1, Supplementary Table S2).

A total of 11 articles showed that high temperature promotes the transmission of DENV. Lourenco-de-Oliveira et al. (2013) compared the transmission of DENV in *Ae. aegypti* mosquito populations from a subtropical region of Argentina (Corrientes), and temperate regions of Uruguay (Salto) and Argentina (Buenos Aires). These authors demonstrated that DENV in mosquito populations from subtropical regions in Argentina and Uruguay exhibited a higher transmission rate than in populations from a temperate region (Buenos Aires) (rates on day 21: 21.7% for mosquitoes from Salto *vs* 34.8% for mosquitoes from Corrientes *vs* 8% for mosquitoes from Buenos Aires). After this observation,

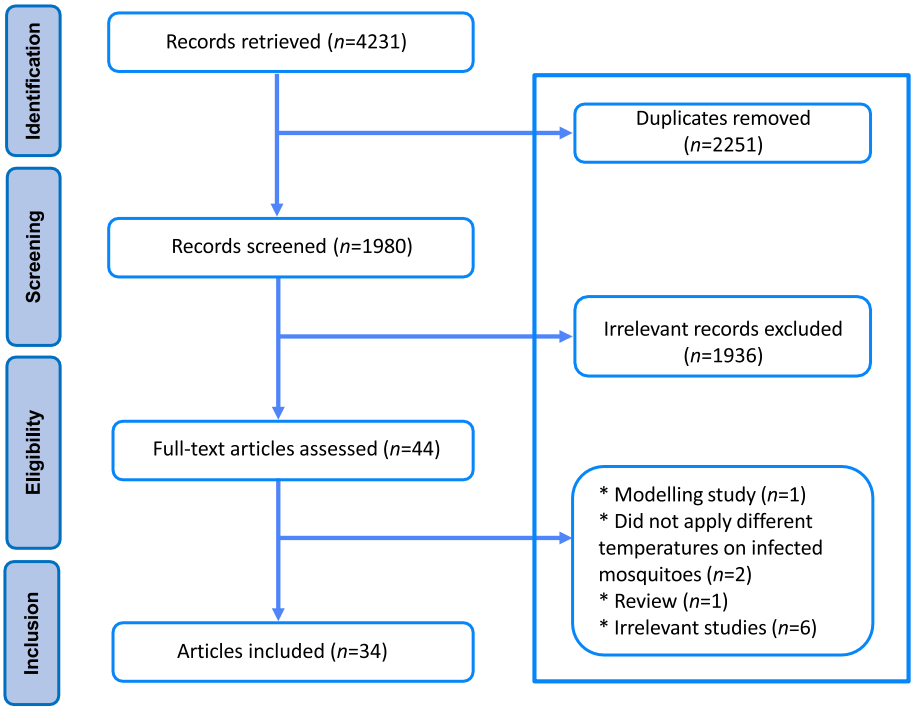

Fig. 1. PRISMA flow diagram for the article selection process.

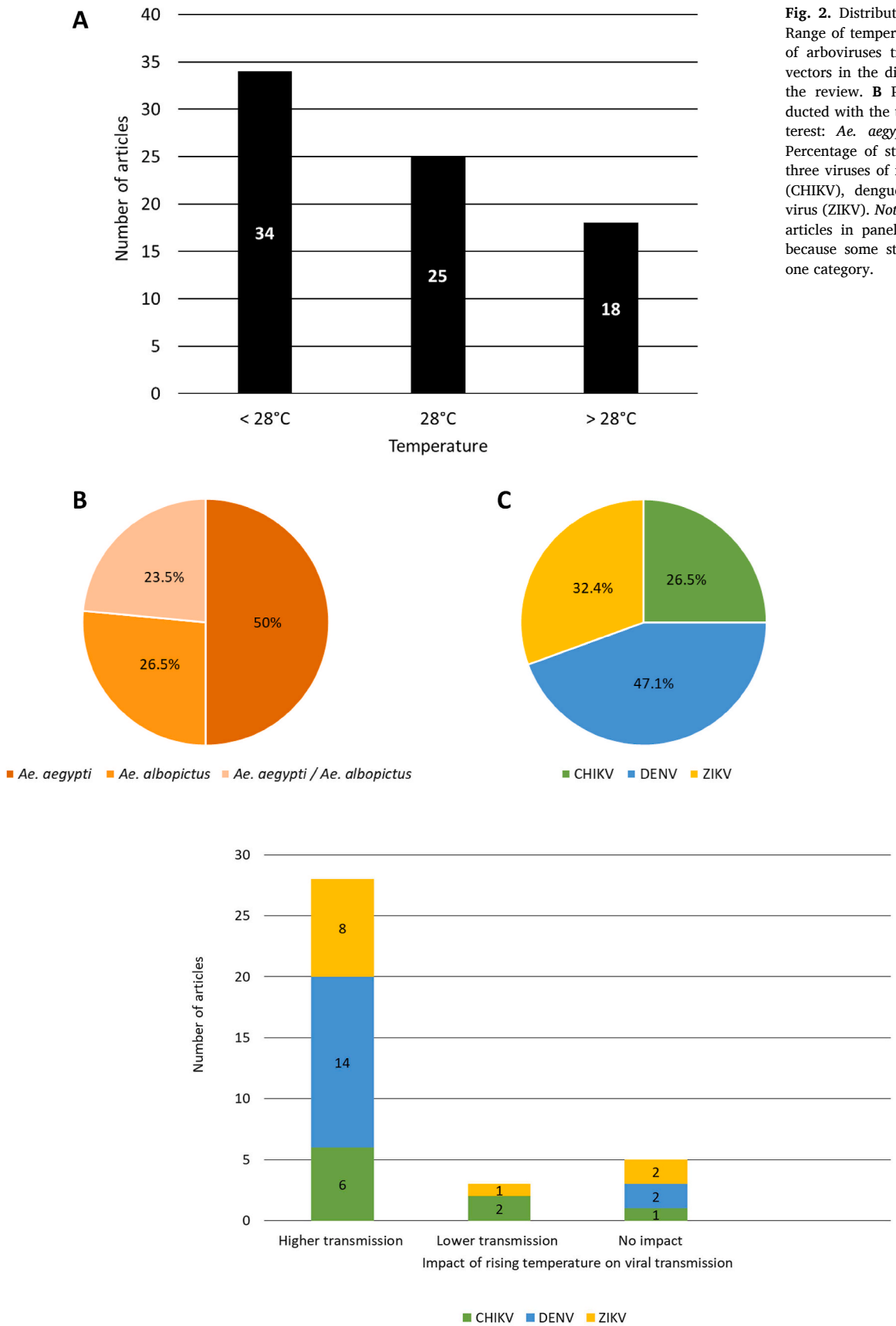

Fig. 2. Distribution of included articles. **A** Range of temperatures applied to the study of arboviruses transmission by *Aedes* spp. vectors in the different articles included in the review. **B** Percentage of studies conducted with the two mosquito species of interest: *Ae. aegypti* and *Ae. albopictus*. **C** Percentage of studies conducted using the three viruses of interest, chikungunya virus (CHIKV), dengue virus (DENV) and Zika virus (ZIKV). *Note*: The numbers of included articles in panel **A** do not sum up to 34 because some studies relate to more than one category.

Fig. 3. Distribution of included articles according to the reported observed impact of increased temperature on transmission (higher, lower, no impact) of arboviruses by mosquito vectors. The number of studies in each category is given. *Note*: The numbers of included articles do not sum up to 34 because some studies relate to more than one category.

Table 1
Summary data for the studies included in the review.

Reference	Mosquito	Virus	Viral titer of blood meal	Larval rearing T (°C)	Experimental exposure T (°C)	IR	DR	TR	TE
Viral transmission increases at higher temperatures									
Alto et al. (2018)	*Ae. aegypti*; *Ae. albopictus* (F1/F3)	CHIKV Asian lineage	$1 \times 10^{6.3}$–$1 \times 10^{6.8}$ PFU/ml	26/28	28; Small DTR: 25.8–31; Large DTR: 23.6–31.3		✓	✓	
Blagrove et al. (2020)	*Ae. albopictus* (F3)	ZIKV Asian genotype	1×10^{6} PFU/ml	25	17/19/21/24/27/31		✓	✓	
Carrington et al. (2013a)	*Ae. aegypti* (F4)	DENV-1	5.86×10^{5} FFU/ml; 7.89×10^{5} FFU/ml	28	16/20/26/30/35 11.7–30.3/27.1–34.7	✓	✓		
Chepkorir et al. (2014)	*Ae. aegypti*	DENV-2	$1 \times 10^{3.03}$ PFU/ml	28	26/30	✓	✓		
Chouin-Carneiro et al. (2020)	*Ae. aegypti*; *Ae. albopictus* (F1/F3)	ZIKV	1×10^{2}–1×10^{6} PFU/ml	28	22/28	✓	✓	✓	✓
Ciota et al. (2018)	*Ae. aegypti* (F1/F4)	DENV;CHIKV	1×10^{4}–1×10^{7} PFU/ml	27	Salta: 24.8 (20–31); Iguazu: 26 (20–35); Posadas: 25.4 (18–34); La Plata: 20 (18–23)	✓	✓		
Ferreira et al. (2020)	*Ae. aegypti* (F5)	ZIKV	1×10^{6} PFU/ml	27	20/28/36	✓			
Gloria-Soria et al. (2017)	*Ae. aegypti* (F6/F9)	DENV-2	1×10^{7} PFU/ml	na	25/27/32	✓			
Hernandez-Triana et al. (2019)	*Ae. aegypti*; *Ae. albopictus*	ZIKV	1.6×10^{6} PFU/ml	25	20/25	✓	✓	✓	
Liu et al. (2017)	*Ae. albopictus*	DENV-2	7.375–7.875 $\log_{10}$TCID$_{50}$/ml	27	18/23/28/32/18–28	✓	✓	✓	✓
Lourenco-de-Oliveira et al. (2013)	*Ae. aegypti* (F1)	DENV-2	1×10^{7} FFU/ml	24	15/20/28		✓	✓	✓
Mbaika et al. (2016)	*Ae. aegypti*	CHIKV	$\log_{10}$5.9 PFU/ml	28	26/32	✓	✓		
McLean et al. (1974)	*Ae. aegypti*	DENV-2; DENN-4	na	na	12.8/26.7/32.2/35		✓	✓	
Murrieta et al. (2021)	*Ae. aegypti* (F13/F18); *Ae. albopictus*	ZIKV	1×10^{7} PFU/ml	27/28	25/28/32/35	✓	✓	✓	
Rohani et al. (2009)	*Ae. aegypti*	DENV-2; DENV-4	na	24	26/28/30	✓			
Tesla et al. (2018a)	*Ae. aegypti* (F4)	ZIKV	2×10^{6} PFU/ml	27	16/20/24/28/32/34/36/38	✓	✓	✓	
Tsai et al. (2017)	*Ae. aegypti* (F1); *Ae. albopictus* (F1)	DENV-1	1.63×10^{7} PFU/ml	20–30	10/16/22/28/34	✓		✓	
Watts et al. (1987)	*Ae. aegypti* (F2)	DENV-2	1×10^{5} PFU/ml	25	20/24/26/28/30			✓	
Wimalasiri-Yapa et al. (2019)	*Ae. albopictus*	CHIKV	1×10^{7} PFU/ml	27	18/28	✓	✓	✓	
Wimalasiri-Yapa et al. (2021)	*Ae. aegypti*	CHIKV	1×10^{7} PFU/ml	na	18/28/32	✓			
Winokur et al. (2020)	*Ae. aegypti* (F4)	ZIKV	$1 \times 10^{5.3}$–$1 \times 10^{5.7}$ PFU/ml	26	18/21/26/30	✓	✓	✓	
Xiao et al. (2014)	*Ae. albopictus* (> F30)	DENV-2	$1 \times 10^{7.9}$ PFU/ml	27	18/21/26/31/36	✓		✓	
Zouache et al. (2014)	*Ae. albopictus*	CHIKV	$1 \times 10^{7.5}$ PFU/ml	26	20/28				✓
Viral transmission decreases at higher temperatures									
Heitmann et al. (2018)	*Ae. albopictus* (F8–F10)	CHIKV	1×10^{6} PFU/ml	26	18/21/24	✓		✓	
Onyango et al. (2020)	*Ae. albopictus* (F15); *Ae. aegypti* (F3/F23)	ZIKV	$\log_{10}$8.3 PFU/ml	28/30/32	24/26/28	✓	✓	✓	✓
Viral transmission is the same at high and low temperatures									
Comeau et al. (2020)	*Ae. aegypti*	ZIKV	1.2×10^{3} PFU/ml	27	27/30/33	✓	✓		
Mercier et al. (2022)	*Ae. albopictus* (F4/F5)	DENV-2; CHIKV East Central South genotype	1×10^{7} FFU/ml	24	20/20 variable (17–23)/28		✓	✓	
Richards et al. (2012)	*Ae. aegypti* (F2); *Ae. albopictus* (F2)	DENV-1	na	28	28/30	✓	✓	✓	
Viral transmission under fluctuating temperatures									
Carrington et al. (2013b)	*Ae. aegypti* (F3)	DENV-1	4.16×10^{5} FFU/ml; 3.09×10^{5} FFU/ml	28	26.7 (7.9 around the average)/26.3 (18.6 around the average)/26	✓	✓		
Hugo et al. (2019)	*Ae. aegypti*; *Ae. albopictus*	ZIKV	$1 \times 10^{8.8}$ CCID$_{50}$/ml	27	28/24.5–32.0 around the average/28	✓	✓	✓	
Lambrechts et al. (2011)	*Ae. aegypti* (F9)	DENV-1	1.3×10^{8} PFU/ml	26	DTR 0/10/20 around the average/26	✓	✓		
	Ae. aegypti (F2)	DENV-2	5×10^{5} FFU/ml	25	DTR 0/10/20 around the average/26	✓	✓		
Viral transmission by vectors placed at different temperatures at the immature stage									
Alto and Bettinardi (2013)	*Ae. albopictus* (F3)	DENV-1	$1 \times 10^{7.09}$ PFU/ml	20/25/30	20/25/30	✓	✓		
Tramonte and Christofferson (2019)	*Ae. aegypti*	ZIKV	8×10^{7} PFU/ml	24/28	24/28	✓	✓		
Westbrook et al. (2010)	*Ae. albopictus*	CHIKV	$\log_{10}$4.7 PFU/ml; $\log_{10}$4.5 PFU/ml; $\log_{10}$3.4 PFU/ml	18/24/32	24	✓	✓		

Note: Tick marks indicate the presence of results in the article.
Abbreviations: T, temperature; IR, infection rate; DR, dissemination rate; TR, transmission rate; TE, transmission efficiency; DTR, diurnal temperature range; na, not available.

Lourenco-de-Oliveira et al. (2013) held mosquitoes from Buenos Aires at different temperatures (15 °C, 20 °C and 28 °C) following a DENV-infected blood meal and found higher disseminated infection at 28 °C (66.7%). DENV transmission rates of 20% and 33% were recorded on day 14 at 28 °C and 20 °C, respectively, and no transmission was detected under 20 °C. Thus, the capacity of *Ae. aegypti* to transmit DENV in temperate zones is reduced at low temperatures, and these mosquitoes can better transmit the virus at higher temperatures. Therefore, Lourenco-de-Oliveira et al. (2013) suggested that increasing temperatures represent a risk of epidemics spreading to temperate regions.

Another study by Carrington et al. (2013a), applied five constant temperatures (16 °C, 20 °C, 26 °C, 30 °C and 35 °C) as well as two fluctuating temperature regimes (11.7 °C–30.3 °C and 27.1 °C–34.7 °C) and focused on rates of infection and dissemination. This study showed that at 16 °C there was a minimal infection with DENV in *Ae. aegypti* (2%) but no dissemination. The highest rate of dissemination (100%) was found at 26 °C. However, there was no significant difference in the rate of dissemination between mosquitoes placed at 20 °C and those placed at fluctuating temperatures (within the range of 11.7 °C–30.3 °C). At higher temperatures, the infection was more rapid and the rates of infection and dissemination were higher. However, there was no difference in infection and dissemination rates between mosquitoes kept at 30 °C and those kept at the second regime of fluctuating temperatures (27.1–34.7 °C) (Carrington et al., 2013a).

Chepkorir et al. (2014) and Gloria-Soria et al. (2017) suggested that *Ae. aegypti* mosquito populations collected from temperate regions are less able to transmit DENV compared to mosquito populations from subtropical regions. Chepkorir et al. (2014) studied the transmission of DENV by *Ae. aegypti* from Kilifi (mean daily temperature of 30 °C) and from Nairobi (mean daily temperature of 25 °C) placed at 26 °C and 30 °C. The infection rate for mosquitoes from Nairobi was significantly greater at the higher temperature (30 °C; 21.3%) than at the lower temperature (26 °C; 12.0%). The infection rate for mosquitoes from Kilifi was also significantly greater at the higher temperature (30 °C; 11.6%) compared to the lower temperature (26 °C; 6.8%). The proportion of mosquitoes with disseminated infection was significantly higher for mosquitoes from Kilifi. Nairobi mosquitoes had a higher dissemination rate at 26 °C (16.7%, $n = 30$) than at 30 °C (7.02%, $n = 57$), although the difference was not significant. Gloria-Soria et al. (2017), studied *Ae. aegypti* mosquitoes from Hanoi (cooler climate) and Ho Chin Minh (warmer climate) infected with two strains of DENV-2 (from Hanoi and Ho Chin Minh). The infected mosquitoes were placed at 3 different temperatures (25 °C, 27 °C and 32 °C) for 10 days. There were no statistically significant differences in infection rates between mosquito populations from Hanoi and Ho Chi Minh at different temperatures, regardless of the virus strain. However, the mosquito population from Ho Chi Minh was more susceptible to infection at lower temperatures (25% at 25 °C, 10% at 27 °C, and 7% at 32 °C) than the mosquito population from Hanoi when infected with DENV-Ho Chi Min strain (8% at 25 °C, 13% at 27 °C, and 4% at 32 °C). Similarly, Mbaika et al. (2016) and Alto et al. (2018) found that mosquito populations collected from temperate regions (Coastal and Western Kenya and Florida, respectively) have lower transmission rates for CHIKV compared to mosquito populations from subtropical regions. Mbaika et al. (2016) observed an increased infection rate as the temperature increased from 26 °C to 32 °C. On day 13, viral dissemination in the legs was higher at 32 °C (Coast: 29.1%; Western Kenya: 26.4%) than at 26 °C (Coast: 17%; Western Kenya: 20.6%). By demonstrating that temperature influences infection and dissemination rates, Mbaika et al. (2016) provided evidence that increasing temperatures have an impact on the transmission of the virus. Alto et al. (2018) studied the transmission of CHIKV by *Ae. aegypti* and *Ae. albopictus*, and particularly how the fluctuation of the temperature around 28 °C influences transmission by mosquitoes from different regions in Florida, USA (Okefenokee, Monroe, Manatee and Alachua). There was no significant difference in the transmission of CHIKV by *Ae. albopictus* among the different regions. In contrast, high fluctuating temperatures resulted in a significantly greater number of *Ae. aegypti* mosquitoes with disseminated CHIKV infection compared with constant and low fluctuating temperature regimes for *Ae. aegypti* from Manatee (65% *vs* 4.1% *vs* 37%, respectively). Taken together, these papers suggest that the introduction of mosquitoes from subtropical into temperate regions may exacerbate the risk of virus transmission.

Studies on the transmission of DENV (Rohani et al., 2009; Xiao et al., 2014; Liu et al., 2017; Tsai et al., 2017) or ZIKV (Tesla et al., 2018a; Winokur et al., 2020; Murrieta et al., 2021) showed that these viruses have better transmission at higher temperatures (26–32 °C) (Table 1, Supplementary Table S2).

Hernandez-Triana et al. (2019), studied the transmission of ZIKV in *Ae. albopictus* collected in Spain and in *Ae. aegypti* from Cuba exposed to two constant temperatures (20 °C and 25 °C). These authors showed for *Ae. aegypti* that infection, dissemination and transmission rates of the virus were higher at 25 °C compared to 20 °C (infection rates: 67 *vs* 15.3%; dissemination rates: 75 *vs* 0%; transmission rates: 55 *vs* 0% on day 21). Furthermore, they noted that the transmission rate of the virus at the same exposure temperature was higher in *Ae. aegypti* than in *Ae. albopictus* (55 *vs* 0% on day 21). (Hernandez-Triana et al., 2019).

Chouin-Carneiro et al. (2020) established that higher temperatures (above 28 °C) contribute to a high transmission rate of ZIKV by *Ae. aegypti* collected in different regions of Brazil, at different blood-meal titers. For an infectious blood-meal titer of 1.10^6 PFU/ml (plaque forming units/ml), the transmission was higher at 28 °C than at 22 °C for mosquitoes from Uca, Rio de Janeiro (76.00 *vs* 43.75%) and from Natal, Rio Grande do Norte (80.77 *vs* 35.71%). For an infectious blood-meal titer of 1.10^6 PFU/ml, the transmission was higher at 28 °C than at 22 °C. At 28 °C, *Ae. aegypti* from Natal infected with a 1.10^4 PFU/ml blood meal had a transmission rate of 19.05% compared to 0% for *Ae. aegypti* from Natal.

Blagrove et al. (2020) showed that a temperature of 31 °C resulted in high transmission of ZIKV in *Ae. aegypti* collected from the field (14%), observed a lower transmission rate at 19 °C (4.1%), and concluded that if the temperature increases, the infection by the virus increases within the vector. The higher the temperature increases, the higher the vector competence (the potential for arthropod vectors to transmit the arthropod-borne viruses) for transmitting ZIKV (Blagrove et al., 2020).

Ferreira et al. (2020), showed that at 28 °C and 36 °C, ZIKV replication in infected *Ae. aegypti* females is higher at 24 and 48 h post-infection compared to mosquitoes maintained at 20 °C. Virus replication was maximal at 36 °C, with higher levels of ZIKV RNA copies in the midguts of vectors than at 28 °C. The authors concluded that low temperatures limit ZIKV replication in the midgut of the *Ae. aegypti* vector (Ferreira et al., 2020).

Zouache et al. (2014) and Ciota et al. (2018), suggested that the higher the temperature, the lower the extrinsic incubation period (EIP), which increases the vectorial competence of the mosquitoes (*Ae. aegypti* and *Ae. albopictus*) for DENV and CHIKV. The EIP corresponds to the time interval between pathogen acquisition and pathogen transmission by the vector. However, these authors highlighted that, in addition to temperature, other factors are involved in viral transmission such as the susceptibility of the mosquito to the virus, the geographical origin of the mosquito population, and the strain or species of the virus (Zouache et al., 2014; Ciota et al., 2018).

Indeed, the results of Ciota et al. (2018), showed that temperature has a greater influence on DENV than on CHIKV in *Ae. aegypti*. Furthermore, susceptibility to infection varied according to the region of origin of the vector mosquitoes (Chepkorir et al., 2014; Mbaika et al., 2016; Gloria-Soria et al., 2017; Alto et al., 2018).

Wimalasiri-Yapa et al. (2019) analyzed the effect of low temperatures on transmission by *Ae. albopictus* of two different CHIKV genotypes (ECSA and Asian) at 3- and 7-days post-infection. At 18 °C, ECSA genotype-infected mosquitoes exhibited a significantly higher transmission rate at 7 days post-infection compared with those infected with the

Asian genotype (25 *vs* 0%). A significant difference in ECSA genotype transmission was observed between the 7th- and 3rd-day post-infection at 18 °C (0 *vs* 25%). It was found that mosquitoes held at 28 °C displayed maximum transmissibility for both the Asian and ECSA genotypes (Wimalasiri-Yapa et al., 2019).

In another study, Wimalasiri-Yapa et al. (2021) sought to determine how different constant temperatures impact CHIKV replication in Australian *Ae. aegypti* mosquitoes. These authors showed that the number of copies of the virus genome in the bodies of mosquitoes placed at 32 °C was significantly higher than in mosquitoes maintained at 18 °C and 28 °C at 3 days post-infection. However, at 7 days post-infection, they noticed a decrease in the number of CHIKV copies at 32 °C. Mosquitoes placed at 28 °C had the highest CHIKV copy number, while those placed at 18 °C had the lowest CHIKV copy number at 3- and 7 days post-infection Wimalasiri-Yapa et al. (2021).

Three studies have described virus transmission under fluctuating temperature regimens (Table 1; Supplementary Table S3). Lambrechts et al. (2011) compared the effect of different diurnal temperature ranges (DTR) on the EIP of DENV-1 and DENV-2. For *Ae. aegypti* females infected by DENV-2, mosquitoes were placed under 26 °C with either 0 °C, 10 °C or 20 °C fluctuation around the mean. For the second experiment, *Ae. aegypti* mosquitoes infected by DENV-1 were placed under the same conditions without the 10 °C fluctuation. In this study, infection rates and dissemination rates were determined at multiple time-points post-infection (5, 7, 11, 14, 20, 27 and 32 days) (Table 1, Supplementary Table S3). Virus dissemination rates are in this study an indicator of the transmission pattern of the virus by the vector. Lambrechts et al. (2011) showed that large DTR (high fluctuation around the mean) decreased the potential for virus transmission. Conversely, small fluctuations increased the potential for transmission.

Carrington et al. (2013b) showed that *Ae. aegypti* mosquito infection with DENV is higher at a smaller fluctuating temperature range than at a larger range, thus enhancing the spread of the virus. Hugo et al. (2019), compared the transmission capacity of ZIKV by *Ae. aegypti* and *Ae. albopictus* at different temperatures, a constant temperature of 28 °C and a fluctuating temperature (24.5–32.0 °C, around 28 °C average). These authors observed that *Ae. albopictus* showed a higher body infection percentage under constant and fluctuating temperatures compared to *Ae. aegypti* (80–100 *vs* 70–70% at 14 days post-infection). They found a significant difference in dissemination percentage between the vector species under fluctuating temperature, with *Ae. albopictus* having a higher dissemination rate compared to *Ae. aegypti* at 14 days post-infection (100 *vs* 70%). Moreover, the dissemination rate at 14 days post-infection was higher under fluctuating conditions than under constant temperature for *Ae. albopictus* (100 *vs* 45%). However, transmission percentages in *Ae. aegypti* were significantly higher than in *Ae. albopictus* under the two temperature regimens 14 days post-infection (28 °C: 60 *vs* 10%; 24.5–32.0 °C: 50 *vs* 10%) (Carrington et al., 2013b).

Hugo et al. (2019) demonstrated that fluctuating temperatures significantly affect viral dissemination, suggesting that applying fluctuating rather than constant temperatures better mimics field conditions.

3.5. Viral transmission decreases at higher temperatures

In contrast to the results above, 2 studies highlighted an increase in arbovirus transmission when mosquitoes were placed at low temperatures (Table 1, Supplementary Table S4). Heitmann et al. (2018) observed a decrease in CHIKV transmission by *Ae. albopictus* mosquitoes from Germany and Italy at 24 °C compared to 18 °C (37.5 *vs* 50–63.3%).

Similarly, in a study by Onyango et al. (2020), *Ae. albopictus* was reared and maintained at 30 °C day/26 °C night and 28 °C day/24 °C night. Although at 7 days post-infection, *Ae. albopictus* had higher dissemination and transmission rates of ZIKV under the 30/26 °C regimen, at 14 days post-infection higher dissemination and transmission rate were observed for mosquitoes placed at the lower temperature regimen (28/24 °C: 52–91% *vs* 30/26 °C: 86–100%). Onyango et al. (2020) also placed *Ae. aegypti* from two different regions (Miami, USA and Poza Rica, Mexico) at 32 °C day/28 °C night and 30 °C day/26 °C night for each population and observed that high temperatures decreased the vectorial capacity of mosquito populations to ZIKV (0.08–0.09 *vs* 0.26–0.33). The infection, dissemination, and transmission rates were lower in mosquitoes kept under the 32/28 °C regimen compared to those kept under the 30/26 °C regimen (see Supplementary Table S4 for details).

3.6. Viral transmission is the same at either high or low temperatures

Of the 34 papers included in this review, 3 did not report any difference between the transmission rates of viruses at different temperatures (Table 1, Supplementary Table S5). Richards et al. (2012) did not find a significant difference in dissemination rate and transmission for DENV by *Ae. aegypti* at 28 °C and 30 °C. These authors placed *Ae. aegypti* mosquitoes from Key West and Stock Island (Monroe County, Florida, USA) under two conditions (28 °C or 30 °C) and *Ae. albopictus* mosquitoes from Vero Beach (Indian River Country, Florida) only at 28 °C. At 30 °C, there was no significant difference in infection and dissemination rates between *Ae. aegypti* with different geographical origins. Richards et al. (2012) also observed a significantly higher dissemination rate in *Ae. aegypti* than in *Ae. albopictus* at 28 °C. They also noticed that at 28 °C only *Ae. albopictus* from Vero Beach and *Ae. aegypti* from Key West transmitted DENV while *Ae. aegypti* from Stock Island did not.

Comeau et al. (2020) attempted to analyze the vertical transmission of ZIKV under different temperatures and gonotrophic cycles. Adult females of *Ae. aegypti* were placed in cages at 27 °C, 30 °C and 33 °C. They were given a ZIKV-infected blood meal; after oviposition substrates were placed in the cages for 72 h. The eggs were then removed, representing the first gonotrophic cycle. After 5 days, mosquitoes were given a non-infected blood meal and a second batch of eggs was collected. This was repeated after 10 days. The offspring were placed at the same temperature as the orally infected females from which they were generated, i.e. 27 °C, 30 °C and 33 °C. At 3, 7 and 14 days after offspring emergence, 10 females from each temperature and gonotrophic cycle batch were analyzed. Comeau et al. (2020) demonstrated that there was no significant difference in infection, dissemination, and transmission rates of ZIKV between the different temperatures in the progeny of engorged *Ae. aegypti* females.

Mercier et al. (2022) aimed to study the effect of different temperatures on the transmission of DENV and CHIKV in *Ae. albopictus* mosquitoes reared at different altitudes. They observed DENV transmission only at 28 °C, whereas CHIKV was transmitted at 20 °C and 28 °C and at a temperature regimen of 17 °C and 23 °C around the average of 20 °C (regimen named "20 °C variable" in the article) and at all altitudes studied. Based on their results, Mercier et al. (2022) concluded that there is an epidemic risk of CHIKV for northern European countries if the distribution of *Ae. albopictus* extends into northern Europe.

3.7. Viral transmission by mosquitoes placed under different temperature in immature stages

Most of the studies included in *Sections 3.4-3.6* were conducted on infected adult mosquitoes placed at different temperatures. In contrast, 3 studies have applied different experimental temperature regimens during the larval stages (Table 1; Supplementary Table S6). Westbrook et al. (2010) reared *Ae. albopictus* larvae (F1 of *Ae. albopictus* generated by collected field mosquitoes at Palm Beach County, Florida) in an incubator at 18 °C, 24 °C and 32 °C. Adults were placed at 24 °C after taking a CHIKV-infected blood meal. The authors observed a higher infection rate at 18 °C (52%) compared to 24 °C (36%) and 32 °C (20%). There was no significant difference in the number of infected females that had disseminated infections at 32 °C and 24 °C (i.e. mosquitoes with disseminated virus in legs, wings and head); however, temperature had a

significant influence on dissemination rate (28% for both temperatures). Compared to adult females reared at 32 °C or 24 °C during the larval stages, the dissemination rate for mosquitoes placed at 18 °C was higher (38%). The dissemination rate was not different between 24 °C and 32 °C. Cooler rearing temperatures, therefore, resulted in higher survival rates and higher CHIKV infection rates, highlighting the importance of the mosquito larval environment in determining CHIKV infection rates (Westbrook et al., 2010).

In contrast, Alto and Bettinardi (2013) demonstrated that high temperature applied at larval stages promotes viral transmission. These authors applied different temperatures on immature and adult stages of *Ae. albopictus* (using environmental chambers) for analysis of the interactions between temperature and DENV-1 transmission. They found no effect of temperature on mosquito infection rates but detected significant differences in the dissemination rates. The highest rates of dissemination (96%) were observed in mosquitoes placed at 30 °C during the immature stage; conversely, the lowest rates of DENV dissemination (6%) were found in mosquitoes placed at 20 °C during the immature stage. Alto and Bettinardi (2013) concluded that dengue virus dissemination in adult mosquitoes is influenced by the temperature applied to immature mosquito stages.

Tramonte and Christofferson (2019), studied *Ae. aegypti* mosquitoes placed during the larval stage at 24 °C and 28 °C (air temperature). After a ZIKV-infected blood meal, 50% of the reared larvae were kept at their rearing temperature (either 24 °C or 28 °C) while the other 50% were moved to the alternate temperature. These authors then tested mosquitoes from those four conditions at 7 days post-infection and found no significant differences in infection and dissemination rate according to rearing temperature. At 10 days post-infection, mosquitoes reared at 28 °C and held at 24 °C post-ZIKV infection had a significantly higher infection rate than those reared at 24 °C and held at 24 °C post-ZIKV infection (80 *vs* 45%), but no difference was observed between the four conditions for dissemination rate (ranges: 3–30%, 8–30%, and 25–58% at 7, 10 and 13 days post-infection, respectively). Tramonte and Christofferson (2019) concluded that there is no relationship between rearing temperature and extrinsic incubation temperature and this temperature difference does not impact the infection and transmission of ZIKV.

4. Discussion

In recent years, climate change has become one of the most pressing global issues, affecting every aspect of human life including health. Climate change may significantly exacerbate the burden of vector-borne diseases in the future. Of these diseases, dengue fever, chikungunya and Zika have been under the spotlight over the past few years due to their significant impact on public health (Bhatt et al., 2013; Servadio et al., 2018; Buchwald et al., 2020; Matthews et al., 2022). In response, substantial research efforts have been undertaken to examine the impact of climate change on future ambient temperatures and the circulation of vector-borne diseases.

Numerous studies have been carried out to anticipate the impact of climate change on the transmission of vector-borne diseases. Some studies used epidemiological data collected through the years, along with climate factors such as temperature and precipitation, to project the future risk of transmission (Hafsia et al., 2022; Marinho et al., 2022). Other studies are focusing on the future geographical distribution of the vectors of DENV, CHIKV and ZIKV in response to climate change (Stewart Ibarra et al., 2013; Fouque and Reeder, 2019; Ryan et al., 2019). Modelling studies are also underway, with data from laboratory experiments feeding into models parameterizing virus transmission as a function of temperature (Barbazan et al., 2010; Brady et al., 2013, 2014; da Cruz Ferreira et al., 2017; Mordecai et al., 2017; Huber et al., 2018; Robert et al., 2020). Most of these studies tend to show an increase in the spread of vector-borne diseases due to higher temperatures. Knowing that an increase in temperature might affect the viral transmission in the vector, we sought to synthesize scientific knowledge from different experimental studies conducted by several research groups in different settings. This review presents 34 studies that examine the effects of temperature on CHIKV, DENV and ZIKV transmission by *Ae. aegypti* and/or *Ae. albopictus*. Most of the studies included in this review show that higher temperatures increase infection rate, dissemination rate and transmission rate of the three viruses in both mosquito vectors. Some authors showing that higher temperatures increase virus transmission suggest that these temperatures facilitate the escape of the virus from the midgut (Chepkorir et al., 2014; Mbaika et al., 2016; Alto et al., 2018; Tesla et al., 2018a; Chouin-Carneiro et al., 2020). Other factors such as the dose of virus ingested by the mosquito, the genetics of the virus and mosquito might also impact the transmission and need to be considered (Pongsiri et al., 2014; Pompon et al., 2017; Tesla et al., 2018b).

With the majority of articles showing that rising temperatures favor the transmission of DENV, CHIKV and ZIKV, it is interesting to note that the higher the temperature is, the earlier mosquitoes become infected (McLean et al., 1974; Rohani et al., 2009; Lambrechts et al., 2011). The EIP is an important parameter to consider. Indeed, temperatures above 30 °C appear to reduce the EIP, especially for DENV, which is between 8 and 14 days at the standard rearing temperature (26–28 °C) (Gubler, 1998; Lambrechts et al., 2011). Most of these studies observed a decrease in the time interval between virus acquisition by the vector and virus transmission with increasing temperature, although EIP analysis was not the objective of those articles. Moreover, there may be some limitations to that observation as temperatures above 32 °C have a negative impact on the vector life span and consequently on arbovirus transmission (Delatte et al., 2009; Rohani et al., 2009; Xiao et al., 2014; Liu et al., 2017; Tsai et al., 2017; Reinhold et al., 2018; Tesla et al., 2018a; Winokur et al., 2020; Murrieta et al., 2021). However, it remains difficult to understand how the EIP changes with increasing temperature due to the lack of studies that adequately address this question.

As presented in the *Results* section above, in most of the studies reviewed here, infected vectors are placed under constant temperature regimes to study the effect of one temperature on virus transmission. However, this does not reproduce the natural conditions in the life of the vector under which the viruses are transmitted. The few studies that applied fluctuating temperatures (Lambrechts et al., 2011; Carrington et al., 2013b; Hugo et al., 2019), showed that infection rates and virus dissemination are higher in mosquitoes placed under smaller DTRs, which correspond to the warm seasons in tropical areas, than in mosquitoes placed under larger DTRs typical of cooler tropical seasons, which correspond to the cool seasons (Lambrechts et al., 2011; Reinhold et al., 2018). Although these experiments are more complicated to perform, they should be carried out more often in the future as they are the most biologically realistic.

Social and societal factors, such as urbanization, have been identified as important factor impacting vector-borne disease spread. Due to population movements and international trade, vectors are colonizing areas where they were not previously reported (Kraemer et al., 2019; Martinet et al., 2019; Reinhold et al., 2018; Robert et al., 2020; Wu and Huang, 2022). Urbanization, combined with increased global travel and trade, is leading to the development of densely populated urban centers with inadequate infrastructure and services, creating ideal conditions for larval breeding sites and thus facilitating the expansion and spread of disease vectors (Kolimenakis et al., 2021). Some articles included in this review highlighted a link between the strain of the virus and the origin and strain of the mosquito. Chepkorir et al. (2014), Gloria-Soria et al. (2017), Mbaika et al. (2016), and Alto et al. (2018) concluded that mosquitoes from tropical areas are more easily infected than mosquitoes from more temperate areas. Additionally, most of the reviewed articles showed that rising temperatures are associated with higher viral transmission, suggesting a greater risk of tropical diseases emerging in temperate regions. This is a major concern in terms of prevention and public health. Although epidemics of DENV, CHIKV, and ZIKV have in their majority been reported in tropical regions, evidence is

accumulating for autochthonous transmission in temperate regions (La Ruche et al., 2010; Sousa et al., 2012; Rey, 2014; Weaver, 2014; Roiz et al., 2015; Robert et al., 2019).

Only three out of 34 studies assessed different air temperature regimens on larval stages, while most studies investigated temperatures applied to the adult mosquito stage. A study of CHIKV-infected *Ae. albopictus* showed that rearing larvae at lower temperatures was correlated with increased rates of dissemination (Westbrook et al., 2010). By contrast, another study showed that higher temperatures during the larval stage increased the rate of dissemination of DENV in *Ae. albopictus* (Alto and Bettinardi, 2013). Finally, a third study, conducted on ZIKV-infected *Ae. aegypti*, demonstrated that rearing larvae at lower or higher temperatures had no effect on ZIKV infection and transmission (Tramonte and Christofferson, 2019). The disparity in the number of studies between mosquito life stages highlights the need for more research to understand how vector competence is affected by the increased temperatures though the entire mosquito life cycle.

Our review has some limitations. We have chosen to focus only on laboratory experimental studies. This review highlights the issue of standard protocols of experimental transmission, hence the difficulty of comparison between settings or clear conclusions (Boyer et al., 2018; Obadia et al., 2022). The protocols for vector competence experiments need to be standardized to enable the data generated to be re-used in future studies such as meta-analysis (Wu et al., 2022). Also, to better measure the impact of climate change, humidity levels, precipitation, or other environmental factors should be considered (Brown et al., 2023); however, these factors remain difficult to incorporate experimentally. We have selected studies focusing only on DENV, CHIKV and ZIKV and two vectors, *Ae. aegypti* and *Ae. albopictus*. However, other viruses and/or vectors have been investigated such as ZIKV transmission by *Aedes japonicus* (Jansen et al., 2018), CHIKV transmitted by *Aedes koreicus* (Ciocchetta et al., 2018), Mayaro virus transmitted by *Ae. aegypti* (Alomar and Alto, 2022) or West Nile virus transmitted by *Culex* mosquitoes (Holicki et al., 2020). The relationship between transmission of yellow fever virus by *Ae. aegypti* and temperature has been poorly studied at the experimental level. An old study from 1932 showed that the EIP of yellow fever decreases with increasing temperature and that infection of *Ae. aegypti* with the virus increases at higher temperatures (Davis, 1932). However, modelling studies have been performed under different scenarios, suggesting transmission of the virus is increased at higher temperatures, which would lead to an increase in the number of yellow fever cases, particularly in Central Africa (Gaythorpe et al., 2020). These studies also showed that higher temperatures (above 28 °C) represent a major risk in transmitting these arboviruses, consistent with the findings from our review. Finally, we have searched articles from three major scientific article databases in the English language, but we cannot rule out the possibility that we may have missed some articles.

Studying how temperature affects transmission is challenging because of the factors involved in vector competence. Most of the studies reviewed demonstrate that increasing temperature promotes viral transmission. Nevertheless, some articles have reached different conclusions. Two articles demonstrated that viral transmission decreased at higher temperatures. Three papers out of 34 included in this review did not show a difference in viral transmission between vectors placed at low temperatures and those placed at high temperatures post-infection. In addition to environmental factors such as temperature, the ability of a virus to infect a mosquito depends on the insect's genetic background and geographical origin (Turell et al., 1992; Richards et al., 2012; Mbaika et al., 2016; Carpenter and Clem, 2023). This may explain some of the variability observed across different studies and settings.

5. Conclusions

Here we have reviewed laboratory studies of the effect of temperature on the transmission of DENV, CHIKV, and ZIKV by the mosquito vectors *Ae. aegypti* and *Ae. albopictus*. Modelling studies have shown that increasing temperatures brought on by climate change will favor the expansion of mosquito vectors and the occurrence of vector-borne diseases such as DENV, CHIKV, and ZIKV, especially in the long-term future. Most of the studies reviewed here demonstrate that increased temperature (above 28 °C) enhances transmission of these viruses. As the geographical range of vectors has expanded over the years, rising temperatures carry the risk that outbreaks of major vector-borne diseases such as dengue, chikungunya, will occur in temperate regions and the burden of these diseases increases in tropical regions. However, current experimental data do not allow us to predict the magnitude of the increase in arbovirus transmission and, for example, the precise impact of each degree Celsius increase on virus transmission. As we do not have much experimental data in the higher temperature range given that temperatures above 32 °C have a negative impact on the life span of the vector, it is also difficult to adequately model what exactly will happen above 32 °C. Whether arbovirus transmission will continue to increase or decrease beyond a higher temperature range requires further investigations.

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Not applicable.

CRediT authorship contribution statement

Méryl Delrieu: Conceptualization, Methodology, Formal analysis, Investigation, Data curation, Writing – original draft, Writing – review & editing, Visualization. **Jean-Philippe Martinet:** Methodology, Validation, Writing – review & editing. **Olivia O'Connor:** Conceptualization, Methodology, Validation, Data curation, Writing – review & editing. **Elvina Viennet:** Writing – review & editing, Funding acquisition. **Christophe Menkes:** Writing – review & editing, Funding acquisition. **Valérie Burtet-Sarramegna:** Conceptualization, Writing – review & editing, Funding acquisition. **Francesca D. Frentiu:** Conceptualization, Validation, Writing – review & editing, Supervision, Project administration, Funding acquisition. **Myrielle Dupont-Rouzeyrol:** Conceptualization, Validation, Writing – review & editing, Supervision, Project administration, Funding acquisition.

Declaration of competing interests

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

The data supporting the conclusions of this article are included within the article and its supplementary files.

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Appendix A. Supplementary data

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