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Arboviral disease outbreaks, *Aedes* mosquitoes, and vector control efforts in the Pacific

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Recurring outbreaks of mosquito-borne diseases, like dengue, in the Pacific region represent a major biosecurity risk to neighboring continents through potential introductions of disease-causing pathogens. *Aedes* mosquitoes, highly prevalent in this region, are extremely invasive and the predominant vectors of multiple viruses including causing dengue, chikungunya, and Zika. Due to the absence of vaccines for most of these diseases, *Aedes* control remains a high priority for public health. Currently, international organizations put their efforts into improving mosquito surveillance programs in the Pacific region. Also, a novel biocontrol method using *Wolbachia* has been tried in the Pacific region to control *Aedes* mosquito populations. A comprehensive understanding of mosquito biology is needed to assess the risk that mosquitoes might be introduced to neighboring islands in the region and how this might impact arboviral virus transmission. As such, we present a comprehensive review of arboviral disease outbreak records as well as *Aedes* mosquito biology research findings relevant to the Pacific region collected from both non-scientific and scientific sources.

KEYWORDS

***Aedes*, Pacific region, arbovirus, mosquito-borne diseases, mosquitoes, insecticide resistance, vector competence, novel biocontrol**

Introduction

Arthropod-borne viral (arboviral henceforth) diseases cause significant burden to global health. Around 400 million people have been infected dengue virus (DENV) per year, and of which 96 million people have undergone dengue fever (1). Chikungunya virus (CHIKV) and Zika virus (ZIKV) spread worldwide over the last decade and currently 77.9% and 48.6% of

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global human populations are living in the countries affected by CHIKV and ZIKV, respectively (2).

Both *Aedes aegypti* and *Aedes albopictus* are known major vectors of these arboviral diseases. *Aedes aegypti* uses artificial habitats to survive even outside of its temperature limit for development and *Ae. albopictus* can survive in much colder regions than *Ae. aegypti*, allowing them to be globally distributed (3). Although both species are similar in that they are highly adaptable, it is important to use different mosquito control strategies to each species since they have different habits and behaviors (3, 4). For example, the WHO recommended targeted indoor residual spraying to control *Ae. aegypti*, while recommending targeted outdoor residual spraying against *Ae. albopictus* (4).

Tropical islands, including the Pacific islands, typically have socio-economic, climatic, and human activity-related factors favorable for arbovirus outbreaks (5). Suboptimal healthcare infrastructure driven by factors including poverty can slow the timely detection of pathogens before outbreaks begin (5). The lack of water management infrastructure also serves to increase potential mosquito-breeding sites (5), and climate change has facilitated the spread of arboviruses in the Pacific (6). It has been suggested that dengue became an endemic disease in New Caledonia due to climate change (7).

The Pacific region experiences recurring outbreaks of arboviral diseases (1). The warm temperatures of the Pacific region make them a suitable environment for the transmission of arboviruses (8), including CHIKV, DENV, and ZIKV. No outbreaks of yellow fever virus (YFV) have been recorded in the region. These three viruses are transmitted by *Aedes* mosquitoes of the subgenus *Stegomyia*, mainly *Aedes aegypti* and *Ae. albopictus*, although additional species in the *scutellaris* group of this subgenus may be important local vectors in the Pacific (e.g., *Ae. hensilli*, *Ae. polynesiensis*, *Ae. scutellaris*, etc.) (9–13). Nonetheless, this review focuses on *Ae. aegypti* and *Ae. albopictus* mosquitoes.

Outbreaks

We collected records from scientific literature, news, reports, and online databases to compile reports of historical outbreaks in the Pacific region (Supplemental Table S1). Outbreak records in the Pacific region appeared in various sources, with gray literatures accounting for 12% of the total sources (Supplemental Table S2) (1). Based on our data, a total of 412 arboviral outbreaks were reported from 25 Pacific nations or territories (Figure 1) through December 2020. From 1971 to 2000, the incidence of arboviral disease in the Pacific remained relatively constant, with no more than thirty outbreaks documented within each ten-year interval (Figure 1). However, during the period between 2001 and 2010, the scale of arbovirus disease increased drastically, with outbreaks documented in 70 locations. From 2011 to 2020, a total of 153 outbreaks were reported, more than two times higher than the number of outbreaks from the previous period. The reason for the recent increase in arbovirus transmission in this region is yet to be determined.

Across the Pacific region, DENV was first reported in Hawaii in the late 1840s (14), and was subsequently reported in French Polynesia in the early 1850s (15). Outbreaks occurred sporadically until the mid-1920s, thereafter they increased until the 1940s when mosquito control was widely implemented, and a slight decrease in the occurrence of outbreaks was observed between 1941 to 1945. As this time frame overlaps with the height of the Pacific campaign of World War II, it is likely that such a major event impacted typical reporting of arboviral illnesses, as well as arbovirus transmission. Reports of dengue-like illness in the Western Pacific Region in the 1950s correlated with troop movements among dengue-endemic and non-endemic areas in the early to mid-1940s (16, 17). Nevertheless, there are no reports of dengue outbreaks following WWII, between 1945 and 1964, potentially due to the commencement of mosquito control activities using DDT, but cases reappeared in the mid-1960s (Figure 1). This gap in dengue outbreak records does not necessarily reflect a lack of DENV transmission during this period and highlights the difficulty to disentangle the issue of underreporting from low occurrence outbreak events. Despite this difficulty, a graph of the number of outbreaks in the Pacific region revealed the overall trend of increasing arboviral disease outbreaks over the entire period (Figure 1).

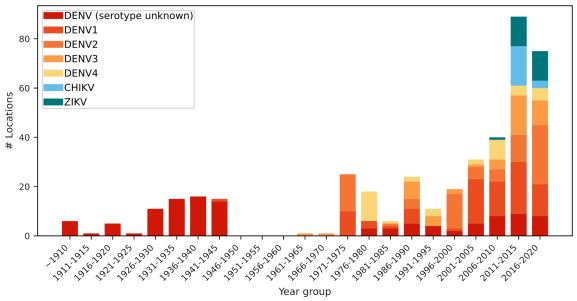

FIGURE 1
The number of arbovirus disease outbreaks in the Pacific region at 5-year intervals.

The first identification of a DENV infection in the Pacific region to the serotype level occurred in 1944, with DENV-1 detected in Tahiti, French Polynesia (15). Subsequently, DENV-3 was reported in the Windward Islands, French Polynesia in 1964 (15). The first reported DENV-2 cases occurred for individuals in American Samoa, Fiji, French Polynesia, Kiribati, New Caledonia, Papua New Guinea (PNG), Tonga, Tuvalu, and Wallis and Futuna in 1971, while the first report of DENV-4 in Pacific was from French Polynesia, New Caledonia, Samoa, and Wallis and Futuna in 1979 (18).

In contrast to DENV, other *Aedes*-transmitted arboviruses have a much shorter history in the region. CHIKV was first detected in the region in 2011 in New Caledonia, with subsequent outbreaks occurring in 2012 in PNG, in 2013 in the Federated State of Micronesia (FSM), in 2014 in the Cook Islands, French Polynesia, Tonga, American Samoa, Samoa, and Tokelau, and in 2015 in Fiji, and RMI, Kiribati, and Tuvalu (19–24). There were 17 total CHIKV outbreaks between 2011 and 2015, and three outbreaks between 2016 and 2020 (Figure 1).

The first ZIKV outbreaks in the Pacific region occurred in 2007 in the FSM, and subsequent cases emerged in 2013 in French Polynesia. The virus then spread to the Cook Islands, Easter Island, and New Caledonia in 2014, followed by Fiji, PNG, RMI, Samoa, Solomon Islands, Vanuatu in 2015, and then American Samoa, Kiribati, Palau, and Tonga in 2016 (22, 23, 25–29). Between 2006 and 2010, there was

one outbreak of ZIKV. There were 12 outbreaks between 2011 and 2015, and 12 outbreaks between 2016 and 2020 (Figure 1).

Distribution of *Aedes aegypti* and *Aedes albopictus*

The *Aedes aegypti* group originated in Madagascar and/or islands in the Southwestern Indian Ocean and then spread to mainland Africa (30). The domesticated subspecies *Ae. aegypti* likely originated in West Africa where the species was initially forest-dwelling and zoophilic (31). It likely shifted its feeding preference from animals to humans and began using artificial containers as breeding sites when human settlements developed adjacent to forests in West Africa (31). A global genetic analysis reported that *Ae. aegypti* populations in the New World were established in the 15th and 16th centuries (32). It is possible that slave traders carried *Ae. aegypti* to European countries on their return from the New World, enabling persistence in the Mediterranean region until around 1950 (31). Their establishment in Asia was estimated to have occurred in the 19th century, and it is hypothesized to have occurred *via* the Mediterranean following the opening of the Suez Canal in 1869 (32).

It is believed that human activities introduced *Ae. aegypti* from Asia and/or the Americas to the Pacific region during the 19th century (33). The whaling industry and migration of Asian people to New Caledonia and French Polynesia may have contributed to the introduction of the Asian lineage of this species (33). Similarly, the whaling industry, international trade, and World War II are thought to have enabled the westward expansion of the American lineage into the Pacific region (33). Within the region, the earliest published record of *Ae. aegypti* was from Brisbane, Australia, in 1887 where the species was described by Skuse as *Culex bancroftii* (34). However, historical records of dengue-like illness and museum specimens that predate Skuse's report suggest that *Ae. aegypti* had a wide distribution in eastern Australia by the latter part of the nineteenth century (35). Regional maritime trade within the Pacific region promoted the movement of *Ae. aegypti* larvae and eggs in water-storage containers from port to port (35), but because of its behavior and reliance on artificial containers for breeding sites, *Ae. aegypti* often stayed localized to port areas and typically only moved inland on larger populated islands when enabled by human activity (35). Consequently, *Ae. aegypti* has been broadly distributed throughout the Pacific for well over a century, but its local distribution within archipelagos has varied substantially between Pacific nations and territories (35–37).

Aedes albopictus is native to the forests of Southeast Asia (38). Like *Ae. aegypti*, it is an invasive species in the Pacific region. Within this region, *Ae. albopictus* has the longest history in Hawaii and was first documented as *Ae. scutellaris* in the early 1900s (39). *Aedes albopictus* was first reported in PNG in 1932 (40). Although some have discredited that record (36), collections from PNG in the 1960s and early 1970s indicate that it was present but relatively sparse compared to *Ae. aegypti* and *Ae. scutellaris* (41, 42). It likely spread to other Pacific region from there in the 1970s, as it was reported in the Solomon and Santa Cruz Islands, east of PNG, from collections made in 1978 (43). Similar to *Ae. aegypti*, *Ae. albopictus* was reported to use a wide variety of artificial containers in contrast to native *Stegomyia* species in the *scutellaris* group (43). Worldwide, the invasion of this species was mediated primarily through the international trade of used tires over the last 40 years (38), a mechanism that may have played a more recent role in the spread of *Ae. albopictus* between neighboring islands (44).

Currently, both species can be found in the Pacific region, but *Ae. aegypti* has colonized more islands than *Ae. albopictus* (Figure 2 and Supplementary Table S2). *Aedes aegypti* has been reported in American Samoa, Australia, the Cook Islands, Easter Island, FSM, Fiji, French Polynesia, Galápagos, Hawaii, Kiribati, Nauru, New Caledonia, Niue, Palau, PNG, Pitcairn Islands, RMI, Samoa, the Solomon Islands, Tokelau, Tonga, Tuvalu, Vanuatu, and Wallis and Futuna (45–51). In contrast, *Ae. albopictus* has been found in Australia, FSM, Fiji, Guam, Hawaii, Kiribati, Nauru, Northern Mariana Islands, Palau, PNG, RMI, Samoa, Solomon Islands, Tonga, and Vanuatu (4, 43–46, 48, 50, 52). Although the two species are not established in New Zealand, interceptions have been recorded from ports in Auckland, New Zealand (53).

Transportation of goods and human travel can contribute to the dispersal of vectors and pathogens (54–57). Also, military activities during WWII and the Vietnam War provided opportunities for mosquitoes and the pathogens they transmit to migrate to the Pacific region (16, 17, 55). The introduction of arbovirus by airplane appears to be through infected humans rather than infected mosquitoes (58). *Aedes aegypti and Ae. albopictus* exhibit an extraordinary ability to move between and adapt to new environments (59). Both species have spread worldwide through cargo containers and tires (59–63). The frequency at which these new introductions occur is unknown. Genetic or genomic studies revealing the population origin and demographic history of various invasive *Aedes* populations could provide vital insight into this issue in the future.

Vector competence of *Aedes aegypti* and *Aedes albopictus*

Aedes aegypti is competent for several arboviruses such as CHIKV, DENV, YFV, and ZIKV. Its competence differs depending on the lineage of each virus and the population of the vector (64).

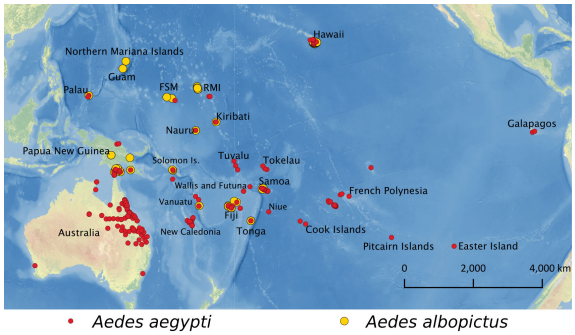

FIGURE 2
Locations where *Ae. aegypti* (red) and *Ae. albopictus* (yellow) have been reported in the Pacific region.

Aedes albopictus is also competent for these same arboviruses, but based on studies utilizing mosquito populations from Africa, Europe, and the United States (Connecticut and New York), it has a greater vector competence for CHIKV than for DENV, ZIKV, or YFV based on (65–68). Both mosquito species can vary in their vector competence for different serotypes or strains of viruses (69–73), which might complicate the risk of disease transmission if multiple competent mosquito species and multiple virus lineages are circulating within a region.

Limited vector competence data are available for the Pacific region. Thus far, only Australia, French Polynesia, New Caledonia, and Samoa have reported the competence of *Aedes* mosquitoes for virus transmissions. Virus transmission efficiencies data from past studies are summarized in Table 1, where transmission efficiency was calculated as the number of mosquitoes with infected saliva divided by the total number of mosquitoes tested (79).

Overall, *Ae. aegypti* populations from the Pacific region appear to be efficient (>20%) at transmitting each DENV, ZIKV, and CHIKV (Table 1). However, across viral lineages and strains, CHIKV seemed to be consistently more infective to *Ae. aegypti* than DENV and ZIKV, with the highest transmission efficiencies observed between 53%-90% (5, 15, 69). Cases of extremely low (0%) and high (100%) efficiency of transmission have only been found for ZIKV (67, 73). Since the vector competent results in Table 1 were derived from different research settings, caution is required for the comparison and interpretation of results.

Specifically, Australian *Ae. aegypti* was particularly efficient in transmitting CHIKV (64% transmission efficiency at 14-15 days post-infection [dpi]) and ZIKV (Table 1). ZIKV strains from Cambodia (87% at 14 dpi) and Brazil (50-60% at 14 dpi) tended to be more efficiently transmitted than those from Tonga and Uganda (>20% at 14 dpi). Comparing with Australian populations, French Polynesian *Ae. aegypti* seemed to be a more efficient dengue vector (35% for DENV-1 at 21 dpi). French Polynesian *Ae. aegypti* was also highly competent in transmitting CHIKV (49% at 14 dpi) and had variable transmission efficiencies for different ZIKV strains. For ZIKV from French Polynesia, however, French Polynesian *Ae. aegypti* had significantly higher transmission efficiencies (36% at 14 dpi) than the Polynesian islands-endemic species *Ae. polynesiensis* (0% at 14 dpi) (81). New Caledonian *Ae. aegypti* was also efficient in CHIKV (20-90% at 14 dpi) and ZIKV (>20%) transmission, particularly for the ZIKV African lineage (max 100% at 14 dpi). Moreover, this mosquito population was more susceptible to DENV-1 than the French Polynesian population. Although its rates of infection and dissemination varied between DENV serotypes and genotypes, transmission efficiencies of New Caledonian *Ae. aegypti* are similar (ranging from 3-16% at 14 dpi) with the exception of a DENV-1 isolated from genotype I (21% at 14 dpi) (82). As for Samoan *Ae. aegypti*, a single study investigated vector competence for ZIKV and reported a low transmission efficiency (2% at 14 dpi), which contrasts with other *Ae. aegypti* populations from Australia, French Polynesia, and New Caledonia (69). In combination, these results highlight the potential importance of local variation in vector competence for arbovirus epidemiology. Vector competencies of *Ae. albopictus* populations among the Pacific region were only tested in the Australian population.

The co-circulation of multiple viruses in a region may increase the occurrence of co-infection and therefore influence arboviral transmissions (71). Studies have implied that *Aedes* mosquitoes could cause concurrent outbreaks when coinfected with arboviruses; however, co-infection led to varying outcomes for transmission depending on the viruses involved in experimental infection. Although *Aedes* mosquitoes from the Pacific regions have not been investigated for co-infection under experimental conditions, co-infection of DENV and ZIKV and even co-infection with three viruses has been observed in Mexican *Ae. aegypti* (84). Besides, *Aedes aegypti* was shown to be capable of transmitting CHIKV and ZIKV simultaneously without a significant reduction in transmission rates (84, 85). *Aedes albopictus* from Reunion Island was able to co-transmit both CHIKV and DENV-1 (86). In nature, little is still known about co-infection and co-transmission of arboviruses, but *Ae. aegypti* and *Ae. albopictus* appear to be capable of transmitting multiple arboviruses in a single bite (87). To date, there have been no studies about simultaneous transmission by the one single mosquito in the Pacific, but two patients co-infected with DENV and ZIKV have been reported in New Caledonia in 2014 (88). Since each patient was infected with a different serotype of DENV and had a different travel history, it is assumed that there were at least two co-infections (88). In the Pacific region where CHIKV, ZIKV, and all of serotypes of DENV are circulating, co-infection is a subject we need to pay close attention to.

Insecticide resistance

Insecticide resistance refers to the ability of insects to survive the exposure to a standard dose of insecticide, with this ability mediated through physiological or behavioral adaptation (4). There are three major mechanisms driving insecticide resistance in mosquitoes: (a) Target-site resistance, which decreases the affinity of insecticides to the target protein by mutation(s) in the protein's gene, (b) metabolic resistance, which is caused by overexpression or conformational change of enzymes involved in detoxification and xenobiotic metabolism, and (c) penetration resistance, which refers to cuticular modifications that interrupt penetration of insecticide into insects' body (89, 90). Insecticide resistance against all four major insecticides has evolved in *Ae. aegypti* and *Ae. albopictus via* both the target-site and metabolic resistance mechanisms while penetration resistance has been largely uncharacterized in *Aedes* mosquitoes (89).

Insecticide resistance management should be included in vector control strategies because there is a limited number of insecticide classes, with many of these used readily in pest management programs on a global scale (91). There are only four insecticide classes approved for adult mosquito control by the World Health Organization (WHO) (pyrethroids, organophosphates, organochlorines, and carbamates), and the threat of insecticide resistance has been increasing due to this limitation (92). Of these four insecticide classes, only pyrethroids and organophosphates were used in the Western Pacific Region from 2000 to 2009, with known usage in the Cook Islands, Fiji, Kiribati, FSM, Nauru, Palau, the Solomon Islands, Tonga, Tuvalu, and Vanuatu (93).

The determination of insecticide resistance of *Aedes* mosquitoes in the Pacific region is performed using the CDC bottle bioassay and/or the WHO insecticide resistance test, two of the most utilized biological assays. Both methods determine mosquito mortality after a

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TABLE 1 Vector competence of *Aedes aegypti* and *Aedes albopictus* from the Pacific region.

Mosquito	Population	Virus	Origin	Passage (passage #, passage history)	Infective unit	Transmission efficiency	Reference
Aedes aegypti	Australia	DENV-2	Australia	Low (1, C6/36)	$10^{3.7}$ $CCID_{50}$/ml	43% at 13 dpi	(12)
				Low (1, C6/36)	$10^{4.5}$ $CCID_{50}$/ml	42% at 13 dpi	(12)
				Low (3, C6/36)	$10^{6.4}$ $CCID_{50}$/ml	0-8% at 8 dpi 0-8% at 12 dpi 20-70% at 16 dpi	(73)
		DENV-4	Indonesia	Low (2, C6/36)	$10^{7.0}$ $CCID_{50}$/ml	0% at 8 dpi 0% at 12 dpi 0-12% at 16 dpi 4-16% at 20 dpi	(73)
		ZIKV	Brazil	Low (3, C6/36)	$10^{8.8}$ $CCID_{50}$/ml	0-5% at 3 dpi 0% at 7 dpi 50-60% at 14 dpi	(74)
			Cambodia	Low (3, C6/36, Vero)	$10^{5.6}$ $TCID_{50}$/ml	87% at 14 dpi	(75)
			Tonga	Moderate (6, mouse, C6/36)	$10^{4.2}$ $TCID_{50}$/ml	3% at 14 dpi 3% at 18 dpi	(76)
					$10^{5.9}$ $TCID_{50}$/ml	0% at 14 dpi	(76)
					$10^{7.2}$ $TCID_{50}$/ml	6-11% at 14 dpi	(76)
					$10^{7.7}$ $TCID_{50}$/ml	6-10% at 14 dpi	(76)
					$10^{8.5 \pm 0.4}$ $TCID_{50}$/ml	27-37% 14 dpi	(76)
			Uganda	Very High (~150, mice, Vero)	$10^{6.7 \pm 0.2}$ $TCID_{50}$/ml	0% at 5 dpi 0% at 7dpi 12% at 10 dpi 27% at 14 dpi	(77)
		CHIKV	Reunion Island	Low (3, Vero)	$10^{4.0}$ $CCID_{50}$/ml	64% at 14-15 dpi	(78)
	French Polynesia	DENV-1	New Caledonia	Moderate (5, Vero)	10^{6} FFU/ml	35% at 21 dpi	(79)
		ZIKV	New Caledonia	Moderate (5, Vero)	10^{7} $TCID_{50}$/ml	0% at 6 dpi 0% at 9 dpi 0% at 14 dpi 17% at 21 dpi	(80)
			French Polynesia	Low (3, C6/36)	10^{7} $TCID_{50}$/ml	0% at 2 dpi 3% at 6 dpi 8% at 9 dpi 36% at 14 dpi 73% at 21 dpi	(81)
		CHIKV	French Polynesia	Low (3, C6/36)	10^{7} $TCID_{50}$/ml	5% at 2 dpi 18% at 6 dpi 34% at 9 dpi 49% at 14 dpi 53% at 21 dpi	(11)
	New Caledonia	DENV-1	New Caledonia	Moderate (5, Vero)	10^{6} FFU/ml	0-3% at 7 dpi 3-13% at 14 dpi 0-13% at 21 dpi	(79)
		DENV-1 Genotype I	New Caledonia	Low (3, C6/36)	10^{7} FFU/ml	4% at 7 dpi 21% at 14 dpi	(82)
		DENV-1 Genotype IV	New Caledonia	Low (3, C6/36)	10^{7} FFU/ml	2% at 7 dpi 13% at 14 dpi	(82)
		DENV-2	New Caledonia	Low (3, C6/36)	10^{7} FFU/ml	0% at 7 dpi 16% at 14 dpi	(82)

(Continued)

TABLE 1 Continued

Mosquito	Population	Virus	Origin	Passage (passage #, passage history)	Infective unit	Transmission efficiency	Reference
		DENV-3	New Caledonia	Low (3, C6/36)	10^7 FFU/ml	0% at 7 dpi 7% at 14 dpi	(82)
		DENV-4	New Caledonia	Low (3, C6/36)	10^7 FFU/ml	4% at 7 dpi 7% at 14 dpi	(82)
		ZIKV	African lineage	Low (4, freeze dried, Vero)	10^7 $TCID_{50}$/ml	57-85% at 7 dpi 69-100% at 14 dpi 22-97% at 21 dpi	(83)
			American lineage	Unknown (freeze dried, Vero)	10^7 $TCID_{50}$/ml	0-7% at 7 dpi 14-20% at 14 dpi 21-40% at 21 dpi	(83)
			Asian lineage	Moderate (5, freeze dried, Vero)	10^7 $TCID_{50}$/ml	0-3% at 7 dpi 20-55% at 14 dpi 20-14% at 21 dpi	(83)
			New Caledonia	Moderate (5, Vero)	10^7 $TCID_{50}$/ml	0% at 6 dpi 3% at 9 dpi 0% at 14 dpi 0% at 21 dpi	(80)
		CHIKV	New Caledonia	Not disclosed	10^7 PFU/ml	40-53% at 3 dpi 54-64% at 8 dpi 20.0-66.7% at 14 dpi	(20)
			Reunion Island	Not disclosed	10^7 PFU/ml	33-73% at 3 dpi 46-57% at 8 dpi 66-90% at 14 dpi	(20)
	Samoa	ZIKV	New Caledonia	Moderate (5, Vero)	10^7 $TCID_{50}$/ml	0% at 6 dpi 0% at 9 dpi 2% at 14 dpi 6% at 21 dpi	(80)
Aedes albopictus	Australia	DENV-2	Australia	Low (1, C6/36)	$10^{4.5}$ $CCID_{50}$/ml	7% at 13 dpi	(12)
		ZIKV	Brazil	Low (3, C6/36)	$10^{8.8}$ $CCID_{50}$/ml	0% at 3 dpi 0-10% at 7 dpi 10% at 14 dpi	(74)
			Cambodia	Low (3, C6/36, Vero)	$10^{5.6}$ $TCID_{50}$/ml	76% at 14 dpi	(75)
		CHIKV	Reunion Island	Low (3, Vero)	$10^{3.9}$ $CCID_{50}$/ml	32% at 14-15 dpi	(78)

Transmission efficiency: The number of infected saliva/the number of the total tested.
dpi, days post-infection;
$CCID_{50}$, Cell culture infectious dose with 50% endpoint;
$TCID_{50}$, Tissue culture infectious dose with 50% endpoint;
FFU, Focus forming unit;
PFU, Plaque forming unit;
C6/36, Aedes mosquito larvae-derived cell line;
Vero, African green monkey kidney epithelial-derived cell lines.
#: Number of.

specific insecticide exposure time (diagnostic time) with minor differences in the guidelines for interpreting results (Table 2) (94, 95). Resistance ratios (RR) are often used in the literature when reporting insecticide resistance of mosquito populations (95). Resistance ratios are defined as the ratio of lethal concentrations of insecticide which results in 50% mortality (LC_{50}) of the test population to the LC_{50} of a susceptible strain. An RR < 5 indicates that the mosquito population is susceptible to the applied insecticide, an RR between 5-10 indicates moderate resistance, and an RR >10 indicates a highly resistant population (95).

Pyrethroid resistance in *Ae. aegypti* and *Ae. albopictus* has been reported worldwide, with a higher level of resistance observed in *Ae. aegypti* (96). Mutations in domains II and III of Voltage-gated sodium channel (VGSC) genes have been observed in *Ae. aegypti* from several populations in the Pacific region (V1016G + S989P in Vanuatu and Kiribati, and F1534C in New Caledonia, Fiji, and Kiribati) (97). Additionally, upregulations of detoxifying cytochrome P450 genes were identified in *Ae. aegypti* from New Caledonia (98). Interestingly, resistance against pyrethroids was not observed in *Ae. aegypti* from Queensland, Australia (97). The overall

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TABLE 2 Guidelines for interpreting results using the CDC bottle bioassay and the WHO insecticide resistance test.

Methods	% Mortality	Interpretation
WHO	≥98%	Susceptible
CDC	≥97%	Susceptible
WHO	90 - 97%	Possible resistance
CDC	90 - 96%	Developing resistance
WHO & CDC	<90%	Resistant

pyrethroids resistance profile of *Ae. aegypti* populations in the Pacific region is shown in Figure 3. Organophosphates ranked first for usage in the Western Pacific Region although the usage of organophosphates worldwide for the control of vector-borne diseases was less than 10% from 2001 to 2009 (93). The majority of *Aedes aegypti* populations in the Pacific region were susceptible to organophosphates. *Aedes aegypti* populations in French Polynesia and PNG were susceptible to organophosphates (malathion and/or temephos) (99, 100). Developments of resistance against organophosphate have been found in two *Aedes* mosquitoes in Fiji, New Caledonia, and Palau since 2010 (Table 3).

Although several populations in the Pacific region are testing for mosquito insecticide resistance, there are still *Aedes* populations where this practice has not been implemented since 2010 or which no information was available (Table 3). Given that insecticide resistance was detected in *Ae. aegypti* populations which inhabit the same island with untested *Ae. albopictus*, it is possible that there are more insecticide resistant *Ae. albopictus* populations. All tested *Ae. aegypti* and *Ae. albopictus* populations showed resistance to organochlorines and carbamates insecticides despite low usages (93). It may be due to the high concentrations of those insecticides remaining in the Pacific region (103). For a better mosquito control, it is important that all countries in the region determine the insecticide resistance status of their mosquito populations, share it with the entire region and work together to find strategies to control and prevent mosquito insecticide resistance which ultimately will reduce the prevalence of mosquito-borne disease in the Pacific region.

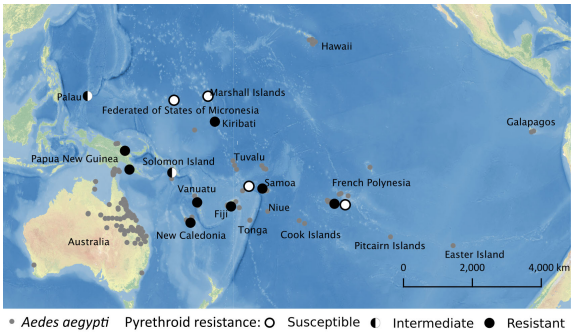

FIGURE 3
Pyrethroid resistance profile of *Ae. aegypti* available as of March 2022 overlaid with historical *Ae. aegypti* occurrence data.

Population genetics

Multiple population genetics studies have been conducted for *Ae. aegypti* populations from the Pacific region (32, 33, 46, 104). A recent study measured genetic differentiation using 12 microsatellite loci in 79 populations of *Ae. aegypti* from 30 countries across six continents, including three Pacific regions – Australia, Hawaii, and Tahiti (32). The Pacific group, including two Australian populations, was genetically closer to the Asian *Ae. aegypti* populations than to those from other continents (32). Another study analyzed nine microsatellites and two mitochondrial DNA loci (COI and ND4) from 270 *Ae. aegypti* individuals collected from Fiji, French Polynesia, New Caledonia, and Tonga, and identified both Asian and American genetic lineages (33). A further study using a double-digest restriction site-associated (ddRAD) sequencing protocol for 224 individuals examined the genetic structure of *Ae. aegypti* populations from the Indo-Pacific regions, including Australia, Kiribati, Fiji, New Caledonia, and Vanuatu (46). Single nucleotide polymorphism (SNP) derived genotypes from ddRAD sequencing indicated that *Ae. aegypti* from the Pacific region were distinct from Asian or Australian *Ae. aegypti* lineages as shown in Figure 4 (46). This suggests that populations from Australia and other Pacific regions may have different invasion histories (46, 104). The genetic relatedness of *Ae. aegypti* within and between other Pacific nations and territories is yet to be investigated.

Aedes aegypti has a longer history in the Pacific region compared to *Ae. albopictus*, which spread more rapidly around the world through trade in a shorter time frame. This difference in time scale has likely influenced the relatedness of populations of the two species across the Pacific region. *Aedes albopictus* populations in Fiji and Nauru may be genetically similar to those from mainland Southeast Asia, but additional specimens must be sequenced to definitively conclude this (52). Population genomics using ddRAD data also demonstrated that Fiji *Ae. albopictus* populations were closely related to those from Southeast Asia, but Vanuatu populations were distinct as shown in Figure 5 (46). Results of analyses from COI and 13 microsatellite loci revealed that *Ae. albopictus* populations from the Southern Fly River in PNG and the Torres Strait Islands in Australia were introduced from the Indonesian region (52, 105). However, *Ae. albopictus* populations from other locations in PNG showed distinct genetic structures when compared with those from the Southern Fly River (105). A study comparing possible historical routes of *Ae. albopictus* invasions indicated that PNG populations, except for the Southern Fly River population, likely came from the mainland of southeast Asia and then became the source of *Ae. albopictus* that was established in the Solomon Islands (52). In contrast, the Hawaii population appeared more closely related to the East Asian population than to the Southeast Asian population (52, 106). It is plausible that *Ae. albopictus* from other Pacific nations and territories would demonstrate close relatedness to either Southeast Asian or East Asian *Ae. albopictus*, but more data from more Pacific nations and territories needs to be collected to test that hypothesis. This is because their genetic structure was not associated with distance, but with human transportation routes, suggesting *Ae. albopictus* enables to disperse even over long distances (46).

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TABLE 3 Outcomes of insecticide resistance testing for *Ae. aegypti* and *Ae. albopictus* from the Pacific region since 2010.

Species	*Ae. aegypti*				*Ae. albopictus*				References
Insecticide Class	P	Op	Oc	C	P	Op	Oc	C	
American Samoa					△	△	△	△	
Australia	○		●	●					(4, 97, 101)
Cook Islands					△	△	△	△	
Easter Island									
Federated States of Micronesia	○				○	○			(4)
French Polynesia	●				△	△	△	△	(4)
Fiji	●	●							(4)
Galápagos									
Guam	△	△	△	△	○	○			(4)
Hawaii									
Kiribati	●	○							(4)
Nauru									
New Caledonia	●	◑			△	△	△	△	(4, 98, 102)
New Zealand									
Niue									
Northern Mariana Islands	△	△	△	△					
Palau	◑	○		●	○	◑		●	(4)
Papua New Guinea	●	○	●	●	○	○	●	◑	(4, 100)
Pitcairn Islands									
Republic of Marshall Islands	○				○	○			(4)
Samoa	●	○							(4)
Solomon Islands	◑				◑				(4)
Tokelau									
Tonga									
Tuvalu									
Vanuatu	●	◑			●				(4)
Wallis and Futuna	○				△	△	△	△	(4)

P, Pyrethroids;
Op, Organophosphates;
Oc, Organochlorines;
C, Carbamates.
White circle: susceptible; circle with half black: developing resistance; black circle: resistance; triangle: absence of mosquito in this locality; and empty space: no information or not tested.

Surveillance and novel mosquito control strategies

The Pacific region continues to experience outbreaks of mosquito-borne diseases representing a major biosecurity threat to the neighboring continents (Figure 1). Due to the high prevalence and invasive characteristics of *Ae. aegypti* and *Ae. albopictus* mosquitoes and the lack of vaccines and treatments for many mosquito-transmitted diseases, it is of utmost importance to conduct continual surveillance to assess outbreak risk and/or assess the response to an active outbreak and enable mosquito control programs to reduce the incidence of these diseases. Figure 6 shows the timeline for an overview of major events related to mosquito-borne diseases in the Pacific region, which are discussed in more detail below.

The Pacific Community (SPC), which was founded in 1947, is a scientific and technical organization with members of 27 Pacific nations and territories. SPC and WHO established the Pacific Public Health Surveillance Network (PPHSN) in 1996 (https://www.pphsn.net). PPHSN prioritizes surveillance of infectious diseases including dengue fever in the Pacific (107). The SPC's Public Health Division, which established in 2009, provides timely alerts of epidemics and emerging diseases in the Pacific region

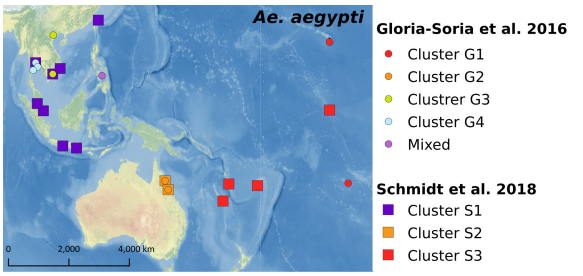

FIGURE 4
Genetic structure of *Ae. aegypti* identified from previous studies.

(https://www.spc.int/phd/epidemics/). This system is based on integrated data collected by routine surveillance systems and informal sources such as media and personal communications.

To improve the capacity for vector surveillance and control across the Pacific region, SPC and WHO have been providing a standardized methodology to mosquito control program staff. SPC and WHO Division of Pacific Technical Support distributed a manual for the surveillance and control of *Aedes* vectors in the Pacific region in 2020 (4). Additionally, the Pacific Mosquito Surveillance Strengthening for Impact (PacMOSSI) was launched by James Cook University, SPC, and WHO in 2021. It focuses on providing systematic surveillance, control of *Aedes* mosquitoes, and training control program staff. This project utilizes an online platform that provides (a) assessments to determine vector surveillance and control strengths and needs for the Pacific region; (b) training to use web-based data management to support the country and regional mosquito surveillance; (c) training on vector surveillance and control best practices, mosquito species identification, and insecticide resistance testing; (d) grants to support country-specific research to generate data for the improvement of mosquito control and surveillance; and (e) support for countries developing *Aedes* surveillance and control plans aligned with best practices (108). Information on *Aedes* vectors generated by these standardized methods will help us understand the current state of the Pacific region consisting of dozens of different countries and territories.

The Incompatible insect technique (IIT) is a control strategy using *Wolbachia*, an endosymbiotic bacterium found in many insect species. Uninfected female mosquitoes are not able to produce viable eggs when they mate with males infected with *Wolbachia* (109).

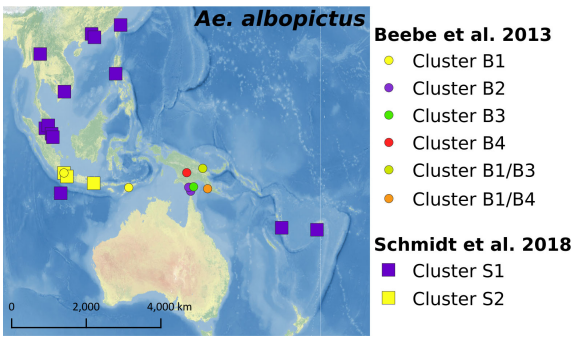

FIGURE 5
Genetic structure of *Ae. albopictus* identified from previous studies.

Wolbachia-based mosquito suppression strategies have been tried in Australia for *Ae. aegypti* control (110), and French Polynesia for *Ae. polynesiensis* control (111). *Aedes aegypti* carrying *w*AlbB2-F4 were released to the Northern Cassowary Coast regions of Australia where wild-type *Ae. aegypti* and *w*Mel-*Wolbachia* infected *Ae. aegypti* coexisted. Over the 20-week period of release in 2018, over 80% of suppression in *Ae. aegypti* populations was achieved in the release sites, and one of the three sites showed over 97% suppression 11 months later (110). *Aedes polynesiensis* carrying *Wolbachia* were released at a hotel operating on the private atoll of Tetiaroa, north of Tahiti occupying approximately 1 km^2 area for a 12-month period between 2015 and 2016. This pilot study achieved successful suppression of the local *Ae. polynesiensis* population and the 2nd trial with an 18-month period was conducted between 2018-2020. The study reported a noticeable drop in mosquito bites perceived by hotel visitors and hotel workers (112).

Another approach involving *Wolbachia* relies on cytoplasmic incompatibility to replace the natural mosquito population with *Wolbachia*-infected mosquitoes (46, 113). *Aedes aegypti* carrying *Wolbachia* have a lower susceptibility to infection with viruses including dengue, Zika, chikungunya, yellow fever, and Mayaro viruses, and also display reduced transmission potential (113–118). *Aedes aegypti* infected with the *w*Mel strain of *Wolbachia* (originally found in *Drosophila melanogaster*) was successfully introduced into two natural *Ae. aegypti* populations in Yorkeys Knob and Gordonvale, Australia (119). Continuous monitoring for two years showed that *Wolbachia* infection frequencies persisted at high levels in both populations (120). In 2013, *Ae. aegypti* carrying *w*Mel *Wolbachia* were released in three areas around Cairns, Australia, and this release suggested the possibility that *w*Mel *Wolbachia*-infected *Ae. aegypti* can become established in urban areas (121). For 28 months from October 2014, 4 million *w*Mel *Wolbachia*-infected *Ae. aegypti* were released across a total area of 66km^2 in Townsville, Australia (122). During this period, although imported DENV cases from overseas were continuously reported, only one case of locally acquired DENV occurred in this region (122).

A similar result in controlling local infection of DENV was also observed during the period of release of *Ae. aegypti* with *w*Mel *Wolbachia* conducted from 2011 to 2017 in Cairns, Australia (123). The same method has been implemented and monitored in Fiji since 2017, Vanuatu since 2018, and Kiribati and New Caledonia since 2019 by the World Mosquito Program (124). Based on these successes, Hawaii departments are considering using *Wolbachia* to control mosquitoes to improve their public health as well as for avian population conservation given high case rates of avian malaria (125). In Australia, experimental releases of another, more pathogenic *Wolbachia* strain (*w*MelPop) were also conducted, but the frequency of the infection steadily decreased within the local *Ae. aegypti* populations after releases were halted (126). Overall, replacement strategies with the *w*Mel strain of *Wolbachia* significantly reduced the possibility of being infected by DENV in the field application.

To overcome the limitation of current insecticide- and environmental maintenance-based current control methods, various novel transgenic-based approaches have been developed. The transgenic approaches for suppressing mosquito populations include producing sterile males or lethal toxic products to offspring and inducing a sex bias ratio. However, careful

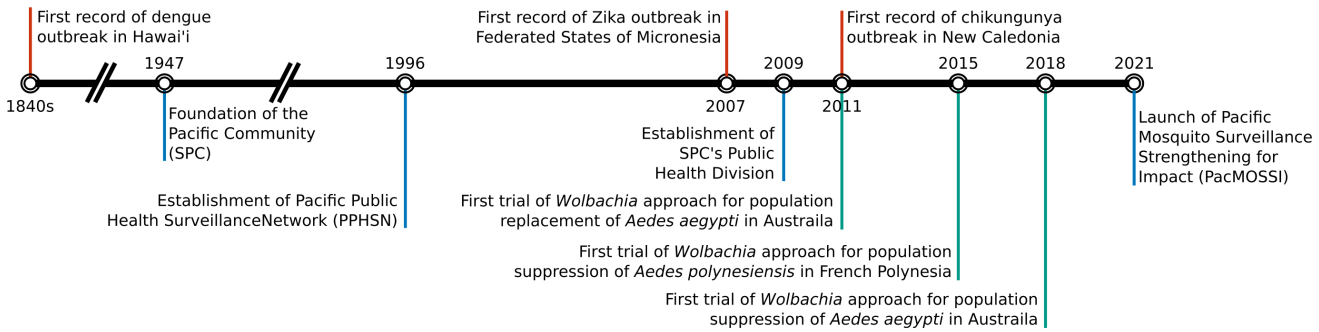

FIGURE 6
Timeline of major events related to mosquito-borne diseases in the Pacific region.

consideration before implementation is required (109). To date, no transgene control approaches have been applied for mosquito control in the Pacific region. However, weekly releases of *Ae. aegypti* eggs generated by the precision-guided sterile insect technique (pgSIT) were simulated on Onetahi, Teti'aroa, French Polynesia to explore the potential of pgSIT to suppress the wild *Ae. aegypti* population (127). The mathematical simulation demonstrated that population elimination was the common result for large release schemes such as 18 weekly releases of 200 pgSIT eggs per wild-type adult.

Future studies needed

There is a paucity of scientific literature on *Aedes* mosquitoes in the Pacific region and scientific understanding of arboviral disease in this region has been complicated because many arboviral disease outbreaks records and *Aedes* surveillance data have not been published in standard scientific journals. This represents vital information for students, scientists, government regulators, mosquito control programs, and public health officials. Obtaining current information about *Aedes* mosquitoes and arbovirus disease outbreak records is critical to improving decision support capacity and will spur future research in this region.

Although *Aedes albopictus* is also a major vector of CHIKV, DENV, and ZIKV in the Pacific regions, it has been less studied than *Ae. aegypti*. For example, its vector competence has only been studied for one Australian population. Due to the lack of information about its vector competence, it is challenging to properly evaluate the risk of *Ae. albopictus* represents as a vector in the Pacific region. Additionally, since insecticide resistance tests have only been conducted on a small number of islands, it is likely that many control programs are proceeding without any consideration of chemical efficacy. Further studies in these areas are essential for the long-term, persistent control of *Ae. albopictus* in this region.

Over the last two decades, there has been rapid development of novel *Aedes* mosquito control strategies (128). In addition to the *Wolbachia* biocontrol strategies, active laboratory studies are being conducted to develop improved sterile insect techniques using a genetic engineering approach (127). All these novel control strategies depend on the ability of mosquitoes to mate and disperse in a natural setting. A comprehensive understanding of mosquito biology is needed to assess the risk of novel mosquito control strategies about introduction to neighboring islands in the region and their potential impact on arboviral disease transmission. In this review, we have outlined several major knowledge gaps that must be addressed to facilitate the development of a road map for future mosquito research and mosquito control activities in the Pacific region.

Author contributions

SS, AV, and YL conceived the study. SS, CR, JM, AM, ME, AR-W, and BG conducted literature search and data collection. SS, CJ, and YL conducted field collection of *Aedes* mosquitoes in Hawai'i Island. AV conducted field collection of *Aedes* mosquitoes in the Republic of Marshall Islands. AV, YL, and JC contributed to *Aedes albopictus* data collection. XW, OA, RR, DM, EC, AV, JC contributed to data analysis and manuscript editing. All authors contributed to the article and approved the submitted version.

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Conflict of interest

OSA is a founder of both Agragene, Inc. and Synvect, Inc. with equity interest. The terms of this arrangement have been reviewed and approved by the University of California, San Diego in accordance with its conflict of interest policies.

The remaining authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fitd.2023.1035273/full#supplementary-material

SUPPLEMENTARY TABLE 1
Arboviral outbreak records in the Pacific Islands.

SUPPLEMENTARY TABLE 2
The number of arbovirus disease outbreaks in the Pacific region at 10-year intervals.

SUPPLEMENTARY DATA SHEET 1
Aedes albopictus and *Aedes aegypti* distribution records in the Pacific Islands.

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