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Quantifying the potential relative roles of *Aedes aegypti* and *Ae. albopictus* in dengue transmission: A systematic literature review and meta-analysis of dengue virus prevalence in both vectors

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ABSTRACT

Objectives: *Aedes aegypti* is the principal dengue virus (DENV) vector, while *Ae. albopictus* is often considered to have a negligible role. However, limited field data comparing their involvement in DENV transmission hampers accurate evaluation of current interventions targeting only one species and dengue outbreak risk assessments in non-endemic areas.

Methods: We conducted a systematic review and meta-analysis of studies assessing DENV prevalence in both *Ae. albopictus* and *Ae. aegypti*. We searched EMBASE, PubMed, SCIELO, and Global Index Medicus up to 15 September 2023. Risk ratios (RR) were calculated using fixed-effects model in meta-analyses, summarizing prevalences in *Ae. albopictus* vs *Ae. aegypti*.

Results: Of 5,432 records screened, 36 studies from 14 countries and territories were included (covering 96,884 *Ae. aegypti* and 106,205 *Ae. albopictus* mosquitoes). Overall, *Ae. albopictus* showed a 35% lower DENV prevalence than *Ae. aegypti* (RR=0.65, 95% CI=0.56-0.75, I^2=93%). The difference was more pronounced pre-2000 (63% lower; RR=0.37; CI=0.30, 0.46), but post-2000 data showed no significant difference (2000s: RR=1.17; 95% CI=0.81, 1.69; since 2010 RR=0.86; 95% CI=0.68, 1.07).

Conclusion: While *Ae. aegypti* remains the primary vector, recent evidence suggests *Ae. albopictus* plays a more notable role in DENV transmission than previously thought. Effective vector control strategies should therefore target both species.

Introduction

Aedes (*Ae.*) *aegypti* and *Ae. albopictus* mosquitoes exert a large toll on global health by transmitting multiple diseases, including dengue, chikungunya, yellow fever, and Zika [1,2]. These mosquitoes are highly invasive, and their global distributions are expanding rapidly [3,4]. Dengue virus (DENV) is the fastest spreading mosquito-borne infection worldwide, with existing vector control methods proving unsustainable or insufficient to block transmission [5].

Aedes aegypti is considered to be the principal vector of dengue, with *Ae. albopictus* having a secondary, even negligible, role in transmission [6–8]. This has been attributed to the fact that, where *Ae. albopictus* is the sole vector, DENV is often absent or transmitted sporadically [7,8]. However, the global distributions of the two species overlap considerably, and the scarcity of locally acquired dengue infections in areas where only *Ae. albopictus* is found may reflect broader environmental conditions that are limiting for both species [3,6,9]. While laboratory studies have often found *Ae. albopictus* to be slightly less competent for DENV transmission, due in part to reduced viral dissemination from the midgut [8], its greater longevity and broader environmental tolerance can com-

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pensate for this difference in certain settings [6,10]. Thus, the relative contribution of *Ae. albopictus* to dengue transmission is context-dependent and may be underestimated if based solely on vector competence measures [6–9,11,12].

Importantly, there is limited evidence quantifying the relative importance of either species in DENV transmission in the field. This has become a pressing evidence gap considering the differential targeting of each species by novel vector control methods (e.g., *Wolbachia*, genetically modified mosquitoes) and the vectors' continued range expansion [3,13]. For example, *Ae. aegypti*-focused interventions would be expected to have a large impact in locations where *Ae. albopictus* is present if the latter has a negligible role in DENV transmission, but the same intervention would have a smaller long-term effect if *Ae. albopictus* is an important (though still secondary) vector. In late 2022, the WHO reported that 42 field studies using human infection or disease endpoints were underway to assess the effectiveness of *Wolbachia* or analogous interventions [14]. Consequently, there is likely to be increased interest in these approaches as more results are published, particularly in understanding factors that could affect their impacts across settings. Quantifying *Ae. albopictus*' and *Ae. aegypti*'s roles in DENV transmission is also pertinent given the anticipated effects of climate change and urbanization on the future distributions of each species [3]. This includes the potential for continued spread of DENV in currently non-endemic locations such as mainland Europe where all locally acquired dengue cases have been due to *Ae. albopictus* since *Ae. aegypti* is absent in those areas [15]. Therefore, it is important to know whether *Ae. albopictus* has a trivial or more substantial role in DENV transmission and to identify what factors might affect its relative importance. Some have proposed using DENV prevalences in each vector as proxies for their roles in transmission, and this is commonly done for assessing the relative importance of other mosquito species in the transmission of West Nile virus and Japanese encephalitis virus [16–19, S7].

We present a systematic literature review and meta-analysis on the relative prevalences of DENV in *Ae. albopictus* and *Ae. aegypti*. Notably, assessing DENV prevalences only in field-caught, female adult mosquitoes focused our analyses on the vectors' abilities to transmit DENV directly to humans and accounted for their different biting behaviours and survival probabilities without needing to directly control for these difficult-to-measure attributes.

Methods

Search strategy and selection criteria

We adhered to the Preferred Reporting Items for Systematic Reviews and Meta-Analysis (PRISMA) guidelines [20]. The study was prospectively registered with PROSPERO (CRD42024500194).

We searched four databases (Embase, Global Index Medicus, PubMed, SCIELO) from their inception until September 15, 2023. Reference lists from selected publications and review articles were also examined to identify additional articles. Briefly, we included field studies that trapped female adult *Ae. aegypti* and *Ae. albopictus*, tested each for DENV, and reported the results. We only included data from articles where both vectors were collected and tested to reduce between-study confounding (e.g., environmental conditions, trapping methods) and differential measurement error (e.g., DENV tests, laboratory personnel skill). To be included, studies must have reported raw data on the numbers of each species examined and testing positive. Articles written in English, Spanish, or Portuguese were included. We excluded studies where results were not clearly separated by species and sex. Conference abstracts, case reports, systematic and literature reviews, and articles without full-texts available were also removed. See Tables S1–S2 for the full search strategy.

Data screening and collation

Duplicate articles were removed, and all search results were exported to Rayyan for screening of titles and abstracts [21]. Three reviewers covered articles in English and Spanish. Portuguese papers were translated using Google Translate and reviewed by two reviewers. Each title, abstract, and full text was assessed by two reviewers. Discrepancies were resolved with a third reviewer through discussion. Reasons for exclusion were documented at each step. All extracted data were collated in English.

The following outcome data were collected using a standardised data extraction sheet: numbers of female mosquitoes screened for DENV and testing positive by species.

We also recorded information on contextual factors to conduct sub-group analyses: WHO region where mosquitoes were collected, country income level during the study [22], urbanicity (urban, rural, urban and rural), place of collection (indoors, peridomestic outdoors, non-peridomestic outdoors, combinations), and whether collections were performed in or around the homes of dengue cases. We also recorded the seasons when mosquitoes were collected (dry, rainy, rainy and dry) and which decade the data were collected in. Lastly, we documented whether mosquitoes were tested for DENV in groups (called "pools") or individually, whether only heads/thoraces/saliva were tested or if other body parts were included, and DENV testing methods. Data on DENV serotypes were also recorded.

We assessed the methodological quality of the included studies using the MASTER scale (Table S3, Figure S1) [23]. Questions 14-17, 24-25, and 27 were excluded as they were not relevant.

Statistical analyses

We calculated minimum infection rates (MIR) for studies analysing mosquitoes in pools [24]. MIR assumes that at most one mosquito per pool is infected and is calculated as:

$$MIR = [number\ of\ positive\ pools/total\ specimens\ tested]\ x\ 1000$$

We conducted meta-analyses using the Mantel-Haenszel fixed-effects method without continuity correction as recommended when data are sparse [25], and summarised their relative prevalences using risk ratios (RR). A RR $>$ 1 indicates an increased prevalence of DENV in *Ae. albopictus* compared with *Ae. aegypti*, RR $\approx$ 1 indicates similar prevalences between species, and RR $<$ 1 indicates a lower prevalence of DENV in *Ae. albopictus* compared with *Ae. aegypti.* Sub-group analyses were performed for the aforementioned contextual factors. Studies that did not state whether they tested heads/thoraces vs other body parts were assumed not to have solely tested heads/thoraces. For any other factors, studies missing data were included as a "Not reported" category. We used chi-squared tests to identify whether results differed across categories within each sub-group analysis. Sensitivity analyses included using a random effects model, leaving one study out at a time, and dichotomizing studies based on whether their MASTER scores were at or above vs below the mean overall score.

We used the I^2 statistic to estimate the percentage of variability in studies' results that was due to between-study heterogeneity rather than random error [25].

Data management was completed via Microsoft Excel 2022. All analyses were conducted in R (v.4.4.1) via Rstudio (v.2024.04.2+764) with the package meta (v.7.0). Visualizations were done in Excel and R.

Role of the funding source

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of Merck Sharp & Dohme LLC, a subsidiary of Merck & Co., Inc., Rahway, NJ, USA during the project.

Results

The search identified 5,412 records, of which 1,529 duplicates were removed. Twenty additional articles were identified from other sources, and 140 articles underwent full-text review, of which 36 met the eligibility criteria (Figure 1) (S1–S36, see Supplementary References for details). Analyses included 96,884 *Ae. aegypti* mosquitoes and 106,205 *Ae. albopictus*.

A list of the studies excluded during full-text screening is provided in Table S4.

Study characteristics, numbers of mosquitoes tested for each species, numbers of DENV positives, and infection rates are provided in Table 1. The geographic distribution of the 36 studies spans Southeast Asia (n=16), Western Pacific (n=8), the Americas (n=8), Eastern Mediterranean (n=2), and Africa (n=2). The highest numbers of articles per country were for Thailand (n=7) and India (n=6). Fifteen studies came from lower-middle-income countries, 16 from upper-middle-income countries, and 5 were from high-income countries. Seventy-two percent of studies (n=26) were published since 2010, while 64% of studies (n=23) collected data since 2010. Seventy-five percent of articles (n=27) only tested pools of mosquitoes for DENV, while 25% (n=9) only tested individual mosquitoes [S2]. Seventy-eight percent of studies (n=28) used a type of PCR to detect DENV. Thirty studies (83%) reported the frequencies of serotypes and DENV-2 was the most common type reported in both species.

The overall meta-analysis found a statistically significant 35% lower prevalence of DENV infection in *Ae. albopictus* compared with *Ae. aegypti* (RR=0.65; 95% CI=0.56, 0.75, I^2=93%) (Figure 2). The I^2 value indicated considerable between-study heterogeneity.

We conducted sixteen subgroup analyses (Table 2). All forest plots are presented in Figures S2–S17.

There were differences in the relative prevalences of DENV across WHO regions. Lower DENV prevalences were observed among *Ae. albopictus* in the Western Pacific (56% lower; RR=0.44, 95% CI=0.34, 0.56) and Southeast Asia (39% lower; RR=0.61, 95% CI=0.49, 0.75) (Fig. S2). When the two regions were combined, the prevalence of DENV was 49% lower among *Ae. albopictus*

Table 1
Summary of articles included in the meta-analysis (n=36). For details see the Supplementary References list in the Supplement.

First author, Publication year	Country	Setting	Method to detect DENV	N of DENV +ve *Aedes* mosquitoes or pools / N of all *Aedes* mosquitoes tested			
				Ae. albopictus	IR/MIR*	*Ae. aegypti*	IR/MIR*
Studies with individual mosquitoes tested							
Chung, 2002[S8]	Singapore	Urban	RT-PCR	67/2256	29.7	54/781	69.1
Dos Santos, 2017[S10]	Brazil	Urban	RT-PCR	0/199	0	24/2469	9.7
Fansiri, 2021[S11]	Thailand	Rural	RT-PCR	0/4	0	22/451	48.8
Johari, 2019[S16]	Malaysia	Urban	Nested PCR	0/42	0	1/10	100
Nonyong, 2021[S22]	Thailand	N/A	qRT-PCR	4/11	363.6	145/891	162.7
Pham Thi, 2017[S24]	Vietnam	N/A	PCR	5/115	43.5	3/989	3
Rangel, 2021[S25]	Brazil	Rural	RT-qPCR	1/27	37	0/18	0
Sarma, 2023[S28]	India	Urban	RT-PCR	1/704	1.4	7/1186	5.9
Thavara, 2006[S34]	Thailand	Rural	RT-PCR	21/58	362.1	53/324	163.6
Studies with mosquito pools tested							
Aragao, 2019[S1]	Brazil	Urban	RT-qPCR	0/4	0	1/172	5.8
Carrasquilla, 2021[S2]†	Colombia	Urban	RT-PCR	0/7	0	6/799	7.5
Chan, 1971[S3]	Singapore	Urban	Cross- complement-fixation test	5/8475	0	1/1961	0.5
Chand, 2021[S4]	India	Mixed	RT-PCR	0/97	0	5/1942	2.6
Chen, 2010[S5]	Taiwan	Urban	RT-PCR	0/57,319	0	12/43,133	0.3
Chetry, 2020[S6]	India	Urban	RT-PCR	19/1809	10.5	14/2073	6.8
Chow, 1998[S7]	Singapore	Urban	RT-PCR	40/784	51	23/409	56.2
Das, 2013[S9]	India	N/A	RT-PCR	1/140	7.1	0/33	0
Gould, 1968[S12]	Thailand	Rural	Cell culture	4/1392	2.9	8/140	57.1
Hasty, 2020[S13]	USA	Mixed	PCR	15/1268	11.8	0/249	0
Isa, 2021[S14]	Nigeria	Urban	RT-PCR	6/160	37.5	17/620	27.4
Jahan, 2014[S15]	Pakistan	Urban	ELISA	1/40	25	31/570	54.4
Khan, 2016[S17]	Pakistan	Mixed	RT-PCR	4/500	8	30/2500	12
Liew, 2021[S18]	Malaysia	Urban	NS1 antigen	3/113	26.6	5/138	36.2
Medeiros, 2018[S19]	Brazil	Urban	RT-PCR	6/67	89.6	21/1293	16.2
Méndez, 2006[S20]	Colombia	Urban	RT-PCR	2/336	6	37/4628	8
Mulyatno, 2018[S21]	Indonesia	Urban	RT-PCR	1/1506	0.7	109/15,099	7.2
Paupy, 2010[S23]	Gabon	Urban	Q-PCR	3/2539	1.2	0/923	0
Rúa-Uribe, 2020[S26]	Colombia	Urban	RT-PCR	20/114	175.4	91/1174	77.5
Rudnick, 1965[S27]	Singapore	Mixed	Mouse infection	1/1250	0.8	5/269	18.6
Selvarajoo, 2022[S29]	Malaysia	Urban	NS1 antigen	6/2602	2.3	71/3867	18.4
Smith, 1971[S30]	Thailand	N/A	Cell culture	38/17,981	2.1	25/480	52.1
Srivastava, 2023[S31]	India	Mixed	RT-PCR	12/1251	9.6	9/1555	5.8
Teerasut, 2012[S32]	Thailand	Rural	RT-PCR	0/69	0	1/1583	0.6
Tewari, 2004[S33]	India	Rural	ELISA and IFA	1/363	2.8	7/3640	1.9
Tuksinvaracharn, 2004[S35]	Thailand	Urban	RT-PCR	0/9	0	2/391	5.1
Withanage, 2020[S36]	Sri Lanka	Urban	RT-PCR	1/2594	0.4	1/124	8.1

* IR = infection rate per 1000 mosquitoes; MIR = minimum infection rate per 1000 mosquitoes. MIR is an estimate of the infection rate when mosquitoes were processed in pools. For studies where individual mosquitoes were processed, an infection rate per 1000 mosquitoes was calculated.

† Carrasquilla et al. (2021)[25] tested some mosquitoes in pooled samples and others individually. For each species, we combined data across pooled and individually tested samples for analyses.

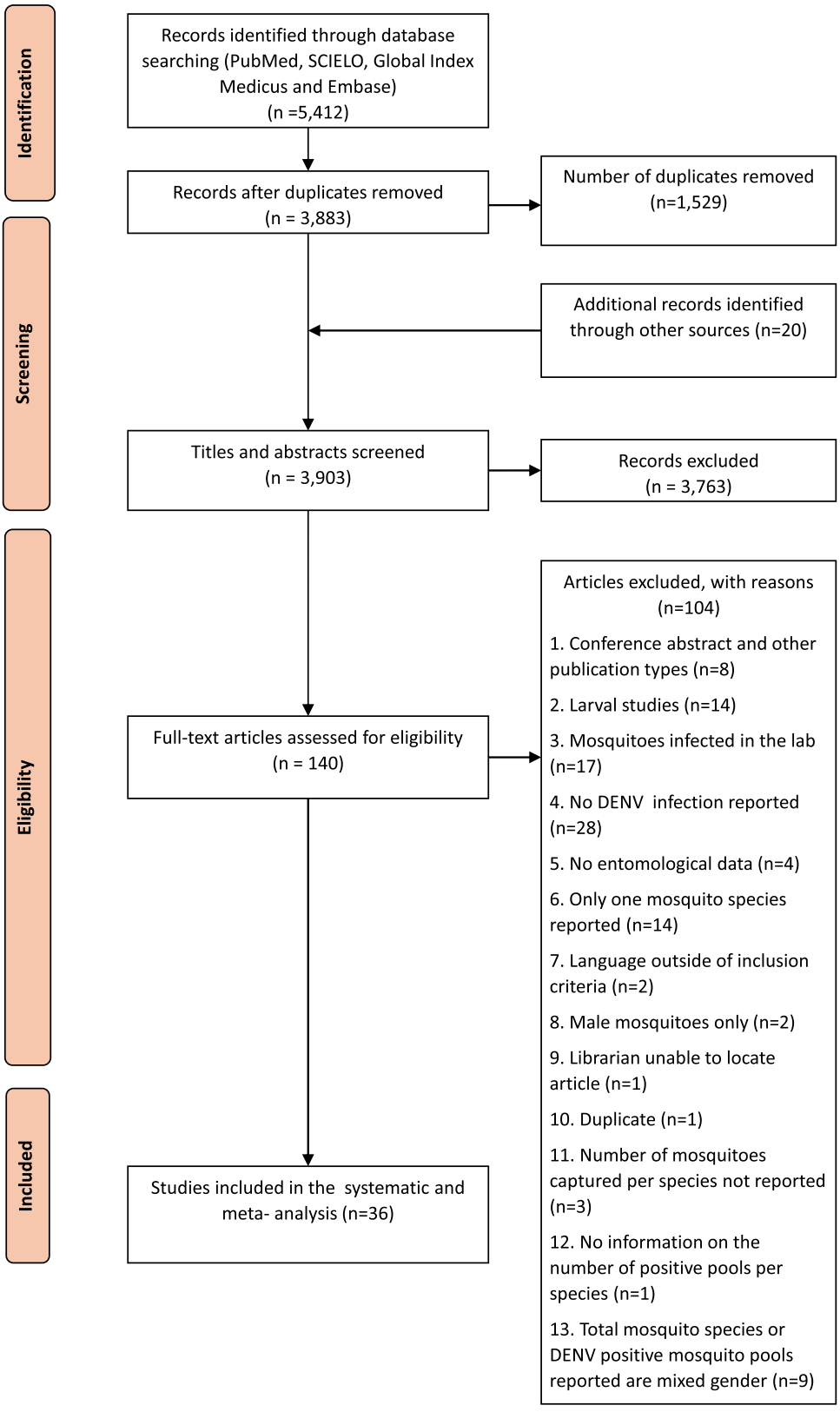

Figure 1. PRISMA flow diagram of selected studies.

(RR=0.51, 95% CI=0.43, 0.60). Contrastingly, DENV prevalence was over 113% higher among *Ae. albopictus* in the Americas (RR=2.13, 95% CI=1.44, 3.14) (Fig. S3). The number of studies in the African (n=2) and Eastern Mediterranean regions (n=2) were too low to provide meaningful results (Table 2).

There was a significantly lower DENV prevalence among *Ae. albopictus* in lower-middle-income countries (52% lower; RR=0.48, 95% CI=0.37, 0.62) and high-income countries (45% lower; RR=0.55, 95% CI=0.42, 0.72), but not for upper middle-income countries (RR=0.94, 95% CI=0.75, 1.18) (Fig. S4).

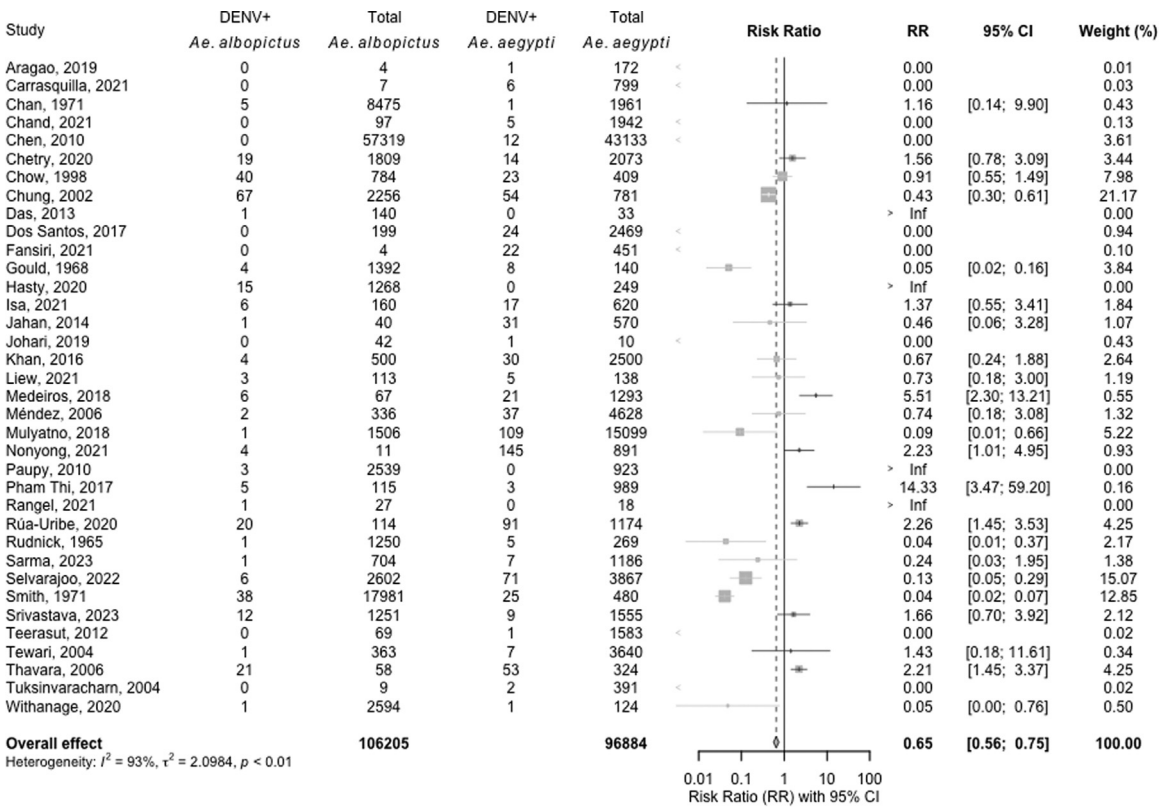

Figure 2. Forest plot of DENV infection rates in Ae. albopictus and Ae. aegypti. The plot shows risk ratio (RR) obtained from meta-analysis of data corresponding to 36 studies with data on DENV-infected mosquitoes for both species. The size of each square represents the weight for each study, and horizontal lines indicate their 95% CI. The diamond at the bottom depicts the overall RR.

In urban settings, there was a 39% lower prevalence of DENV among *Ae. albopictus* (RR=0.61, 95% CI=0.50, 0.73), but prevalences were similar in rural settings (RR=1.20, 95% CI=0.87, 1.67) (Fig. S5). There were also similar prevalences between species in studies that collected data from both urban and rural settings (Table 2).

Sixteen studies collected mosquitoes both indoors and peridomestically outdoors, and we found a 26% lower DENV prevalence among *Ae. albopictus* in this group (RR=0.74, 95% CI=0.61, 0.90). Six studies exclusively collected mosquitoes indoors with a 72% lower DENV prevalence among *Ae. albopictus* (RR=0.28, 95% CI=0.11, 0.70) (Fig. S6). There were too few studies in other specific categories to provide meaningful results (Table 2).

The prevalence of DENV was lower among *Ae. albopictus* irrespective of whether collections were done around the homes of dengue patients (65% lower; RR=0.35, 95% CI=0.26, 0.46) or independent of people's infection status (21% lower; RR=0.79, 95% CI=0.67, 0.93) (Fig. S7). However, the chi-squared test indicated that these RR were significantly different from each other (P<0.01).

One study (3%) collected mosquitoes exclusively during the dry season, while three studies (8%) collected mosquitoes only during the rainy season. Seventeen studies (44%) trapped mosquitoes in both rainy and dry seasons, and DENV prevalence was 18% lower among *Ae. albopictus* in this group (RR=0.82, 95% CI=0.69, 0.96) (Fig. S8).

Studies collected mosquitoes between 1960-2022, and there were significant differences in results across calendar periods. There was a 63% lower prevalence of DENV in *Ae. albopictus* for data collected pre-2000 (RR=0.37; 95% CI=0.30, 0.46; n=7 studies), with lower estimates for studies from the 1960s (RR=0.07; 95% CI=0.04, 0.10; n=4) versus those from the 1990s (RR=0.57; 95% CI=0.43, 0.75; n=3) (Fig. S9-S10). However, vectors' DENV prevalences were statistically indistinguishable for data collected in the 2000s (RR=1.17; 95% CI=0.81, 1.69) and since 2010 (RR=0.86; 95% CI=0.68, 1.07).

In studies that tested the DENV infection status of each mosquito, there was a borderline significant 20% lower prevalence of DENV among *Ae. albopictus* (RR=0.80, 95% CI=0.63, 1.01). In studies that tested mosquitoes in pools, there was a 41% lower prevalence of DENV in *Ae. albopictus* (RR=0.59, 95% CI=0.49, 0.70) (Fig. S11), and these RR were significantly different from each other (P=0.04).

When all mosquito body parts were processed together, DENV prevalence was 32% lower among *Ae. albopictus* (RR=0.68, 95% CI=0.57, 0.81). Similarly, when heads/thoraces were tested alone, there was a 41% lower prevalence of DENV among *Ae. albopictus* (RR=0.59, 95% CI=0.45, 0.76) (Fig. S12).

When stratifying by DENV testing methods, DENV prevalence was 77% lower among *Ae. albopictus* when immunological assays were used (RR=0.23, 95% CI=0.13, 0.42; n=5 studies) (Fig. S13). However, DENV prevalences were similar when PCR was used (RR=0.95, 95% CI=0.80, 1.12; n=28). There were too few studies using other testing methods to provide meaningful results (Table 2).

Thirty studies identified one or more DENV serotypes and were included in meta-analyses. Seventeen studies detected DENV serotype 1 (DENV-1), 24 studies detected DENV-2, 13 detected DENV-3, and 12 detected DENV-4. Prevalences were similar between species for DENV-1, DENV-2, and DENV-3 (Table 2; Fig. S14-S16). However, the prevalence of DENV-4 was significantly lower in *Ae. albopictus* compared to *Ae. aegypti* (RR=0.35, 95% CI=0.26, 0.47) (Fig. S17).

Using the MASTER scale (Fig. S1, Table S3), we found that few studies addressed equal prognosis (equivalence in prognostic variables between mosquitoes) scoring 18.9%. Ascertainment (accuracy

Table 2
Summary of the results of the subgroup meta-analyses.

Sub-group analysis	Number of studies	RR	95% CI	I^2
MOSQUITO COLLECTION				
WHO region				
Africa region	2	1.60	0.64, 3.98	NC
Americas	8	2.13	1.44, 3.14	67%
Eastern Mediterranean	2	0.61	0.24, 1.52	0%
Western Pacific & Southeast Asia combined	24	0.51	0.43, 0.60	93%
Southeast Asia	16	0.61	0.49, 0.75	95%
Western Pacific	8	0.44	0.34, 0.56	87%
Subgroup differences:†		χ^2_3=47.99	df=3	P<0.01
Country income level				
High-income	5	0.55	0.42, 0.72	68%
Upper-middle income	16	0.94	0.75, 1.18	87%
Lower-middle income	15	0.48	0.37, 0.62	93%
Subgroup differences:		χ^2_2=16.91	df=2	P<0.01
Location (urban vs rural)				
Rural	6	1.20	0.87, 1.67	94%
Urban	21	0.61	0.50, 0.73	85%
Urban and rural	5	0.94	0.55, 1.63	80%
Not reported	4	0.36	0.29, 0.46	98%
Subgroup differences:		χ^2_3=37.98	df=3	P<0.01
Location (indoors vs peridomestic outdoors vs non-peridomestic outdoors)				
Indoors	6	0.28	0.11, 0.70	58%
Indoors and peridomestic outdoors	16	0.74	0.61, 0.90	96%
Indoors and non-peridomestic outdoors	1	0.00	-	N/A
Indoors, peridomestic and non-peridomestic outdoors	3	0.64	0.27, 1.51	44%
Indoors and outdoors*	5	0.71	0.55, 0.90	81%
Peridomestic outdoors	2	0.15	0.07, 0.33	NC
Non-peridomestic outdoors	2	5.90	2.34, 14.91	NC
Peridomestic and non-peridomestic outdoors	1	NC	-	N/A
Subgroup differences:		χ^2_7=39.75	df=7	P<0.01
Collection in/around houses of dengue patients				
No	26	0.79	0.67, 0.93	86%
Yes	10	0.35	0.26, 0.46	96%
Subgroup differences:		χ^2_1=23.44	df=1	P<0.01
Season				
Dry	1	0.00	-	N/A
Rainy	3	1.32	0.52, 3.32	NC
Rainy and dry	17	0.82	0.69, 0.96	89%
Not specified	15	0.20	0.14, 0.28	87%
Subgroup differences:		χ^2_3=57.88	df=3	P<0.01
Period when data were collected				
Pre-2000	7	0.37	0.30, 0.46	94%
1960s	4	0.07	0.04, 0.10	66%
1990s	3	0.57	0.43, 0.75	70%
2000s	6	1.17	0.81, 1.69	52%
2010 onwards	23	0.86	0.68, 1.07	83%
Subgroup differences:†		χ^2_2=40.03	df=2	P<0.01
MOSQUITO PROCESSING				
Pooled samples vs individual mosquitoes				
Pooled mosquito samples	27	0.59	0.49, 0.70	93%
Individual mosquitoes	9	0.80	0.63, 1.01	93%
Subgroup differences:		χ^2_1=4.34	df=1	P=0.04
Processing of mosquito heads separately				
No	27	0.68	0.57, 0.81	95%
Yes	9	0.59	0.45, 0.76	71%
Subgroup differences:		χ^2_1=0.87	df=1	P=0.35
Mosquito testing methods				
Culture‡	2	0.04	0.0, 0.07	17%
Immunology	5	0.23	0.13, 0.42	18%
Mouse‡	1	0.04	0.01, 0.37	2%
PCR	28	0.95	0.80, 1.12	63%
Subgroup differences:		χ^2_3=163.77	df=3	P<0.01
Serotypes§				
DENV-1	17	0.85	0.55, 1.29	40%
DENV-2	24	0.97	0.73, 1.28	81%
DENV-3	13	0.76	0.47, 1.21	2%
DENV-4	12	0.35	0.26, 0.47	97%

Notes: CI = confidence interval; df = degrees of freedom; N/A = not applicable; NC = not calculable; RR = risk ratio.
* Insufficient information provided to classify sampling location as peridomestic outdoors vs non-peridomestic outdoors.
† Chi-squared test results provided for the analysis that included Western Pacific & Southeast Asia combined and studies from the 1960s and 1990s combined respectively.
‡ Note that the studies that detected DENV with culture-based methods or infecting mice used samples collected in the 1960s.
§ No chi-squared test results are provided because the studies that reported data for each serotype are not mutually exclusive (i.e., some studies reported >1 serotype).

and reliability of methods for detecting DENV) scored 75% due to lack of blinding of researchers. Most studies achieved equal recruitment for mosquito species or mosquito sampling locations (e.g., indoor vs outdoor were selected consistently), equal retention (all mosquitoes were collected, processed, and analyzed with the same rigour), temporal precedence (conditions influencing mosquito infection occurred prior to testing) and sufficient analysis safeguards (e.g., absence of numerical contradictions and data dredging).

Using a random effects meta-analysis, the overall point estimate changed little but was no longer statistically significant (RR=0.64; 95% CI=0.33, 1.23) (Fig. S18). In the leave-one-out analysis, five studies appeared to be more influential than the others (Fig. S19). Three studies [S8, S29, S30] (8% of studies) comprised 49% of the weight of the overall meta-analysis and each had a low RR (0.04, 0.13, 0.43), while the other two comprised 7% of the overall weight and had high RR (2.26, 2.21) [S26, S34]. Finally, results were similar when studies were stratified by their overall MASTER quality score (higher quality ($\geq$ 25): RR=0.62; 95% CI=0.53, 0.72; lower quality ($\leq$24): RR=0.88; 95% CI=0.63, 1.23) (Fig. S20).

Discussion

Our systematic literature review identified 36 studies reporting DENV prevalences in both *Ae. albopictus* and *Ae. aegypti*. These studies were conducted across 14 countries and territories on five continents over six decades.

The overall meta-analysis showed a 35% lower DENV prevalence among *Ae. albopictus* compared with *Ae. aegypti*, which is consistent with *Ae. albopictus* being a secondary vector. However, the prevalence of DENV in *Ae. albopictus* was far from negligible, which is compatible with it potentially having a meaningful role in DENV transmission in locations where both vectors are present. In subgroup analyses, eighteen specific sub-groups that included at least five studies were in line with the overall result. However, DENV prevalences were significantly higher among *Ae. albopictus* in studies performed in the Americas, and a further ten subgroup analyses showed no significant differences in prevalences between the two species. This may be explained in part by known differences in the bionomics of *Ae. albopictus* in the Americas, compared to its native Asian range. In the Americas, *Ae. albopictus* is thought to exhibit greater ecological plasticity, exploiting a wider range of habitats, including both artificial and natural breeding sites [9,26]. Populations have also adapted their diapause responses to local temperature and photoperiodic conditions [27]. While generally regarded as an opportunistic feeder and highly anthropophilic in Asia, *Ae. albopictus* in temperate regions of the USA shows a strong preference for mammals, with no bird-derived blood meals recorded [28]. These adaptations have important implications for its role as vector of arboviruses, particularly those affecting mammals, such as DENV.

Notably, three influential studies (8% of studies) likely drove the overall result and many subgroup analyses, since they comprised 49% of the weight of the overall meta-analysis, each had a low RR, and they were all conducted in the Western Pacific or Southeast Asia [S8, S29, S30]. Two of the studies were done in urban settings, primarily collected data prior to 2000, collected mosquitoes during rainy and dry seasons, did not conduct collections in or around the homes of dengue cases, processed mosquito abdomens or whole bodies, or tested them in pools. These papers may also have driven the significant results for the location subgroups of "indoors and peridomestic outdoors" and "indoors and outdoors" despite there only being one such study in each of these categories since the upper bounds of the confidence intervals were close to 1 (Table 2).

A recent meta-analysis reported higher DENV prevalences among *Ae. albopictus* vs *Ae. aegypti* in Asia [29]. However, these results were likely skewed by how data from testing mosquitoes in pools were analysed. Specifically, the authors estimated prevalences for pooled data by dividing the number of positive pools by the total number of pools rather than dividing by the total number of mosquitoes across pools as is standard for estimating the widely used MIR. The results are also not comparable to ours because data were combined across mosquito sexes and life stages.

Aedes aegypti and *Ae. albopictus* were respectively classified as primary and secondary DENV vectors in the 1960s based on the frequencies of isolating DENV from them and their apparent spatial association with dengue cases in Asia [16,30]. Interestingly, one of the lowest RR for any specific subgroup that included at least five studies was for the subset that collected data pre-2000 (RR=0.37, 95% CI=0.30, 0.46), and where the two studies published in the 1960s had RR of 0.04 and 0.05. *Aedes aegypti* displaced *Ae. albopictus* throughout much of Asia in the late 19th and early 20th centuries [31]. However, it is *Ae. albopictus* that has expanded the fastest in recent decades [4], and we found similar DENV prevalences between the vectors for data collected since 2000 [S3, S7].

Vector indices go beyond comparing pathogen prevalences between species by estimating the numbers of infected mosquitoes. They have been used to study the roles of *Culex* mosquitoes in West Nile virus transmission [17,19], and future work could assess whether vector indices would be useful in quantifying the roles of *Aedes* species in DENV transmission. The numbers of each species or capture rates are inputs to vector indices, but the studies we identified were not designed to obtain valid estimates (e.g., arbitrary split in sampling efforts between indoors and outdoors or between neighbourhoods, collections rarely occurred in non-domestic settings though dengue can be acquired outside the home). However, ongoing entomological surveillance ("xenosurveillance") by public health authorities could provide contemporary longitudinal data, especially if collections were suitably designed.

Our study has limitations. First, the results are susceptible to within-study confounding. For example, indoor traps may preferentially collect *Ae. aegypti* due to its propensity for resting indoors, which could bias the relative prevalence of DENV across species, especially for studies that collected mosquitoes from the homes of cases. In such instances, the DENV prevalence among *Ae. aegypti* would be biased upwards, which would bias the RR downwards. Second, there were few studies in certain subgroups, which precluded conducting multivariate analyses. Third, we used MIR values for studies that tested mosquitoes in pools, though MIR can underestimate prevalence, especially when large pools are used or if true prevalence is high, because it assumes only one infected mosquito per positive pool [24]. Studies frequently used variable pool sizes but did not provide sufficient details to calculate corrected prevalences. Future studies should report both the number and size of pools tested and the rationale for pool size selection, as pool size directly affects prevalence estimates. Reporting pool sizes would enable calculation of corrected estimates, such as maximum likelihood estimator (MLE), and support cross-study comparison [24,32]. Pools size is important as well and should be guided by the sensitivity and specificity of the assay used for detection of viral particles, as well as the true proportion of infected mosquitoes so as to correctly estimate infection rates and better understand local infection dynamics [32]. Lastly, some studies have reported similar DENV prevalences in larvae or adult male mosquitoes as in females [S6, S9, S16, S17, S26]. Because larvae and males can only be infected through vertical transmission, these data could help estimate and adjust for the vertical transmission component in females. This would improve estimates of the proportions of females infected by feeding on viraemic humans, providing a better proxy for their role in direct DENV transmission.

Our study also has several important strengths. We conducted a systematic review that identified many studies on DENV preva-

lences among females of each vector, including dozens more than included in previous reviews [7,29]. Only using results from articles that included both species was a major strength since it minimised between-study confounding and differential measurement error. Matched comparisons may have broader applicability since *Ae. albopictus* was reported to take a smaller proportion of bloodmeals from humans than *Ae. aegypti* when data on each species came from separate studies but to have similar host preferences when data on both were obtained from the same studies [33–36, S33] or further matched on being collected from the same sites within studies [37,38]. Using risk ratios instead of risk differences helped reduce bias due to imperfect sensitivities of the DENV laboratory tests. Lastly, our results could be used to parameterise simulations of the long-term impacts of vector control interventions that only target one species and quantitative risk assessments for dengue outbreaks in currently non-endemic locations.

In summary, while our results are consistent with *Ae. albopictus* being a secondary vector for DENV, its role in transmission appears to be non-trivial in locations where both it and *Ae. aegypti* are found. This was shown by: a) the RR being substantially larger than zero in the overall meta-analysis as well as some subgroup analyses, and b) the DENV prevalences being statistically indistinguishable between species in many subgroup analyses. Interestingly, the overall result and many subgroup results that showed significantly lower DENV prevalences in *Ae. albopictus* appeared to be driven by data collected pre-2000, and especially in the 1960s, with more recent studies showing similar prevalences between species. *Wolbachia* or analogous sterile insect technique or incompatible insect technique interventions have been tested in at least two dozen countries, and there is substantial government involvement in scaling up such interventions in Brazil, Indonesia, Malaysia, and Singapore [39,40]. Therefore, the roles of each vector in DENV transmission should be examined further. This would improve evaluations of the potential long-term impacts of vector control interventions that only target *Ae. aegypti* in locations where there are many *Ae. albopictus* (and vice versa) and risk assessments for outbreaks in currently non-endemic locations where *Ae. albopictus* occurs.

Author contributions

JOH conceptualised the project, provided technical guidance for literature searches and data analyses, and contributed to the writing, reviewing and editing of the manuscript. MK provided technical guidance for literature searches, reviewed full-text papers, extracted, accessed and verified the data, prepared the first draft of the manuscript, and contributed to the writing, reviewing and editing of the manuscript. FA conducted the literature search, reviewed full-text papers, extracted, accessed and verified the data, and contributed to the writing and reviewing of the manuscript. KS conducted the data analyses and contributed to the writing and reviewing of the manuscript. KA conducted the literature search, reviewed full-text papers, extracted the data, and contributed to the writing and reviewing of the manuscript. LY provided technical guidance for literature searches, and contributed to the writing, reviewing and editing of the manuscript. MC provided technical guidance for literature searches, and contributed to the writing, reviewing and editing of the manuscript. All authors had full access to all the data in the study, approved the final version of the manuscript, and had final responsibility for the decision to submit for publication.

Data sharing statement

All data used in the study has been included in the manuscript and supplementary material.

Declaration of competing interest

JOH was an employee of Merck Sharp & Dohme LLC, a subsidiary of Merck & Co., Inc., Rahway, NJ, USA during the project and may hold stock or stock options in Merck & Co., Inc., Rahway, NJ, USA. MK, MC, FA, KA, and LY received funding for this study from Merck Sharp & Dohme LLC, a subsidiary of Merck & Co., Inc., Rahway, NJ, USA.

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Ethical approval

This study is a systematic review of previously published data and did not involve any human participants nor identifiable data. Therefore, ethical approval is not required.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.ijid.2025.108004.

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