RESEARCH ARTICLE

A systematic review and meta-analysis of the potential non-human animal reservoirs and arthropod vectors of the Mayaro virus

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Abstract

Improving our understanding of Mayaro virus (MAYV) ecology is critical to guide surveillance and risk assessment. We conducted a PRISMA-adherent systematic review of the published and grey literature to identify potential arthropod vectors and non-human animal reservoirs of MAYV. We searched PubMed/MEDLINE, Embase, Web of Science, SciELO and grey-literature sources including PAHO databases and dissertation repositories. Studies were included if they assessed MAYV virological/immunological measured occurrence in field-caught, domestic, or sentinel animals or in field-caught arthropods. We conducted an animal seroprevalence meta-analysis using a random effects model. We compiled granular georeferenced maps of non-human MAYV occurrence and graded the quality of the studies using a customized framework. Overall, 57 studies were eligible out of 1523 screened, published between the years 1961 and 2020. Seventeen studies reported MAYV positivity in wild mammals, birds, or reptiles and five studies reported MAYV positivity in domestic animals. MAYV positivity was reported in 12 orders of wild-caught vertebrates, most frequently in the orders Charadriiformes and Primate. Sixteen studies detected MAYV in wild-caught mosquito genera including *Haemagogus*, *Aedes*, *Culex*, *Psorophora*, *Coquillettidia*, and *Sabethes*. Vertebrate animals or arthropods with MAYV were detected in Brazil, Panama, Peru, French Guiana, Colombia, Trinidad, Venezuela, Argentina, and Paraguay. Among non-human vertebrates, the Primate order had the highest pooled seroprevalence

at 13.1% (95% CI: 4.3–25.1%). From the three most studied primate genera we found the highest seroprevalence was in *Alouatta* (32.2%, 95% CI: 0.0–79.2%), followed by *Callithrix* (17.8%, 95% CI: 8.6–28.5%), and *Cebus/Sapajus* (3.7%, 95% CI: 0.0–11.1%). We further found that MAYV occurs in a wide range of vectors beyond *Haemagogus* spp. The quality of evidence behind these findings was variable and prompts calls for standardization of reporting of arbovirus occurrence. These findings support further risk emergence prediction, guide field surveillance efforts, and prompt further *in-vivo* studies to better define the ecological drivers of MAYV maintenance and potential for emergence.

Author summary

Mayaro virus (MAYV) is an emerging tropical public health threat in the Americas. We conducted a georeferenced, quality-graded systematic review to evaluate the current evidence regarding MAYV occurrence in non-human vertebrates and arthropods. Overall, 57 studies were eligible out of 1523 screened, published between the years 1961 and 2020. Seventeen studies reported MAYV positivity in wild mammals, birds, or reptiles and five studies reported MAYV positivity in domestic animals. MAYV positivity was reported in 12 orders of wild-caught vertebrates, most frequently in the orders Charadriiformes and Primate. Our systematic review identified 12 orders of wild-caught vertebrates and seven mosquito genera with evidence of MAYV occurrence. Primates had the highest pooled MAYV seroprevalence according to a seroprevalence meta-analysis. The graded quality of evidence behind these findings was variable and prompts calls for standardization of reporting of MAYV and perhaps other emerging arbovirus occurrence in animals and vectors. This study provides important information for public health authorities and disease ecologists concerned with the growing threat of MAYV in Latin America. Our analysis provides a foundation for future laboratory and field studies focused on the MAYV transmission cycle.

Introduction

First detected in Trinidad in 1954 [1], Mayaro virus (MAYV) is a zoonotic *Alphavirus* that is endemic in several Latin American countries. Like Chikungunya virus (CHIKV), MAYV may cause complications such as debilitating arthralgia but often presents with a non-specific constellation of symptoms and signs that may be clinically indistinguishable from other vector borne diseases such as dengue or Zika [2]. There is no current licensed vaccine or antiviral treatment for MAYV infections, and the current standard of clinical treatment is supportive care only [2,3].

MAYV has caused periodic outbreaks in humans in Brazil [4,5], Bolivia [6], and Venezuela [7], while surveillance studies and serological surveys have detected MAYV in humans in several countries throughout the Americas including Peru [8], Suriname [9], Mexico [10], Colombia [11], French Guiana [12], and Haiti [13]. These findings demonstrate widespread circulation of the virus throughout the region. A recent 2019 epidemiological alert by the Pan American Health Association (PAHO) has emphasized the need for increased awareness of and extended surveillance for this emerging virus in the Americas [3]. However, the precise areas of risk from MAYV throughout the Americas remain unclear. Understanding the ecology and distribution of MAYV remains a major obstacle in predicting areas that are at high risk of transmission to humans and domestic animals.

Current evidence suggests that MAYV is maintained in nature through a sylvatic transmission cycle involving mosquito vectors and non-human animal reservoirs. Therefore, human MAYV cases reported to date likely represent direct sylvatic spillovers. Residing near forested areas [12] and hunting in the rainforest [14] have been identified as risk factors for MAYV infection in humans, highlighting the importance of the sylvatic transmission cycle and the potential for spillover events.

Identification of the non-human vertebrate animals (i.e., reservoirs) involved in MAYV transmission is an important step in delineating the human populations at greatest risk. The spillover of MAYV into humans represents a complex interaction of processes involving the density and distribution of reservoirs and vectors, as well as the prevalence and intensity of infection among reservoirs [15].

Identifying the non-human vertebrates that may serve as MAYV reservoirs is a difficult task due to a myriad of issues including, but not limited to, the challenges associated with establishing evidence of infection in wild animal populations [16,17]. High seroprevalence of a pathogen in an animal population does not necessarily implicate a given host as an efficient reservoir; conversely, low seroprevalence at a single point in time cannot definitively rule out an animal as a reservoir [17]. Due to the relatively short viremia of MAYV (approximately 3–10 days) molecular assays may be unsuccessful in detecting virus [18], necessitating the use of serological assays such as hemagglutination-inhibition (HI) assays, enzyme-linked immunosorbent assays (ELISA), or plaque-reduction neutralization tests (NT).

Several studies have been conducted to clarify the precise vertebrate hosts that may serve as MAYV reservoirs. High seroprevalence among non-human primates (NHPs) in Brazil [19], French Guiana [12], and Panama [20] provides evidence that NHPs may play an important role in the MAYV transmission cycle. MAYV antibodies have also been detected in mammals including rodents and marsupials [21] as well as several avian species [19]. Unfortunately, there is significant heterogeneity in the study methods used to identify potential MAYV reservoirs and there remains a high level of uncertainty surrounding the role of various non-human vertebrate species in the MAYV transmission cycle.

Studies have also been conducted in wild-caught mosquito populations as well as in controlled laboratory conditions in order to identify potential arthropod vectors of MAYV. One study in Brazil [19] suggested that the canopy-dwelling *Haemagogus janthinomys* mosquito is an important vector of MAYV. Additional mosquito species including *Aedes aegypti*, *Ae. albopictus*, and several anopheline species have been shown to be competent vectors in laboratory settings [22–24], posing a potential but as yet theoretical risk of urban MAYV cycles. The occurrence of MAYV in the city of Manaus has also led to concerns about the involvement of *Aedes* mosquitoes in a MAYV urban transmission cycle [25]. In addition, mathematical modeling has demonstrated the potential for urban outbreaks of MAYV in Brazil [26] and Colombia [27].

Although many non-human vertebrate animals and arthropod species have been proposed as capable MAYV reservoirs or vectors, our understanding of the MAYV transmission cycle and ecology remains limited. Collating and evaluating the current evidence regarding the potential MAYV reservoirs and vectors are important steps in characterizing MAYV transmission ecology and identifying the communities at greatest risk for MAYV outbreaks. Therefore, the goal of this systematic review is to evaluate the current evidence regarding MAYV occurrence in non-human vertebrates and arthropods. We present here the first structured evaluation of the potential vector and non-human reservoir range of MAYV, including the development of custom criteria for grading the quality of evidence of arbovirus occurrence in invertebrate and vertebrate non-human hosts.

Methods

This systematic review and meta-analysis were conducted according to the PRISMA 2020 Checklist [28] (see S1 File). A protocol was developed but was not uploaded to PROSPERO.

Information sources

We conducted a systematic review of original research articles, reports, and dissertations that attempted to identify potential non-human animal reservoirs or arthropod vectors of MAYV. We first searched Embase, Web of Science, PubMed/MEDLINE, and SciELO databases for English, Spanish, and Portuguese language articles published between 1954 (the year MAYV was first isolated) and March 21, 2020. We searched all databases using the highly sensitive search term "Mayaro". A PubMed/MEDLINE alert using the search term "Mayaro" was also set to capture any additional studies that were published between the initial search and May 2021. This database search was extended using bioRxiv (https://www.biorxiv.org/) and medRxiv (https://www.medrxiv.org/) pre-print databases. We complemented these database search results with 'grey literature,' including hand-searched bibliographies of the included articles and MAYV review articles (including systematic reviews), dissertations from several Brazilian university repositories, the Pan American Health Organization (PAHO) Institutional Repository for Information Sharing database (iris.paho.org), the GIDEON database (https://www.gideononline.com/), and GenBank [29] (https://www.ncbi.nlm.nih.gov/genbank/). In addition, we searched conference handbooks that are available online (2004–2019) from the American Society of Tropical Medicine and Hygiene (https://www.astmh.org/annual-meeting/past-meetings).

Eligibility criteria

We included studies that evaluated past or current MAYV infection in non-human vertebrates using methods including virus isolation, molecular detection, and serosurveys. We also included studies that screened arthropods for MAYV using virus isolation and molecular detection. Original research studies were considered for eligibility if they assessed MAYV positivity in field-caught, captive, or sentinel non-human vertebrates or field-caught arthropods. Studies that met any of the following exclusion criteria were not included: studies not reporting original data (e.g., review articles, perspective pieces, editorials, recommendations, and guidelines); duplicate studies; *in vitro* studies such as vector cell-line or mammal cell line experiments; laboratory-based vector competence studies that did not explicitly demonstrate the detection of MAYV in a wild-caught vector; *in-vivo* lab-reared animal studies or any laboratory-based study that experimentally inoculated an animal to test theoretical reservoir status.

Selection process

All articles were organized using EndNote software version X9 (Clarivate, Philadelphia, Pennsylvania, USA), and data were abstracted into a Microsoft Excel table. Two reviewers independently screened all titles and abstracts to determine articles that could immediately be excluded and articles that should be included in the second stage of review. Results were compared to reconcile any differences between the two reviewers. The first and second reviewers then independently read the full text of potentially eligible articles identified through screening and selected the articles that were candidates for inclusion in the study. Results were compared to reconcile any differences between the two reviewers. A third-party reviewer adjudicated when consensus was not reached between the two reviewers during the first or second stage review. From those studies deemed eligible, data were extracted from articles by one reviewer using the data abstraction tool in Microsoft Excel.

Data abstraction

Relevant information was abstracted by one reviewer in an Excel sheet. Information for each article was abstracted across several domains including publication details (author and affiliation, study title, study funding), study methods (date and location of study, study design, laboratory methods to assess MAYV positivity), and study results (sample size, taxonomic classification, proportion of animals testing positive for MAYV, location of vertebrates/arthropods testing positive for MAYV). A second reviewer randomly selected and reviewed five articles for review to validate the data abstraction process.

Grading quality of evidence

We developed a customized grading system to assess the quality of each study included in our review. Several published studies have employed a similar grading system to assess evidence quality of included articles [30–32]. We assigned each study in our systematic review a grade for each of four quality items: clarity of research question/objective (*Was the research question/ objective clearly described and stated*?); description of study methods (*Were the study methods presented in a reproducible way*?); description of sampling methods (*Was the sampling method described in detail*?); and validity of diagnostic tests (*Was MAYV positivity measured in a valid way*?). For each quality item, eligible studies were assigned a score of 3 (strong evidence), 2 (moderate evidence), 1 (weak evidence), or unable to judge. Studies were deemed unable to judge if the information provided was insufficient to assign quality scores (e.g., a single GenBank entry or conference abstract).

A score of 3 was assigned for the *description of sampling methods* item if authors thoroughly described the type of trap used, the habitats in which traps were set, how often traps were checked, and the results of trapping (i.e., were animals reported to the species level). For studies that assessed MAYV in vertebrate animals, a score of 3 was assigned for the *validity of diagnostic tests* item if MAYV positivity was assessed using RT-PCR, viral culture, or high-specificity serological method (i.e., plaque reduction NT); a score of 2 was assigned if MAYV positivity was assessed using non-specific serological assay (i.e., HI and ELISA); and a score of 1 was assigned if MAYV positivity was based on presumptive exposure only with no confirmatory assay. For studies that assessed MAYV in arthropods, a score of 3 was assigned for this item if MAYV positivity was assessed using viral culture; a score of 2 was assigned if MAYV positivity was assessed using RT-PCR or metagenomics; and a score of 1 was assigned if MAYV positivity was based on presumptive exposure only with no confirmatory assay. A score of "NA" was assigned for the *validity of diagnostic tests* item if studies did not detect MAYV positivity in any animal or arthropod samples.

Quality review scores were recorded in two different Excel documents for animal reservoir studies and arthropod vector studies, respectively. Two reviewers independently graded the evidence quality for each study and results were compared to reconcile any differences between the two reviewers. A third-party reviewer adjudicated if consensus was not reached between the two reviewers.

Data analysis

Descriptive analysis

Descriptive statistics were presented by species for potential animal reservoirs showing the total sample size, proportion infected, and locations of infected animals. Descriptive statistics were presented by species for potential arthropod vectors showing the total sample size and total pools tested for virus (if applicable), the number of MAYV isolates or PCR-positive pools,

and locations of infected arthropods. Maps were developed using ArcGIS software [33] to display the geographic distribution of MAYV-positive animals and vectors.

Pooled analysis

Due to the heterogeneity of study designs and outcome measurements, a quantitative meta-analysis across all eligible studies was not possible. Instead, we conducted a seroprevalence meta-analysis using the studies that reported MAYV seroprevalence (i.e., using serological methods including HI, ELISA, or NT) in non-human vertebrate animals. Pooled seroprevalence estimates were stratified by taxonomic order and an additional analysis was conducted among the various Primate genera. Orders were excluded from the analysis if the total sample size was less than 10 or if no MAYV-positive samples were reported within that order. Pooled seroprevalence was first calculated based on all available data, regardless of test method. This included the samples that tested MAYV-positive based on HI alone (when no confirmatory assay was performed) as well as the samples that were confirmed positive by an NT. Only monotypic reactions to MAYV were included in the meta-analysis in the absence of confirmatory NT. A sensitivity analysis was then conducted using only the MAYV-positive samples that were confirmed using NT. Positive samples that were based on HI alone (without confirmatory NT) were excluded from this analysis, although all MAYV-negative samples were retained. This sensitivity analysis was conducted to account for the low specificity of HI compared to NT [34] and provided a more conservative estimate of seroprevalence.

Due to the substantial differences across studies including sample size, study design, species sampling methods, and geographical location, a random effects model was used for analysis [35,36]. The Freeman-Tukey double-arcsine transformation was implemented to calculate a proportion, based on the recommendation of Barendregt et al. [37]. A sensitivity analysis was conducted using a generalized linear mixed model (GLMM) with a logit transformation, due to the potential for misleading results with the double-arccosine transformation [38,39]. Measures of variance (τ^2), heterogeneity (I^2), and statistical significance are presented for each random effects model. An additional sensitivity analysis was conducted using a fixed effects model. Results of sensitivity analyses are presented in the S4–S8 Tables.

The I^2 statistic measures inconsistency across study results and is calculated as $I^2 = 100\%$ x (Q—df) /Q [40]. The I^2 statistic ranges between 0% and 100%, where a value of 0% represents no heterogeneity and larger values represent increased heterogeneity. Following recently published systematic reviews, we defined high heterogeneity as $I^2 > 50\%$ [41,42]. Animal seroprevalence estimates with 95% confidence intervals (CIs) weighted by sample size are presented as forest plots. All analyses were conducted using the '*meta*' package in R statistical software version 4.0.2 (R Project for Statistical Computing, Vienna, Austria) [43,44].

Estimation of bias

An assessment of publication bias was carried out for meta-analyses that included five studies or more. Bias was assessed using funnel plots and tests for funnel plot asymmetry based on methods proposed by Egger [45]. If the Egger's test revealed bias, the Trim and Fill technique was used to estimate the effect of missing studies on the outcomes of the meta-analysis [46].

Georeferencing of MAYV occurrence

All available location information from each confirmed MAYV infection (animal and mosquito) was extracted from each article and georeferenced based on methods that have been described previously [47,48]. Each occurrence of MAYV was designated as either a point or polygon location according to the spatial resolution provided in the study. When specific

latitude and longitude coordinates were provided, they were verified in GoogleMaps and designated as a point location. If a neighborhood, town, village, or small city was explicitly mentioned in the article and fell within a 5x5 km grid cell, it was designated as a point location and its centroid coordinates were recorded. For studies that report a less precise spatial resolution such as states or counties, first level (ADM1) or second level (ADM2) administrative divisions were recorded as polygons. If the size of a specific named location was greater than a 5x5 km grid cell the occurrence was assigned to a custom polygon created in ArcGIS that encompassed the extent of that location. If place names were duplicated (i.e., the ADM1 and ADM2 units had the same name), the coarsest spatial resolution was used. Country shapefiles were accessed through the geoBoundaries Global Administrative Database [49].

Results

General findings

We identified a total of 57 research items that met our eligibility criteria out of 1523 research items screened, including 46 research articles, seven dissertations, two GenBank entries, one laboratory report, and one abstract (see Table 1 for a full list of eligible items and citations). Thirty-nine (68%) of the included items assessed MAYV infection in non-human vertebrates while 29 (51%) items assessed MAYV infection in arthropods. Of the 57 eligible items, 24 (42%) were included in the vertebrate seroprevalence meta-analysis, and the remaining items were only included in the qualitative analysis. A flow chart describing the article search and selection process is presented in Fig 1. Five articles were identified that met the inclusion criteria but were deemed to be reporting the same data as other included articles. These include de Thoisy *et al.*, (2001) [50] and Talarmin *et al.*, (1998) [12] (both reporting the same data as de Thoisy *et al.*, (2003) [21]), Aitken *et al.*, (1960) [51] (reporting the same data as Aitken *et al.*, (1969) [52]), Batista *et al.*, 2013 [53] (reporting the same data as Paulo *et al.*, (2015) [54]), and Woodall (1967) [55] (reporting the same data as Taylor, (1967) [56]). These articles were excluded from this systematic review.

Studies were conducted in the following countries: Brazil (n = 34), Panama (n = 5), Colombia (n = 4), Peru (n = 3), Trinidad and Tobago (n = 2), French Guiana (n = 1), Venezuela (n = 1), Costa Rica (n = 1), and the United States of America (n = 1). Several studies reported data from multiple countries including Argentina/Paraguay (n = 1), Panama/Colombia (n = 1), and Brazil/Trinidad and Tobago (n = 1). The majority of studies were conducted after the year 2000 (n = 33), although some studies were conducted between 1950–1969 (n = 9), 1970–1989 (n = 8), or 1990–1999 (n = 4). Quality scores for all included studies are reported in Table 2.

MAYV in wild-caught non-human vertebrate animals

Thirty-nine (68%) studies in our systematic review assessed MAYV infection in wild-caught non-human vertebrate animals (including birds, mammals, and reptiles). Seventeen (44%) of these studies identified at least one non-human vertebrate that was positive for MAYV infection. Of the 27 taxonomic orders studied, 12 (44.4%) had evidence of MAYV infection: Artiodactyla (even-toed ungulates), Caprimulgiformes (nightbirds), Carnivora, Charadriiformes (shorebirds), Cingulata (armadillos), Columbiformes (pigeons and doves), Didelphimorphia (opossums), Passeriformes (passerine birds), Pilosa (sloths and anteaters), Primate, Rodentia, and Squamata (scaled reptiles). The greatest number of MAYV-positive animal species were found in the order Charadriiformes (n = 16 positive species) and the order Primate (n = 15 positive species). (See S1 Table for complete mammal data and S2 Table for complete avian data).

Table 1. Eligible Study Characteristics.

Reference	Study Period	Country	Arthropods Tested (n)	Vertebrate non-human animals tested (n)[a]	MAYV infection reported
Aitken, 1969 [52]	1953–1963	Trinidad	1,568,439	- - -	Yes
Araujo, 2003 [57]	2002	Brazil	- - -	555	Yes
Araujo, 2004 [58]	2003	Brazil	- - -	202	No
Araujo, 2004b [59]	2003	Brazil	- - -	495	Yes
Araujo, 2012 [60]	2007–2008	Brazil	- - -	95	Yes
Araujo, 2012b [61]	2009	Brazil	- - -	102	Yes
Azevedo, 2009 [62]	2008	Brazil	832	- - -	Yes
Batista, 2012 [63]	2010	Brazil	122	65	Yes
Calisher, 1974 [64]	1967	USA[b]	- - -	1,300	Yes
Carrera, 2020 [65]	2017	Panama	113	- - -	No
Casseb, 2010 [66]	2009	Brazil	- - -	2191	Yes
Casseb, 2016 [67]	2009	Brazil	- - -	753	Yes
Catenacci, 2017 [68]	2006–2014	Brazil	239	142	Yes
Cruz, 2009 [69]	2006–2008	Brazil	- - -	85	No
Degallier, 1992 [70]	1974–1988	Brazil	2,005,069	6,248	Yes
De Thoisy, 2003 [21]	1994–1995	French Guiana	- - -	579	Yes
Diaz, 2007 [71]	1994	Argentina, Paraguay	- - -	90	No
Esposito, 2015 [72]	1960	Brazil	NA[d]	- - -	Yes
Ferreira, 2020 [73]	2017–2018	Brazil	10,569	- - -	Yes
Galindo, 1966 [74]	1959–1962	Panama	377,492	2,444	Yes
Galindo, 1967 [75]	1966	Panama	11,829	- - -	Yes
Galindo, 1983 [76]	1972–1979	Panama	NA[c]	NA[c]	Yes
GenBank KY618129	1991	Brazil	NA[d]	- - -	Yes
GenBank KY618130	2011	Brazil	NA[d]	- - -	Yes
Gibrail, 2015 [77]	2011–2014	Brazil	- - -	50	No
Gomes, 2019 [78]	2018	Brazil	- - -	213	Yes
Groot, 1961 [79]	1958–1960	Colombia	41,564	- - -	Yes
Groot, 1964 [11]	1956–1961	Colombia	- - -	34	Yes
Henriques, 2008 [80]	2002–2005	Brazil	37,519	- - -	No
Hoch, 1981 [19]	1978–1979	Brazil	10,667	1785	Yes
Kubiszeski, 2017 [81]	2014–2015	Brazil	778	- - -	Yes
Laroque, 2014 [82]	2008–2010	Brazil	- - -	131	Yes
Maia, 2019 [83]	2017	Brazil	4786	- - -	Yes
Martinez, 2020 [84]	2018–2019	Colombia	169	- - -	No
Medlin, 2016 [85]	2005–2007	Costa Rica	- - -	94	No
Medina, 2015 [86]	1999	Venezuela	- - -	NA[d]	Yes
Moreira-Soto, 2018 [87]	2012–2017	Brazil	- - -	103	Yes
Nunes, 2009 [88]	2005	Brazil	- - -	181	No
Paulo, 2015 [54]	2012–2014	Brazil	- - -	43	Yes
Pauvolid-Correa, 2010 [89]	2007	Brazil	- - -	135	No
Pauvolid-Correa, 2015 [90]	2009–2011	Brazil	- - -	748	Yes
Pauvolid-Correa, 2008 [91]	2007	Brazil	1,759	NA[e]	No
Perez, 2019 [92]	2007–2008	Peru	- - -	90	Yes
Pinheiro, 1974 [93]	1971–1974	Brazil	NA[c]	NA[c]	Yes
Pinheiro, 2019 [94]	2017	Brazil	867	- - -	No
Powers, 2006 [95]	N/A	N/A	NA[d]	NA[d]	Yes
Price, 1978 [96]	1972–1974	Trinidad	- - -	997	No

(Continued)

Table 1. (Continued)

Reference	Study Period	Country	Arthropods Tested (n)	Vertebrate non-human animals tested (n)[a]	MAYV infection reported
Ragan, 2019 [97]	N/A	N/A	---	NA[c]	No
Sanmartin, 1973 [98]	1967	Colombia	27,437	480	No
Scherer, 1975 [99]	1970–1971	Peru	1,500	NA[c]	No
Serra, 2016 [100]	2013	Brazil	4,556	---	Yes
Seymour, 1983 [20]	1974–1976	Panama	---	304	Yes
Silva, 2017 [101]	2016	Brazil	3,750	---	No
Srihongse, 1974 [102]	1967	Panama/Colombia	---	2026	Yes
Tauro, 2019 [103]	2017	Brazil	125	---	No
Taylor, 1967 [56]	N/A	Brazil/Trinidad	NA[c]	NA[c]	Yes
Turell, 2019 [104]	2001–2002	Peru	---	20	No

[a] Includes wild-caught, sentinel, and domestic animals.

[b] Migratory birds captured in Louisiana.

[c] Unable to determine the total number of animals or arthropods tested for MAYV.

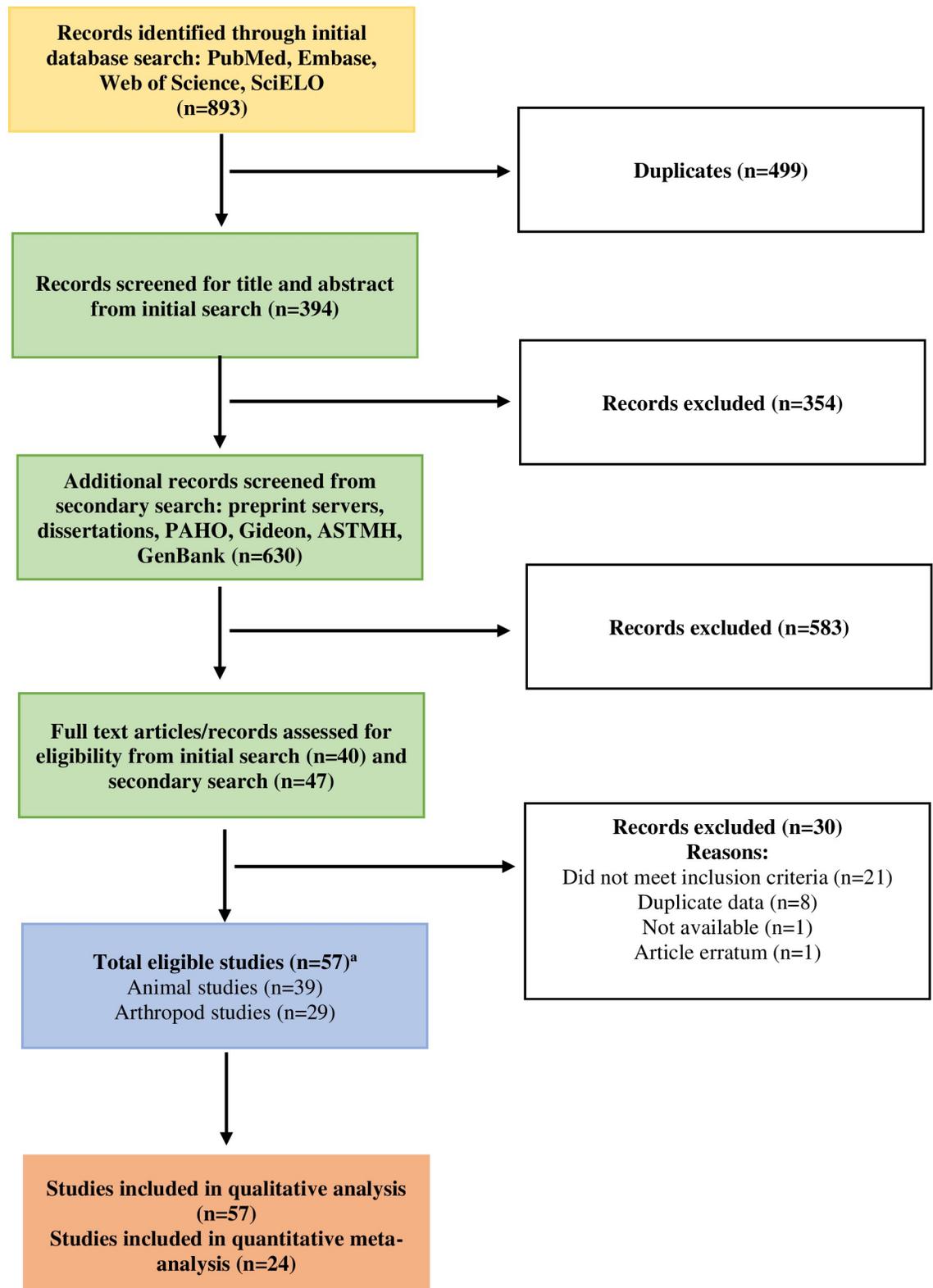[d] Genomic sequence only. No additional information provided.

[e] Horse seroprevalence data collected but recorded in another study.

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Table 3 reports NHP species that were detected with MAYV antibodies. Only studies with positive results are shown on Table 3; other negative studies are listed in the S1 Table. High MAYV seroprevalence was confirmed by NT among *Alouatta seniculus* monkeys in individual studies in French Guiana [21] (n = 51/98) and among *Callithrix argentata* monkeys in Brazil [19] (n = 32/119). In addition, 29 *Cebus libidinosus* monkeys from wildlife screening centers were detected with MAYV antibodies according to HI, although only six were reported as monotypic reactions [82]. Diagnosis in these monkeys was not confirmed by NT. An additional *Cebus libidinosus* monkey presented a heterotypic reaction to MAYV (titer of 1:20) and four additional viruses according to HI (including a titer of 1:640 for Oropouche virus) [77]. However, based on the study's protocol, confirmatory NT was only performed for viruses with titers $\geq$ 1:40.

Among the 12 additional NHP species with evidence of past MAYV infection, nine were confirmed by NT and three by HI alone. In addition, MAYV positivity was reported in the following NHP genera, although animals were not reported to species: *Aotus* (n = 1/4), *Alouatta* (n = 7/11), *Cebus* (n = 4/13), *Sapajus* (n = 3/43), and *Saimiri* (n = 1/1). The authors reporting MAYV positivity in the *Aotus*, *Alouatta*, *Cebus*, and *Saimiri* genera noted that these results should be interpreted with caution due to potential for cross-reactivity with Una virus (UNAV) [11]. In one study conducted in Brazil, two of 11 Chikungunya virus (CHIKV)-positive serum samples (in the species *Sapajus xanthosternos* and *Ateles marginatus*) neutralized MAYV with titers of 1:40 in plaque reduction NTs [87]. These two samples were considered MAYV-positive and included in our meta-analysis. One additional study [71] detected neutralizing antibodies against both UNAV and MAYV in 21 *Alouatta caraya* monkeys. However, all 21 monkeys were diagnosed with UNAV based on a 4-fold titer difference between the two viruses. Therefore, we considered these monkeys MAYV-negative and did not include them in our meta-analysis. Finally, in 1963 the Belem Virus laboratory reported MAYV infection in seven NHPs based on HI tests alone [56]. These monkeys were described as Tamarin, Pithecia, and Cebus although no further information was provided regarding sampling method, testing protocol, or primate species.

MAYV antibodies were also detected in 21 bird species from the order Charadriiformes (n = 16) and Passeriformes (n = 5). All MAYV-positive birds were found in Brazil, with the

Records identified through initial database search: PubMed, Embase, Web of Science, SciELO (n=893)

Duplicates (n=499)

Records screened for title and abstract from initial search (n=394)

Records excluded (n=354)

Additional records screened from secondary search: preprint servers, dissertations, PAHO, Gideon, ASTMH, GenBank (n=630)

Records excluded (n=583)

Full text articles/records assessed for eligibility from initial search (n=40) and secondary search (n=47)

Records excluded (n=30)
Reasons:
Did not meet inclusion criteria (n=21)
Duplicate data (n=8)
Not available (n=1)
Article erratum (n=1)

Total eligible studies (n=57)[a]
Animal studies (n=39)
Arthropod studies (n=29)

Studies included in qualitative analysis (n=57)
Studies included in quantitative meta-analysis (n=24)

[a] Eleven articles assessed MAYV in both non-human animals and arthropods

Fig 1. Flow diagram for search and selection of articles.

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Table 2. Quality Review Scores.

	Vertebrate animals				Arthropods			
	Research question	Study methods	Sampling method	MAYV+ test method[a]	Research question	Study methods	Sampling method	MAYV+ test method[a]
Aitken, 1969 [52]	---	---	---	---	3	2	2	3
Araujo, 2003 [57]	3	3	2	2	---	---	---	---
Araujo, 2004 [58]	3	3	3	NA	---	---	---	---
Araujo, 2004b [59]	3	3	2	2	---	---	---	---
Araujo, 2012 [60]	3	3	3	2	---	---	---	---
Araujo, 2012b [61]	3	3	2[b]	2	---	---	---	---
Azevedo, 2009 [62]	---	---	---	---	2	2	2	3
Batista, 2012 [63]	2	3	2	2	2	3	2	NA
Calisher, 1974 [64]	3	3	2	3	---	---	---	---
Carrera, 2020 [65]	---	---	---	---	3	3	3	N/A
Casseb, 2010 [66]	3	3	2[b]	2	---	---	---	---
Casseb, 2016 [67]	3	3	3[b]	2	---	---	---	---
Catenacci, 2017 [68]	3	3	3	N/A	3	3	2	2
Cruz, 2009 [69]	2	3	2	N/A	---	---	---	---
Degallier, 1992 [70]	3	2	2	2	3	2	3	N/A
De Thoisy, 2003 [21]	3	3	2	3	---	---	---	---
Diaz, 2007 [71]	3	2	2	3	---	---	---	---
Esposito, 2015 [72]	---	---	---	---	Unable to judge	Unable to judge	Unable to judge	3
Ferreira, 2020 [73]	---	---	---	---	3	3	3	3
Galindo, 1966 [74]	3	3	2	N/A	3	3	3	3
Galindo, 1967 [75]	---	---	---	---	3	3	2	2
Galindo, 1983 [76]	3	3	3	N/A	3	2	2	3
GenBank KY618129	---	---	---	---	Unable to judge	Unable to judge	Unable to judge	3
GenBank KY618130	---	---	---	---	Unable to judge	Unable to judge	Unable to judge	3
Gibrail, 2015 [77]	3	3	2	2	---	---	---	---
Gomes, 2019 [78]	3	3	3[b]	3	---	---	---	---
Groot, 1961 [79]	---	---	---	---	3	3	3	3
Groot, 1964 [11]	3	3	3	2	---	---	---	---
Henriques, 2008 [80]	---	---	---	---	3	3	3	N/A
Hoch, 1981 [19]	3	3	3	3	3	3	3	3
Kubiszeski, 2017 [81]	---	---	---	---	3	3	3	2
Laroque, 2014 [82]	3	3	2	2	---	---	---	---
Maia, 2019 [83]	---	---	---	---	3	3	3	3
Martinez, 2020 [84]	---	---	---	---	3	3	2	N/A
Medlin, 2016 [85]	3	3	3	N/A	---	---	---	---
Medina, 2015 [86]	3	2	2[c]	3	---	---	---	---
Moreira-Soto, 2018 [87]	3	3	3	3	---	---	---	---
Nunes, 2009 [88]	2	3	2	N/A	---	---	---	---
Paulo, 2015 [54]	3	3	3	2	---	---	---	---
Pauvolid-Correa, 2010 [89]	3	2	2[b]	N/A	---	---	---	---
Pauvolid-Correa, 2015 [90]	3	3	3	3	---	---	---	---

(Continued)

Table 2. (Continued)

	Vertebrate animals				Arthropods			
	Research question	Study methods	Sampling method	MAYV+ test method[a]	Research question	Study methods	Sampling method	MAYV+ test method[a]
Pauvolid-Correa, 2008 [91]	---	---	---	---	3	3	2	N/A
Perez, 2019 [92]	3	2	2	3	---	---	---	---
Pinheiro, 1974 [93]	3	2	2	2	3	2	2	N/A
Pinheiro, 2019 [94]	---	---	---	---	3	3	3	N/A
Powers, 2006 [95]	3	2	Unable to judge	3	3	2	Unable to judge	3
Price, 1978 [96]	3	2	2	N/A	---	---	---	---
Ragan, 2019 [97]	Unable to judge	Unable to judge	Unable to judge	Unable to judge	---	---	---	---
Sanmartin, 1973 [98]	3	3	3	N/A	2	3	2	N/A
Scherer, 1975 [99]	2	3	3[c]	N/A	2	2	2	N/A
Serra, 2016 [100]	---	---	---	---	3	3	3	3
Seymour, 1983 [20]	2	3	2	3	---	---	---	---
Silva, 2017 [101]	---	---	---	---	3	3	3	N/A
Srihongse, 1974 [102]	3	2	2	2	---	---	---	---
Tauro, 2019 [103]	---	---	---	---	3	2	2	N/A
Taylor, 1967 [56]	Unable to judge	Unable to judge	Unable to judge	3	Unable to judge	Unable to judge	Unable to judge	3
Turell, 2019 [104]	3	2	3[c]	N/A	---	---	---	---

[a] Studies were assigned a score of NA for this criterion if no MAYV-positive samples were reported.

[b] Domestic animals only.

[c] Sentinel animals only.

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exception of one MAYV isolate from a migrating bird captured in Louisiana USA [64]. A high MAYV-seroprevalence (n = 34/122) was reported by the Belem Laboratory in 1963 among *Columbigallina* birds, although no additional information was provided regarding sampling method or bird species. MAYV antibodies were also detected in seven avian families that were not identified to genus or species. Only one study that detected MAYV antibodies in birds performed confirmatory NT [19]. All other diagnoses (with the exception of the virus isolation) were made by HI tests alone. See Table 4 for additional information regarding avian species that were infected with MAYV.

Additional wild-caught mammals with evidence of MAYV infection are presented in Table 5. Six rodent species as well as unidentified rodents in the *Echimys* and *Proechimys* genera were detected with MAYV antibodies in French Guiana [21], Peru [92], and Panama [20]. In addition, four species in the order Didelphimorphia, three species in the order Pilosa, and one species each in the orders Carnivora, Artiodactyla, and Cingulata were detected with MAYV antibodies in French Guiana [21] and Peru [92]. Additional positive samples were detected in the orders Rodentia, Didelphimorphia, and Pilosa although the species were not identified.

Successful isolation of MAYV was reported from the following viremic animals: a silvery marmoset (*Callithrix argentata*) captured during a MAYV outbreak in Belterra, Brazil [19] and a migrating orchard oriole (*Icterus spurius*) captured in Louisiana [64]. In addition, the Belem Virus Laboratory reported MAYV isolation from two lizard species in 1963 [56] (*Tropidurus torquatus* and *Ameiva ameiva*) although no further information was provided regarding study methods or procedures.

Table 3. Evidence of MAYV infection in non-human primates.

Species	Positive (n)	Total tested (n)[a]	% Pos	Test method	Notes	Citation
Alouatta seniculus	51	98	**52.0**	HI with confirmatory NT[d]	NA	[21]
	1	1	**100.0**	ELISA with confirmatory plaque-reduction NT	NA	[92]
Callithrix argentata	32	119	**26.9**	HI with confirmatory NT	One isolation also reported but not included in this table.	[19]
Cebus libidinosus[b]	6	100	**6.0**	HI	Six reactions were monotypic, and 23 were heterotypic, with titers of 1:20 (n = 1), 1:80 (n = 6), 1:160 (n = 2), 1:320 (n = 6), 1:640 (n = 6), and 1:1280 (n = 8). Only 6 of the 29 reactions were monotypic.	[82]
Tamarin, Pithecia, Cebus (species not specified)	7	21	**33.3**	HI	Results presented as a table from the Belem Virus Laboratory, but no further information is provided regarding the study methods or primate species.	[56]
Cebus apella	10	62	**16.1**	HI	Titer results for monotypic reactions were 1:80 (n = 2), 1:160 (n = 7) and 1:640 (n = 1). Three additional samples showed positive results for MAYV and another virus.	[63]
Saguinas midas	8	42	**19.1**	HI with confirmatory NT[d]	NA	[21]
Alouatta sp.[c]	7	11	**63.6**	HI	NA	[11]
Lagothrix poeppigii	6	11	**54.5**	ELISA with confirmatory plaque-reduction NT	NA	[92]
Saimiri sciureus	4	6	**66.7**	HI with confirmatory NT[d]	NA	[21]
Pithecia pithecia	4	5	**80.0**	HI with confirmatory NT[d]	NA	[21]
Cebus sp.[c]	4	13	**30.8**	HI	NA	[11]
Alouatta villosa	3	5	**60.0**	Plaque-reduction NT	Samples considered positive if 90% plaque reduction by plasma 1:16 or weaker. The median positive titer was 1:128 (range 1:32–1:512).	[20]
Sapajus sp.	3	43	**7.0**	HI and RT-PCR	Positive samples had a monotypic reaction to MAYV with titers of 1:80 (n = 1) and 1:160 (n = 2). All samples negative by RT-PCR.	[54]
Sapajus xanthosternos	1	2	**50.0**	Plaque-reduction NT	Plaque reduction NTs were performed against MAYV for all CHIKV-positive samples. The sample neutralized both MAYV and CHIKV at titers of 1:40.	[87]
Ateles marginatus	1	1	**100.0**	Plaque-reduction NT	Plaque reduction NTs were performed against MAYV for all CHIKV-positive samples. The sample neutralized both MAYV and CHIKV at titers of 1:40.	[87]
Alouatta belzebul	1	1	**100.0**	HI with confirmatory NT	NA	[19]
Sapajus macrocephalus	1	6	**16.7**	ELISA with confirmatory plaque-reduction NT	NA	[92]
Cacajao calvus	1	3	**33.3**	ELISA with confirmatory plaque-reduction NT	NA	[92]
Callicebus brunneus[e]	1	N/A	**NA**	HI	Sera reacted against MAYV and Tacaiuma virus. No additional information provided.	[70]
Aotus sp.[c]	1	4	**25.0**	HI	NA	[11]
Saimiri sp.[c]	1	1	**100.0**	HI	NA	[11]

MAYV: Mayaro virus; HI: hemagglutination inhibition; ELISA: enzyme-linked immunosorbent assay; RT-PCR: reverse transcription polymerase chain reaction; NT: neutralization test; CHIKV: Chikungunya virus

[a] Denominators presented in this table reflect only studies that reported MAYV positivity. Complete data (including MAYV-negative samples) are included in the seroprevalence meta-analysis and the S1 Table.

[b] Captive primates from a wildlife rescue facility.

[c] Sera analyzed for MAYV may have had cross reactivity with Una virus because the authors used a Colombian isolate that was initially characterized as MAYV but was later identified as Una virus. A differential test was not performed for MAYV. However, the authors identified human sera that was reactive to MAYV alone in the same study region.

[d] Serum samples with titers >1:20 confirmed by seroneutralization. Positive reaction was considered with the total inhibition of the cytopathic effect in the cell monolayer.

[e] Authors also reported that seven monkey sera among the 14 examined were positive for yellow fever and MAYV, of which five were positive for the two agents. The species of these positive samples were: *Pithecia pithecia* (n = 1), *Alouatta seniculus* (n = 2), *Saimiri sciureus* (n = 1), *Saguinus midas* (n = 1), and *Ateles paniscus* (n = 2). However, they did not note the specific primate species that were positive for MAYV.

Table 4. Evidence of MAYV infection in birds.

Order	Species	Positive (n)	Total (n)[a]	% Pos	Test method	Notes	Citation
Columbiformes	*Columbigallina* sp.	34	121	**28.1**	HI	Results presented as a table from the Belem Virus Laboratory, but no further information is provided regarding the methods or species.	[56]
Charadriiformes	*Sterna hirundo*	23	342	**6.7**	HI	NA	[57]
Charadriiformes	*Sterna trudeaui*	12	56	**21.4**	HI	NA	[57]
Charadriiformes	*Arenaria interpres*	8	28	**28.6**	HI	NA	[57]
		1	NA	**NA**	HI	Titers 1:40	[59]
Charadriiformes	*Calidris canutus*	7	51	**13.7**	HI	NA	[57]
Passeriformes	Fringillidae family, unspecified species	6	131	**4.6**	HI with confirmatory NT	NA	[19]
Passeriformes	Formicariidae family, unspecified species	5	444	**1.1**	HI with confirmatory NT	NA	[19]
Charadriiformes	*Limosa haemastica*	5	17	**29.4**	HI	NA	[57]
Charadriiformes	*Tringa flavipes*	4	5	**80.0**	HI	NA	[57]
Charadriiformes	*Calidris pusilla*	3	NA	**NA**	HI	Titers 1:40 for all positive samples	[59]
		1	30	**3.3**	HI	Monotypic reaction with titers ≥ 1:20 to MAYV	[60]
Charadriiformes	*Sterna superciliaris*	2	8	**25.0**	HI	N/A	[57]
Charadriiformes	*Actitis macularius*	2	22	**9.1**	HI	Monotypic reaction with titers ≥ 1:20 to MAYV	[60]
Passeriformes	Dendrocolaptidae family, unspecified species	1	97	**1.0**	HI with confirmatory NT	NA	[19]
Passeriformes	*Icterus spurius*	1	223	**0.45**	Virus isolation by inoculation into suckling mice	NA	[64]
Passeriformes	*Arremon tactiturnus*	1	NA	**NA**	HI (confirmatory NT unclear)	NA	[70]
Passeriformes	Pipridae family, unspecified species	1	229	**0.44**	HI with confirmatory NT	NA	[19]
Passeriformes	*Cercomacra tyrannina*	1	NA	**NA**	HI (confirmatory NT unclear)	NA	[70]
Passeriformes	*Formicivora grisea*	1	NA	**NA**	HI (confirmatory NT unclear)	NA	[70]
Passeriformes	*Tyrannus melancholicus*	1	NA	**NA**	HI (confirmatory NT unclear)	NA	[70]
Passeriformes	Tyrannidae family, unspecified species	1	102	**0.98**	HI with confirmatory NT	NA	[19]
Charadriiformes	*Pluvialis squatarola*	1	4	**25.0**	HI	Monotypic reaction with titers ≥ 1:20 to MAYV	[60]
Charadriiformes	*Haematopus palliatus*	1	6	**16.7**	HI	NA	[57]
Charadriiformes	*Sterna eurygnatha*	1	7	**14.3**	HI	NA	[57]
Charadriiformes	*Sterna maxima*	1	1	**100**	HI	NA	[57]
Charadriiformes	*Sterna niotica*	1	1	**100**	HI	NA	[57]
Charadriiformes	*Calidris fuscicollis*	1	11	**9.1**	HI	NA	[57]
Charadriiformes	*Calidris minutilla*	1	6	**16.7**	HI	Monotypic reaction with titers ≥ 1:20 to MAYV	[60]
Caprimulgiformes	Caprimulgidae family, unspecified species	1	5	**20.0**	HI with confirmatory NT	NA	[19]
Columbiformes	Columbidae family, unspecified species	1	34	**2.9**	HI with confirmatory NT	NA	[19]
Passeriformes	*Molothrus* sp.	1	NA	**NA**	HI	Titers 1:80	[59]

MAYV: Mayaro virus; HI: hemagglutination inhibition; NT: neutralization test

[a] Denominators presented in this table reflect only studies that reported MAYV positivity. Complete data (including MAYV-negative samples) is reflected in the seroprevalence meta-analysis and the S2 Table.

**Table 5. Evidence of MAYV infection in mammals (excluding non-human primates).**

Order	Species	Positive (n)	Total (n)[a]	% Pos	Test method	Notes	Citation
Rodentia	Wild rodents, unspecified	71	960	**7.4**	HI	Results presented as a table from the Belem Virus Laboratory, but no further information is provided regarding the methods or species.	[56]
Didelphimorphia	Opossum, unspecified	9	122	**7.4**	HI	Results presented as a table from the Belem Virus Laboratory, but no further information is provided regarding the methods or species.	[56]
Pilosa	*Choloepus didactylus*	7	26	**26.9**	HI with confirmatory NT[b]	NA	[21]
Didelphimorphia	*Marmosa* sp.	7	46	**15.2**	HI	NA	[56]
Pilosa	*Tamandua tetradactyla*	6	26	**23.1**	HI with confirmatory NT[b]	NA	[21]
Cingulata	*Dasypus novemcinctus*	4	40	**10.0**	HI with confirmatory NT[b]	NA	[21]
		2	4	**50.0**	ELISA with confirmatory plaque reduction NT	NA	[92]
Rodentia	*Dasyprocta leporina*	5	29	**17.2**	HI with confirmatory NT[b]	NA	[21]
Didelphimorphia	*Philander opossum*	5	27	**18.5**	HI with confirmatory NT[b]	NA	[21]
Rodentia	*Coendou prehensilis*	3	26	**11.5**	HI with confirmatory NT[b]	NA	[21]
Rodentia	*Dasyprocta punctata*	3	5	**60.0**	Plaque reduction NT	Samples considered positive if 90% plaque reduction by plasma 1:16 or weaker. The median positive titer was 1:128 (range 1:32–1:512).	[20]
Rodentia	*Dasyprocta fuliginosa*	3	27	**11.1**	ELISA with confirmatory plaque reduction NT	NA	[92]
Rodentia	*Coendou melanurus*	2	15	**13.3**	HI with confirmatory NT[b]	NA	[21]
Didelphimorphia	*Didelphis albiventris*	2	19	**10.5**	HI with confirmatory NT[b]	NA	[21]
Rodentia	*Echimys* sp.	1	21	**4.8**	HI with confirmatory NT[b]	NA	[21]
Rodentia	*Agouti paca*	1	10	**10.0**	ELISA with confirmatory plaque reduction NT	NA	[92]
Rodentia	*Proechimys* sp.	1	18	**5.6**	HI with confirmatory NT[b]	NA	[21]
Didelphimorphia	*Caluromys philander*	1	5	**20.0**	HI with confirmatory NT[b]	NA	[21]
Didelphimorphia	*Didelphis marsupialis*	1	29	**3.5**	HI with confirmatory NT[b]	NA	[21]
Carnivora	*Potos flavus*	1	9	**11.1**	HI with confirmatory NT[b]	NA	[21]
Artiodactyla	*Pecari tajacu*	1	6	**16.7**	ELISA with confirmatory plaque reduction NT	NA	[92]
Pilosa	*Bradypus tridactylus*	1	29	**3.5**	HI with confirmatory NT[b]	NA	[21]
Pilosa	*Bradypus* sp.	1	3	**33.3**	HI	NA	[56]

MAYV: Mayaro virus; HI: hemagglutination inhibition; ELISA: enzyme-linked immunosorbent assay; RT-PCR: reverse transcription polymerase chain reaction; NT: neutralization test

[a] Denominators presented in this table reflect only studies that reported MAYV positivity. Complete data (including MAYV-negative samples) is reflected in the seroprevalence meta-analysis and the S1 Table.

[b] Serum samples with titers >1:20 confirmed by seroneutralization. Positive reaction was considered with the total inhibition of the cytopathic effect in the cell monolayer.
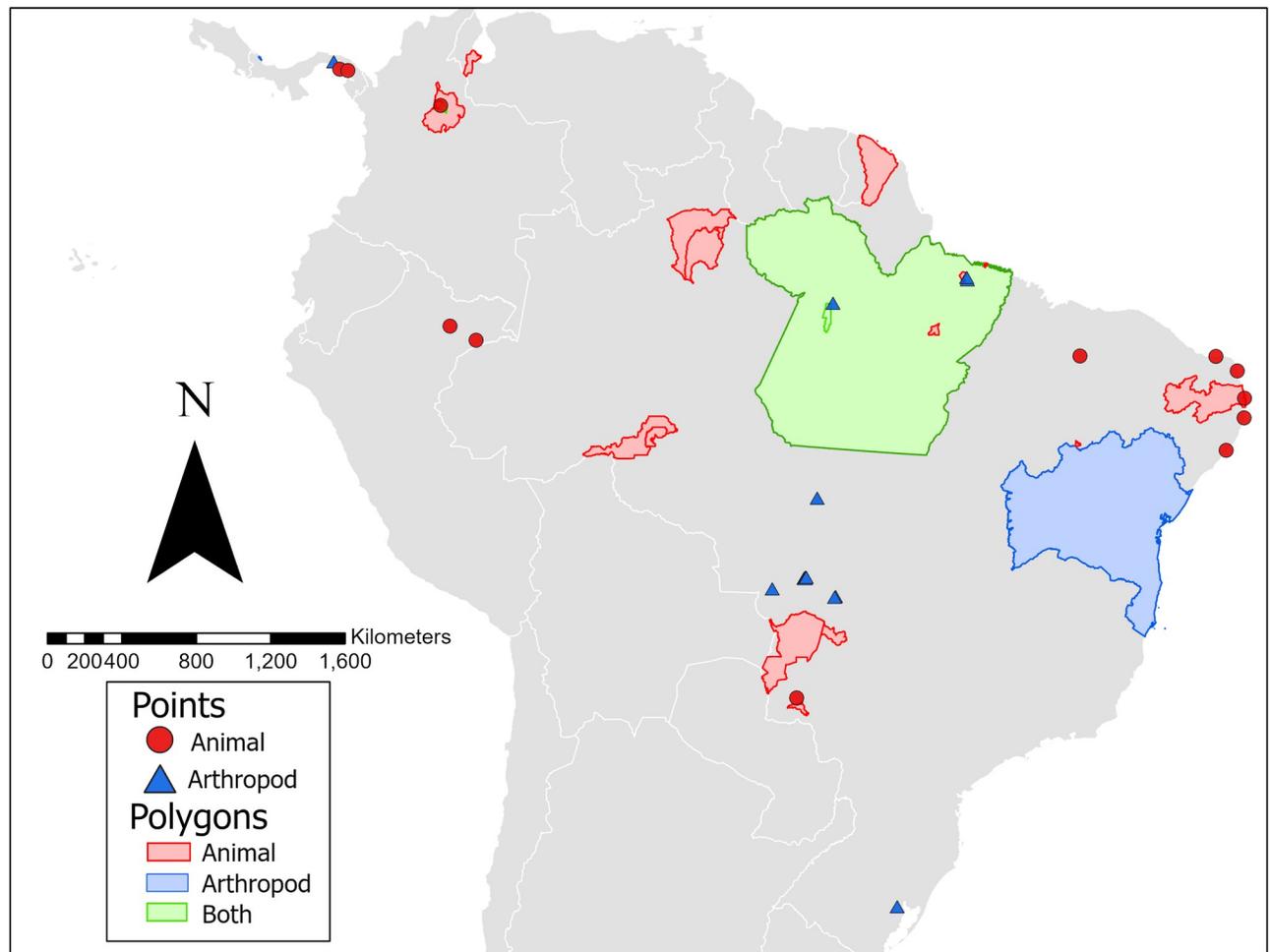
Fig 2. Georeferenced locations of MAYV positivity in non-human animals and arthropods. The finest spatial scale is presented where possible. One MAYV isolate detected in a migrating bird in Louisiana is not included in the map. The base map layer was generated using the geoBoundaries Comprehensive Global Administrative Zones (CGAZ) dataset available at https://www.geoboundaries.org/downloadCGAZ.html.

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The geographic distribution of animals (wild-caught, domestic, and sentinel) infected with MAYV is presented in Fig 2. The infected animals were identified in six countries overall, including Brazil, Peru, French Guiana, Colombia, Venezuela, and Panama, although the majority of infected animals were found in Brazil. Overall, 12 locations were geo-referenced as points, four locations as ADM1 polygons, 15 locations as ADM2 polygons, and two locations as custom polygons.

MAYV in domestic or sentinel animals

Nine studies analyzed MAYV seroprevalence in domestic animals (equids, sheep, poultry, dogs, pigs, cattle, and buffaloes), and five studies analyzed MAYV seroprevalence in sentinel animals (monkeys, mice, and hamsters). Domestic and sentinel animals with evidence of MAYV positivity are reported in Table 6 and complete results are reported in the S3 Table. In domestic animals, evidence of MAYV infection was detected in equids, cattle/buffalo, and dogs. Six studies assessed MAYV seroprevalence in Brazilian equids [58,61,67,78,89,90], and antibodies against MAYV were detected in four of these studies. Notably, Gomes et al. [78]

Table 6. Domestic and sentinel animals with evidence of MAYV infection.

Animal Type	Total Positive	Number Tested[a]	% Pos	Test Method	Notes	Citation
Domestic Equids	16	213	7.5	ELISA with confirmatory plaque reduction NT	Forty-eight horses had antibodies to MAYV by ELISA. Sixteen of 48 (33%) were considered positive by plaque reduction NT_{90} for MAYV with titers 1:10 (n = 12), 1:20 (n = 3) and 1:40 (n = 1).	[78]
	4	753	0.5	HI	Forty reactions overall. Four of 40 reactions were monotypic while 36 of 40 were heterotypic.	[67]
	11	102	10.8	HI	Not clear if the 11 reactions are monotypic or heterotypic.	[61]
	10	748	1.5	Plaque reduction NT	Forty-four horses had neutralizing antibody (titer $\geq$ 10) against MAYV, but only ten met the diagnostic criteria of 4-fold greater plaque reduction NT_{90} titer than the three other viruses (VEEV, EEEV, WEEV). Positive samples had titers of 1:20 (n = 6) and 1:40 (n = 4)	[90]
Domestic Cattle/Buffalo	5	1103	0.5	HI	Positive reactions were considered any reaction with a titer equal to or greater than 1:20. Fourteen reactions overall, and five of 14 reactions were monotypic.	[66]
Domestic Dog	2	7	28.6	HI	N/A	[57]
Sentinel Hamster	1	N/A	N/A	RT-PCR		[86]
Sentinel Monkeys	2	13	15.4	HI	N/A	[102]

MAYV: Mayaro virus; HI: hemagglutination inhibition; ELISA: enzyme-linked immunosorbent assay; RT-PCR: reverse transcription polymerase chain reaction; NT: neutralization test; VEEV: Venezuelan equine encephalitis virus; EEEV: Eastern equine encephalitis virus; WEEV: Western equine encephalitis virus

[a] Denominators presented in this table reflect only studies that reported MAYV positivity. Complete data (including MAYV-negative samples) are reflected in the seroprevalence meta-analysis and the S3 Table.

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reported MAYV neutralizing antibodies in 48 equids out of 213 (23%) based on ELISA. However, only 16 of the 48 equids were considered positive based on the study's diagnostic criterion of 4-fold greater plaque reduction NT_{90} titer than that of the other viruses under study. In addition, Casseb et al. [67] detected MAYV antibodies in 40 horses using HI, although only four of the 40 reactions were monotypic, and confirmatory NTs were not performed. Additional domestic animals with evidence of MAYV infection included cattle/buffalo (n = 14/1103 positive reactions by HI; 5/14 monotypic reactions [66]) and dogs (n = 2/7 positive reactions by HI [57]). In addition, neutralizing antibodies (plaque reduction NT_{90} titer $\geq$10) against MAYV were detected in three sheep in Brazil [90]. However, these animals did not meet the original study's diagnostic criterion for MAYV diagnosis based on 4-fold greater plaque reduction NT_{90} titer than that of the other viruses under study. Evidence of MAYV infection was also detected by HI in two sentinel monkeys placed in the tree canopy in Panama [102], and one MAYV isolate was obtained from a sentinel hamster in Venezuela [86].

Pooled seroprevalence of MAYV in non-human vertebrate animals

Twenty-four studies overall were included in the pooled seroprevalence meta-analysis. Eight studies were excluded because they did not clearly state how many animals were tested for MAYV within each order [59,70,76,88,93,97] or did not present serologic results [64,74]. Another study was excluded because authors reported the number of "Group A" positive serum samples, but did not specify individual viruses [102]. Studies were also excluded if they only reported sequence data or only included sentinel animals [86,95,99,104]. Finally, a study that sampled bats exclusively was excluded because no MAYV-positive samples were reported in the order Chiroptera [96].

Eleven orders of nonhuman vertebrate animals (including domestic equids) were included in the meta-analysis. Orders were excluded from the analysis due to insufficient sample size (N<10) or if no MAYV-positive samples were reported. These include the orders Apodiformes (MAYV seroprevalence: 0/3), Caprimulgiformes (MAYV seroprevalence: 1/6), Chiroptera (MAYV seroprevalence: 0/1546), Crocodilia (MAYV seroprevalence: 0/87), Cuculiformes (MAYV seroprevalence: 0/5), Galliformes (MAYV seroprevalence: 0/1), Gruiformes (MAYV seroprevalence: 0/2), Psittaciformes (MAYV seroprevalence: 0/3), Tinamiformes (MAYV seroprevalence: 0/2), Pelecaniformes (MAYV seroprevalence: 0/2), and Podicipediformes (MAYV seroprevalence: 0/2).

The primate order appeared in 14 studies that were included in the meta-analysis. A forest plot for the primate order is presented in Fig 3. When all positive samples were included, the pooled MAYV seroprevalence among primates was 13.1% (95% CI: 4.3–25.1%) according to the random effects model, with statistically significant and high heterogeneity across studies (I^2 = 95%, p < 0.01). After excluding positive samples that were not confirmed by NT, the pooled MAYV seroprevalence among primates decreased to 4.9 (95% CI: 0.0–15.2; I^2 = 96%; p < 0.01) according to the random effects model. When the analyses were repeated using the GLMM with logit transformation, seroprevalence estimates for primates decreased to 8.7% (95% CI: 3.1–22.0%) overall and to 0.7% (95% CI: 0.0–9.1%) when only NT-positive samples were included. Additional meta-analysis results for the various primate genera are presented in S5 and S6 Tables. The seroprevalence for the most frequently sampled primate genera was 32.2% (95% CI: 0.0–79.2%) for the *Alouatta* genus, 17.8% (95% CI: 8.6–28.5%) for the *Callithrix* genus, and 3.7% (95% CI: 0.0–11.1%) for the *Cebus/Sapajus* genus.

Meta-analysis results for additional non-human vertebrate orders are presented in Table 7 and forest plots for mammal orders (excluding non-human primates) and avian orders are presented in Figs 4 and 5, respectively. When all positive samples were included in the analysis,
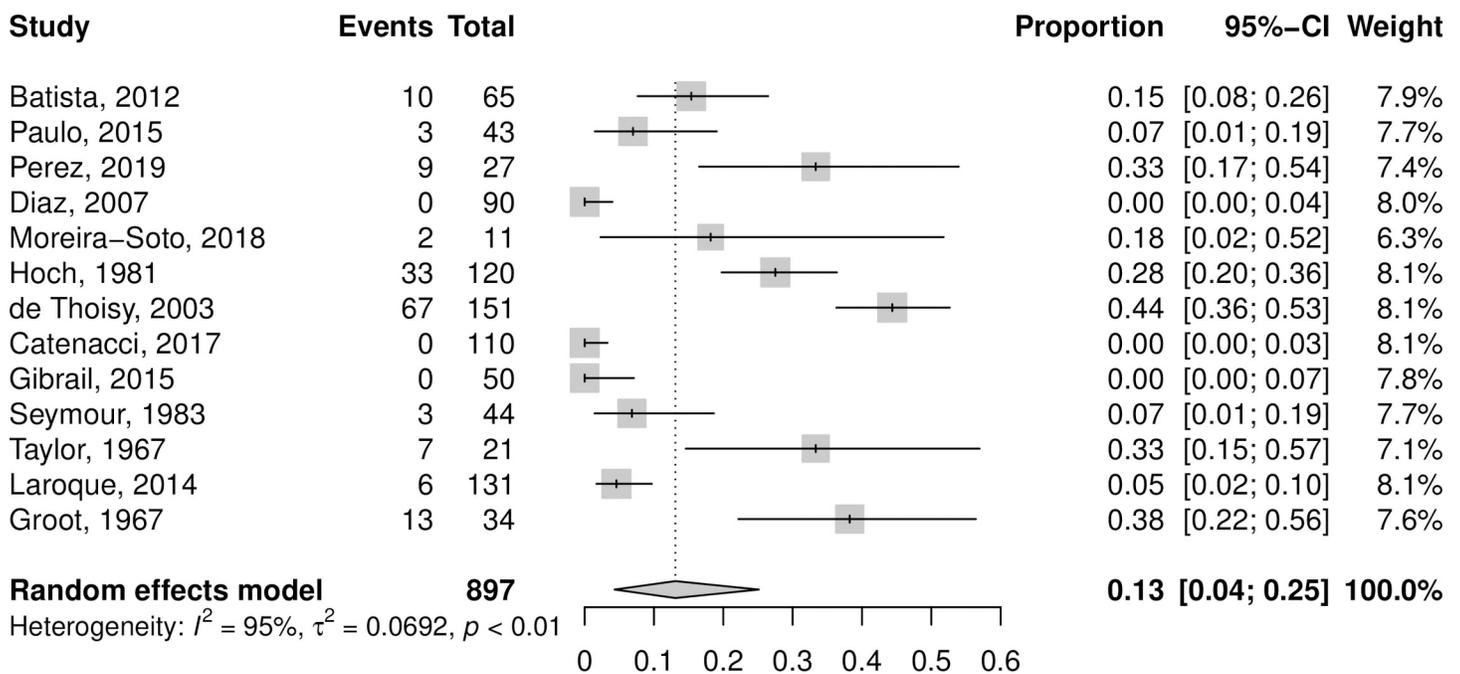
Study	Events	Total		Proportion	95%–CI	Weight
Batista, 2012	10	65		0.15	[0.08; 0.26]	7.9%
Paulo, 2015	3	43		0.07	[0.01; 0.19]	7.7%
Perez, 2019	9	27		0.33	[0.17; 0.54]	7.4%
Diaz, 2007	0	90		0.00	[0.00; 0.04]	8.0%
Moreira–Soto, 2018	2	11		0.18	[0.02; 0.52]	6.3%
Hoch, 1981	33	120		0.28	[0.20; 0.36]	8.1%
de Thoisy, 2003	67	151		0.44	[0.36; 0.53]	8.1%
Catenacci, 2017	0	110		0.00	[0.00; 0.03]	8.1%
Gibrail, 2015	0	50		0.00	[0.00; 0.07]	7.8%
Seymour, 1983	3	44		0.07	[0.01; 0.19]	7.7%
Taylor, 1967	7	21		0.33	[0.15; 0.57]	7.1%
Laroque, 2014	6	131		0.05	[0.02; 0.10]	8.1%
Groot, 1967	13	34		0.38	[0.22; 0.56]	7.6%
Random effects model		**897**		**0.13**	**[0.04; 0.25]**	**100.0%**

Heterogeneity: I^2 = 95%, τ^2 = 0.0692, p < 0.01

0   0.1   0.2   0.3   0.4   0.5   0.6

Fig 3. Forest plot of non-human primates from meta-analysis of pooled MAYV seroprevalence. Estimates are based on random effects model with Freeman-Tukey double arcsine transformation. All samples that tested MAYV-positive are included, regardless of test method.

Table 7. Pooled Seroprevalence Table (Random effects with Freeman-Tukey double arcsine transformation).

Order	Positives Included[a]	Studies (n)	Total (n)	Positive (n)	Pooled Seropreval-ence (%)	95% CI	I² (%)	τ²	p-value
Mammals									
Primate	HI and NT	13	897	153	13.1	4.3; 25.1	95	0.0692	<0.01
	NT only	13	858	114	4.9	0.0; 15.2	96	0.0851	<0.01
Pilosa	HI and NT	7	297	15	0.0	0.0; 6.6	84	0.0338	<0.01
	NT only	7	296	14	0.0	0.0; 3.9	82	0.0305	<0.01
Rodentia	HI and NT	7	1557	90	1.3	0.0; 6.5	91	0.0160	<0.01
	NT only	7	1486	19	0.1	0.0; 3.7	90	0.0153	<0.01
Domestic Equids	HI and NT	6	1955	41	1.1	0.0; 4.5	90	0.0085	<0.01
	NT only	6	1940	26	0.0	0.0; 1.9	90	0.0087	<0.01
Didelphimorphia	HI and NT	6	369	25	2.0	0.0; 7.2	68	0.0101	<0.01
	NT only	6	353	9	0.1	0.0; 4.2	74	0.0141	<0.01
Carnivora Order	HI and NT	5	40	2	0.1	0.0; 8.1	0	0	0.71
	NT only	5	40	2	0.1	0.0; 8.1	0	0	0.71
Cingulata Order	HI and NT	4	70	6	3.0	0.0; 24.5	35	0.0198	0.20
	NT only	4	70	6	3.0	0.0; 24.5	35	0.0198	0.20
Artiodactyla	HI and NT	2	26	1	2.3	0.0; 20.7	46	0.0172	0.17
	NT only	2	26	1	2.3	0.0; 20.7	46	0.0172	0.17
Birds[b]									
Charadriiformes	HI and NT	3	641	71	7.1	2.2; 13.8	61	0.0045	0.08
Passeriformes	HI and NT	4	1166	14	0.0	0.0; 0.0	27	0.0010	0.25
Columbiformes	HI and NT	4	171	35	2.2	0.0; 27.1	87	0.0591	<0.01

MAYV: Mayaro virus; HI: hemagglutination inhibition; NT: neutralization test; CI: confidence interval

[a] The first analysis (HI and NT) included all positive samples, regardless of test method. A sensitivity analysis was conducted that included only positive samples that were confirmed with NT.

[b] Only one study reporting MAYV positivity in birds used confirmatory NT. Therefore, a sensitivity analysis was not conducted.

the highest seroprevalence was observed in the orders Charadriiformes (seroprevalence: 7.1%; 95% CI: 2.2–13.8%) and Cingulata (seroprevalence: 3.0%; 95% CI: 0.0–24.5%). When the analysis was repeated using GLMM with logit transformation, the seroprevalence increased to 10.0% (95% CI: 2.7–30.8%) for the order Cingulata and 9.2% (95% CI: 4.4–18.2%) for the order Charadriiformes. All results of the sensitivity analysis using GLMM with logit transformation are reported in the S4 Table. An additional sensitivity analysis using fixed effects models is presented in the S7 and S8 Tables.

MAYV in wild-caught arthropods

Twenty-eight of the studies in our systematic review analyzed MAYV infection in wild-caught arthropods. Seventeen (61%) of the 28 studies reported at least one arthropod that was positive for MAYV infection. Of the mosquito genera studied, seven were found to be infected with MAYV: *Aedes*, *Culex*, *Haemagogus*, *Psorophora*, *Sabethes*, *Wyeomyia*, and *Mansonia*. For detailed information on all infected mosquito species, see Table 8. The majority of infected vectors were identified using viral isolation techniques, although three studies reported MAYV positivity using RT-PCR alone. In addition, one study reported isolation of MAYV from an *Ixodes* tick [95] while another study reported isolation from a *Gigantolaelaps* mite [56]. Complete results, including studies that did not detect MAYV in arthropods, are reported in the S9 Table.
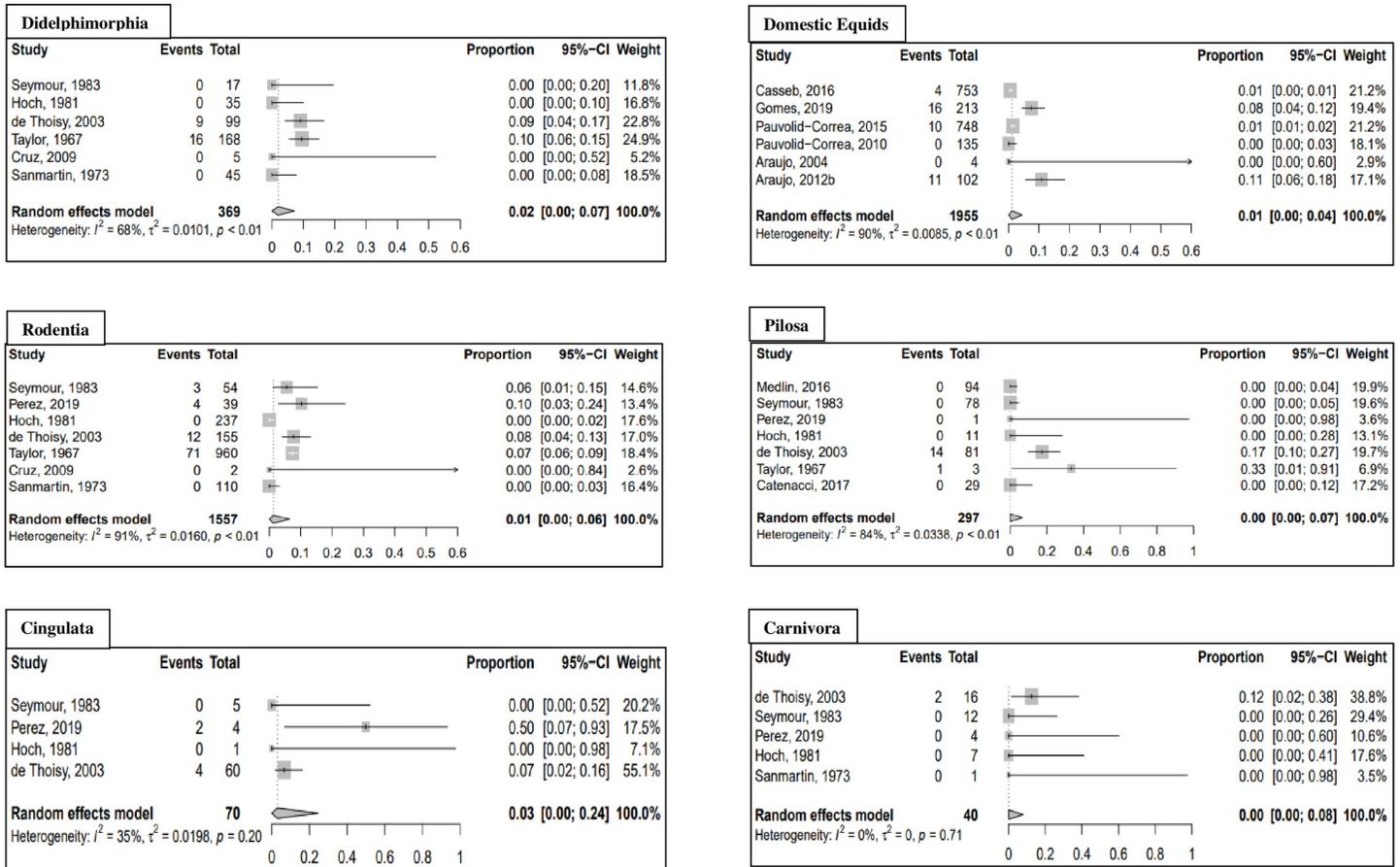
Fig 4. Forest plots of mammal orders (excluding primates) from meta-analysis of pooled MAYV seroprevalence. Estimates are based on random effects model with Freeman-Tukey double arcsine transformation. All samples that tested MAYV-positive are included, regardless of test method.

The geographic distribution of vectors infected with MAYV is presented in Fig 2. MAYV-positive arthropods were identified in four countries overall, including Brazil, Colombia, Panama, and Trinidad. Overall, 15 locations were geo-referenced as points, two locations as ADM1 polygons, two locations as ADM2 polygons, two locations as ADM3 polygons, and two as custom polygons.

Analysis of publication bias

Publication bias was assessed among six animal orders (including domestic equids) and two primate genera. The results of Egger's test did not reveal evidence of publication bias for the included studies. Therefore, the Trim fill technique was not carried out. Funnel plots are presented in S1 and S2 Figs, and results of Egger's test are reported in the S10 Table.

Discussion

In this study, we attempted to systematically review the existing evidence of non-human animal reservoirs and arthropod vectors of MAYV. We extended this comprehensive literature review with a pooled seroprevalence analysis of potential MAYV reservoirs. We identified 57 studies that assessed MAYV infection in non-human vertebrate animals and arthropods. Overall, the studies found evidence of MAYV infection in 12 wild-caught animal orders and
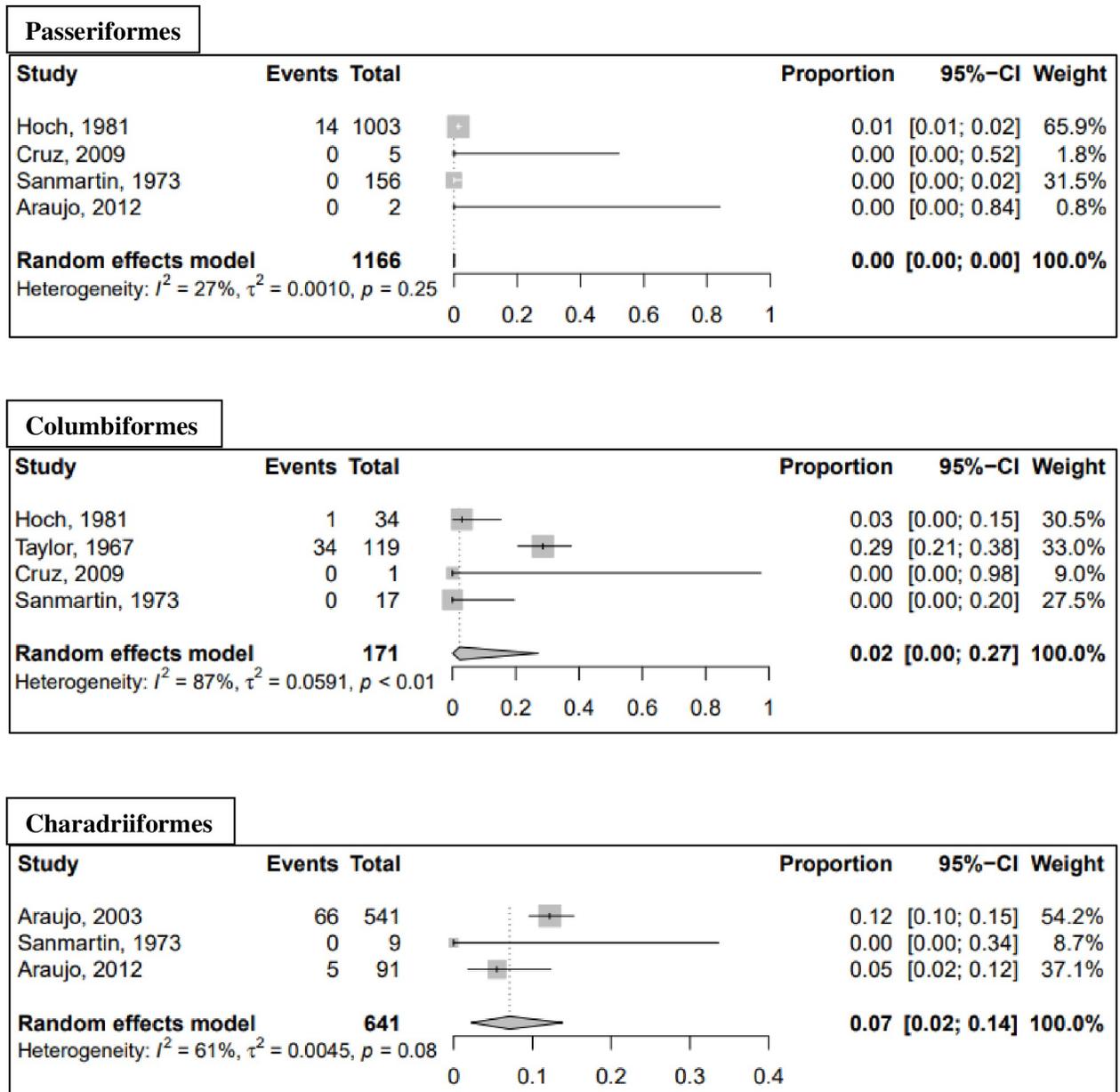
Passeriformes

Study	Events	Total		Proportion	95%-CI	Weight
Hoch, 1981	14	1003		0.01	[0.01; 0.02]	65.9%
Cruz, 2009	0	5		0.00	[0.00; 0.52]	1.8%
Sanmartin, 1973	0	156		0.00	[0.00; 0.02]	31.5%
Araujo, 2012	0	2		0.00	[0.00; 0.84]	0.8%
Random effects model		**1166**		**0.00**	**[0.00; 0.00]**	**100.0%**

Heterogeneity: $I^2 = 27\%$, $\tau^2 = 0.0010$, $p = 0.25$

(axis: 0 0.2 0.4 0.6 0.8 1)

Columbiformes

Study	Events	Total		Proportion	95%-CI	Weight
Hoch, 1981	1	34		0.03	[0.00; 0.15]	30.5%
Taylor, 1967	34	119		0.29	[0.21; 0.38]	33.0%
Cruz, 2009	0	1		0.00	[0.00; 0.98]	9.0%
Sanmartin, 1973	0	17		0.00	[0.00; 0.20]	27.5%
Random effects model		**171**		**0.02**	**[0.00; 0.27]**	**100.0%**

Heterogeneity: $I^2 = 87\%$, $\tau^2 = 0.0591$, $p < 0.01$

(axis: 0 0.2 0.4 0.6 0.8 1)

Charadriiformes

Study	Events	Total		Proportion	95%-CI	Weight
Araujo, 2003	66	541		0.12	[0.10; 0.15]	54.2%
Sanmartin, 1973	0	9		0.00	[0.00; 0.34]	8.7%
Araujo, 2012	5	91		0.05	[0.02; 0.12]	37.1%
Random effects model		**641**		**0.07**	**[0.02; 0.14]**	**100.0%**

Heterogeneity: $I^2 = 61\%$, $\tau^2 = 0.0045$, $p = 0.08$

(axis: 0 0.1 0.2 0.3 0.4)

Fig 5. Forest plots of avian orders from meta-analysis of pooled MAYV seroprevalence. Estimates are based on random effects model with Freeman-Tukey double arcsine transformation. All samples that tested MAYV-positive are included, regardless of test method.

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seven arthropod genera across seven Latin American countries and the USA. We identified 17 studies that reported MAYV occurrence in non-human animals and 17 studies that reported MAYV occurrence in arthropods. A recently published study reviewed the occurrence of MAYV in animals, arthropods, and humans and used this information to estimate key parameter estimates for modeling [105]. The additional focus of our seroprevalence meta-analysis adds to the existing literature on MAYV ecology and provides important information for public health authorities that are concerned with MAYV spread.

We also noted that some vertebrates and arthropods were found to be infected with multiple viruses of medical importance. For example, during the MAYV outbreak in Belterra, Brazil,

Table 8. Evidence of MAYV infection in arthropods.

Genus	Species	Notes	Year	Citation
Haemagogus	Hg. janthinomys	Pools of Hg. janthinomys yielded nine isolates by injection into suckling mice	1978	[19]
		A pool of two Hg. janthinomys yielded one strain by inoculation into newborn mice and C6/36 cells and confirmed by complement fixation and immunofluorescent assays	2008	[62]
		Mayaro virus isolate BeAr505578, complete genome. GenBank accession no. KY618129	1991	GenBank: KY618129
		Mayaro virus isolate BeAr505411. Genbank accession no. DQ487382	1991	[95]
	Hg. equinus	One MAYV isolate detected by viral culture using Vero cells with confirmation in microplates.	1973–76	[76]
	Hg. lucifer	Two MAYV isolates detected by viral culture using Vero cells with confirmation in microplates.	1973–76	[76]
	NA	Twenty-five isolates reported. No further information provided.	NA	[56]
		Mayaro virus isolate BeAr350396. GenBank accession no. DQ487388	1978	[95]
		Complete Genome Sequence of Mayaro Virus Strain BeAr 20290. GenBank accession no. KT754168.	1960	[72]
Aedes	Ae. aegypti	Two out of 57 (3.5%) pools positive by PCR and isolated in C6/36 cells.	2017	[83]
		Four out of 171 (2.3%) pools positive by RT-PCR. One pool yielded an isolate after inoculation in Vero cells.	2013	[100]
	Ae. serratus	Addendum to the article states that one additional MAYV strain was isolated from Ae. serratus pools. No further information provided.	1960	[79]
Mansonia	M. venezuelensis[a]	MAYV was isolated in baby mice from a pool of 49 wild-caught M. venezuelensis mosquitoes.	1957	[52]
		One isolation. No further information provided. GenBank accession no. DQ487384.	1957	[56,95]
Culex	C. nigripalpus	One pool out of 152 (0.7%) positive by RT-PCR.	2014–15	[81]
	C. quinqefasciatus	Twelve out of 403 (3%) pools positive by RT-PCR. One pool was isolated after inoculation in Vero cells.	2013	[100]
		Twelve out of 179 (6.7%) pools positive by RT-PCR and isolation in Vero cells.	2017–18	[73]
	C. vomerifer	Wild-caught mosquitoes were allowed to feed on caged hamsters. The sera of one hamster produced MAYV antibodies by HI.	1966	[75]
	NA	Mayaro virus strain BeAr757954, complete genome. GenBank accession no. KY618130.	2011	GenBank: KY618130
		One isolation. No further information provided.	NA	[56]
Psorophora	P. ferox	A pool of P. ferox yielded one isolate by inoculation into Swiss mice.	1959–62	[74]
		Addendum to the article states that five additional MAYV strains were isolated from P. ferox pools. No further information provided.	1960	[79]
	NA	Four out of 748 (0.5%) pools yielded strains isolated by inoculation into Swiss mice from. Pools of 50 mosquitoes each were composed of P. albipes, P. ferox, or a combination of the two.	1958	[79]
Wyeomyia	NA	One pool out of 304 (0.3%) positive by RT-PCR.	2006–14	[68]
Sabethes	NA	Two isolations. No further information provided	NA	[56]
Gigantolaelaps	NA	One isolation. No further information provided	NA	[56]
Ixodes	NA	Genbank accession no. DQ487378	1961	[95]

[a] The mosquito Mansonia venezuelensis is now referred to as Coquillettidia venezuelensis.

both YFV and MAYV were isolated from pools of Hg. janthinomys mosquitoes and MAYV and YFV antibodies were detected in primates [19]. Another study reported that serum samples of primates neutralized both MAYV and CHIKV antibodies [87]. The co-circulation of multiple medically important viruses in reservoirs and vectors is an important consideration in the ecology and control of these pathogens. Further studies could clarify the precise distribution of other reservoirs and vectors of these other medically important arboviruses.

The majority of animal species that were found to be infected with MAYV belonged to the orders Primate and Charadriiformes (shorebirds). Several MAYV-positive species were also detected in the orders Rodentia, Didelphimorphia, and Pilosa. Overall, the highest MAYV pooled seroprevalence occurred in the Primate order. This finding points to the potential role of NHPs as an important reservoir in the MAYV transmission cycle.

The role of NHPs in sylvatic transmission cycles of arboviruses has been demonstrated with varying degrees of evidence [106]. Several arboviruses have been successfully isolated from wild NHPs, including dengue [107], CHIKV [108], and Zika [109] viruses. While isolation of a virus from NHPs is important for establishing the existence of a sylvatic cycle, it is difficult to achieve due to the short duration of viremia [106]. In our review, we identified only one study that successfully isolated MAYV from a NHP [19]. In the absence of viral detection, antibody seroprevalence has been used as evidence of the role of NHPs in sylvatic transmission cycles [110,111]. Therefore, the high seroprevalence of MAYV among NHPs, including 52% seropositivity among *A. seniculus* monkeys in a 1994–95 survey in French Guiana [21], points to the potential importance of NHPs as MAYV reservoirs. Furthermore, Hoch et al. [19] reported substantial viremia in *C. argentata* marmosets that were experimentally infected with MAYV and noted that viremia titer was likely sufficient to infect vectors. Due to the high MAYV seroprevalence among marmosets during the Belterra outbreak, the isolation of MAYV from a single *C. argentata* marmoset, and the results of experimental infection studies, the authors concluded that marmosets were likely the amplifying hosts of MAYV.

The importance of birds in the MAYV transmission cycle was hypothesized following viral isolation from a migrating oriole (*Icterus spurius*) in Louisiana [64]. Avian species have been implicated as definitive or potential reservoirs of several Alphaviruses, including Sindbis virus [112], Ross River virus [113], and Eastern/Western equine encephalitis virus [114]. However, their role in MAYV transmission remains poorly understood. Our systematic review identified seven studies that found MAYV positivity in birds in the orders Passeriformes, Caprimulgiformes, Columbiformes, and Charadriiformes with relatively high seroprevalence reported in several bird species in the latter two orders [56,57]. While some have theorized that MAYV has been introduced into certain areas by migratory birds [63], this hypothesis requires further study in order to elucidate the role of birds in MAYV transmission.

Although evidence of MAYV infection was detected in several vertebrate species, identifying the primary non-human animal reservoirs remains a difficult task. The precise definition of a disease "reservoir" has been a source of disagreement [17,115]. One definition proposed by Haydon et al., (2002) defined a reservoir as "one or more epidemiologically connected populations or environments in which the pathogen can be permanently maintained and from which infection is transmitted to the defined target population" [17]. In addition, in 2005 Kuno and Chang outlined three basic criteria for the identification of reservoirs including isolation of the virus from the suspected reservoir population, high antibody prevalence in field-caught animals, and evidence of viremia in laboratory settings, although they posited that definitive identification of a reservoir requires evidence of long-term infection [116]. The role of various non-human vertebrates in the MAYV transmission cycle should be explored further in longitudinal seroprevalence surveys and experimental transmission studies in laboratory settings.

The sylvatic *Hg. janthinomys* mosquito has long been considered as the primary vector of MAYV. This is in part based on the isolation of MAYV from several pools of *Hg. janthinomys* mosquitoes in the context of a major MAYV outbreak in Belterra, Brazil in 1978 [19]. Since our systematic review was conducted, additional research has been published using a meta-transcriptomic-based approach to identify MAYV in *Hg. janthinomys* mosquitoes [117]. Our systematic review also identified several additional mosquito species including *Ae. aegypti* and

Cx. quinqefasciatus with evidence of MAYV infection. A caveat, however, is that the isolation of a virus or detection of viral RNA through PCR is not sufficient to establish that arthropod as a biological vector [118], i.e. involved in the biological transmission of pathogens [116]. The World Health Organization (WHO) established three criteria to define a confirmed vector: (1) viral isolation in the absence of vertebrate blood; (2) biological transmission of the virus in experimental conditions; and (3) presence of certain temporal, geographic and other epidemiological or ecological parameters that allow transmission to occur [118]. Thus, certain arthropods that are capable of ingesting and transmitting a virus may not be established as confirmed vectors if the other parameters are not in place.

Experimental transmission studies support the role of *Ae. aegypti* as a possible MAYV vector with high MAYV infection rates and transmission potential [22–24,119]. For example, Long et al., revealed *Ae. aegypti* to be a capable MAYV vector with a relatively short extrinsic incubation period [22]. Furthermore, MAYV titers in the saliva of *Ae. aegypti* were similar to other Alphavirus-vector systems including EEEV in *Culiseta melanura* and VEEV in *Ae. albopictus* and *Ae. taeniorhynchus*. In contrast, *Cx. quinquefasciatus* mosquitoes exhibited low MAYV infection rates and inability to transmit MAYV in laboratory settings [119]. It is also important to note that the competence of a given vector species to transmit MAYV may be impacted by the MAYV genotype that is present in a given area. In laboratory conditions, genotype L infection rates were significantly higher than genotype D infection rates among *Ae. aegypti* mosquitoes [119].

The spillover of MAYV into urban populations has been a source of concern for Latin American health authorities [120]. The implication is that anthropophilic, urban-dwelling mosquitoes like *Ae. aegypti* as effective vectors of MAYV would increase the potential for urban MAYV outbreaks [121]. The detection of MAYV antibodies in peri-domestic animals such as horses and chickens may perhaps also increase the likelihood of an urban cycle. Although *Ae. aegypti* primarily feed on humans, bloodmeal analysis has revealed an eclectic mix of vertebrate hosts including domestic and peri-domestic animals such as horses, dogs, cats, and chickens [122]. Furthermore, a susceptible-exposed-infected-recovered (SEIR) model estimated the reproductive number (R_0) of MAYV to be between 1.18 and 3.51 in Rio de Janeiro. These findings suggest that MAYV has the potential for epidemic spread in an urban setting. [26]

Concerns of urban MAYV transmission were amplified after antibodies to MAYV were discovered in 33 of 631 sera (5.2%) in the city of Manaus, Brazil in 2007–08 [25] although it is unclear if humans can serve as amplification hosts. For example, Long et al. noted that the short duration of MAYV viremia and the relatively low viremic titers in humans reduces the probability of urban spread [22]. Our systematic review identified two recent studies conducted in the city of Cuiaba in which MAYV was isolated from pools of wild-caught *Ae. aegypti* mosquitoes [83,100]. One of these studies also reported vertical transmission of MAYV in mosquitoes [83]. This represents another mechanism that may lead to maintenance of the virus in urban mosquito populations. Although *Ae. aegypti* mosquitoes have not been conclusively implicated as MAYV vectors, the isolation of MAYV from wild-caught *Ae. aegypti* mosquitoes combined with the evidence of vector competence in laboratory settings [22–24,119] suggests that MAYV could spill over into an urban cycle. This hypothesis requires further study to explore natural MAYV infection in city-dwelling mosquitoes and in domestic animals as well as additional controlled vector competence studies.

Our systematic review revealed high heterogeneity ($I^2 > 50\%$) across included studies, even within animal orders. Heterogeneity may complicate the interpretation of pooled seroprevalence estimates [40]. The importance of temporal heterogeneity should also be considered when interpreting these results. Because MAYV may act as both an endemic and epidemic

disease, point estimates of seroprevalence may not accurately capture the complexities of MAYV transmission dynamics in animals and arthropods. Longitudinal surveys may provide a more accurate picture of MAYV prevalence. An additional limitation involves the validity of serological assays used to detect MAYV infection in animals. While plaque reduction NT is considered the "gold standard test" for detecting neutralizing antibodies to MAYV, some of the studies in the review instead relied on the less-specific HI test for antibody detection [106]. Furthermore, antibodies to other alphaviruses in the Semliki Forest serocomplex (e.g., CHIKV) may cross-react in serological tests [123]. Therefore, interpretation of seroprevalence estimates should be done with caution especially in the absence of confirmatory NT. Finally, unpublished data and articles with low quality scores were included in this review due to the paucity of eligible studies. Therefore, readers should consider the heterogeneity of study quality when interpreting the results of pooled seroprevalence estimates.

Conclusions

MAYV is an emerging arbovirus that poses a major threat to human populations in Latin America. In order for public health authorities to effectively design MAYV surveillance and control programs, an understanding of the disease ecology is essential. This systematic review adds to existing knowledge regarding the potential animal reservoirs and arthropod vectors that are involved in the MAYV transmission cycle. These baseline data and maps of MAYV occurrence can direct risk emergence modeling and prediction efforts. Future studies involving experimental infection of primates and other non-human vertebrates are necessary to determine the animal species that may serve as amplifying hosts. Furthermore, additional experimental transmission studies may provide critical information regarding the potential for *Ae*. *aegypti* to facilitate urban spread of MAYV.

Supporting information

S1 File. PRISMA Checklist.
(DOCX)

S1 Table. MAYV positivity by taxa of wild mammals and reptiles in included studies.
Includes all positive samples regardless of test method.
(DOCX)

S2 Table. MAYV positivity by taxa of wild birds in included studies. Includes all positive samples regardless of test method.
(DOCX)

S3 Table. MAYV positivity in domestic or sentinel animals studied.
(DOCX)

S4 Table. Pooled Prevalence Table (Random effects using GLMM with logit transformation).
(DOCX)

S5 Table. Primate Genera Pooled Prevalence Table (Random effects with Freeman-Tukey double arcsine transformation).
(DOCX)

S6 Table. Primate Genera Pooled Prevalence Table (Random effects using GLMM with logit transformation).
(DOCX)

S7 Table. Pooled Prevalence Table (Fixed effects with Freeman-Tukey double arcsine transformation).
(DOCX)

S8 Table. Pooled Prevalence Table (Fixed effects using GLMM with logit transformation).
(DOCX)

S9 Table. Complete arthropod results by genus.
(DOCX)

S10 Table. Egger's test for publication bias.
(DOCX)

S1 Fig. Funnel plots for estimates of MAYV seroprevalence in non-human animal reservoirs. Funnel plots presented for: A) Primate order, B) Rodentia order, C) Domestic equids, D) Pilosa order, E) Didelphimorphia order, F) Carnivora order.
(TIF)

S2 Fig. Funnel plots for estimates of MAYV seroprevalence in non-human primate genera. Funnel plots presented for: A) *Alouatta* genus and B) *Cebus/Sapajus* genus.
(TIF)

Acknowledgments

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