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# Dynamics of invasive mosquitoes: introduction pathways, limiting factors, and their potential role in vector-borne pathogen transmission

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The blooming of global trade and travel and the intensification of global changes over the past decades are thought to be important drivers of accelerated range expansions of vector-borne pathogens (VBPs), with the potential to cause severe disease outbreaks around the world. As a bridge between hosts and pathogens, mosquitoes play a central role in the transmission of VBPs. With modern oversea/air transportation facilitating the introduction of different mosquito species into novel regions, there is concern that this may escalate the introduction and subsequent spread of introduced VBPs in those regions. Despite these potential impacts, there is still a lack of comprehensive understanding of the ecology of invasive mosquitoes and the consequences they have for VBP introductions and transmission intensity. Here we review common introduction pathways, limiting factors for the establishment and spread of invasive mosquito species and explore their role in the transmission of VBPs in invaded regions. We also highlight the major challenges in invasive mosquito surveillance and control and identify key research questions for advancing future control strategies and practices. This body of knowledge may contribute to the prevention of mosquito introductions, as well as risk assessment and risk management of VBPs.

KEYWORDS

**mosquito-borne diseases, mosquito invasion, vector surveillance and control, alien species introduction, pathogen transmission**

## Introduction

Vector-borne pathogens (VBPs) are disease agents (e.g., viruses, parasites or bacteria) of human and animal illness transmitted by arthropod vectors including flies, fleas, midges, mites, ticks and most deadly, mosquitoes (1). Over the past decades, the emergence or re-emergence of VBPs has accelerated, posing a heavy burden on public health and biodiversity conservation (2–5). According to the World Health Organization, for example, the annual number of estimated cases of dengue and malaria were up to 390 and 249 million, respectively, accounting for a considerable portion of the global infectious disease burden (6, 7). Blooming global trade and travel has most likely facilitated the movement of VBPs via infected humans, livestock, or vectors. As a result, many VBPs are expanding their distribution ranges, some even breaking through the intercontinental barriers and threatening new regions remote from their native ranges (5). A notorious recent example likely involving infected travelers was Zika virus (8), whose endemic regions consist of Africa and with infections later sporadically occurring in Asia. Following introduction to Yap Island in the western Pacific in 2007 and then French Polynesia in the southern Pacific in 2013-2014, a large epidemic occurred in Brazil in 2015-2016 and the virus continued to spread through Latin America, the Caribbean, and parts of Europe (9, 10). In Brazil, studies have shown that subsequent lower levels of incidence following the large outbreaks were most likely caused by the build-up of population immunity (11). Although there was no major outbreak of Zika in the US, locally acquired cases were also reported in Southern Texas and Florida in 2016-2017 ( (12) and references therein). Another example is the transmission of West Nile virus (WNV). Originally discovered in Uganda in 1937, WNV gradually spread throughout Africa, Middle East and Europe over the course of 60 years, and it spread to the Western hemisphere starting from the outbreak of WNV infection in avian communities in New York 1999, followed by thousands of reported human cases, including hundreds of deaths in the US and Canada in 2002 and 2003 ( (13) and references therein). This is a prime example of an arbovirus that not only was introduced and led to major outbreaks, but then rapidly spread over the course of a 4-year period across the continental United States and has become established in local avian populations (14).

Given these examples of recent invasions of vector-borne pathogens, and the threat associated with potential novel invasive pathogens, understanding the drivers for local and regional expansion of VBPs is of top priority. Global trade and travel have been suggested as the main driver for the introduction of VBPs into novel regions while land use and social changes (e.g., poverty) are more likely drivers of local expansion of already-circulating VBPs (5). In addition, global climate change may also contribute to the range expansion or shifts of VBPs if increasing temperatures enable certain vectors to expand their distribution range by latitude or elevation (15). In this context, the introduction of VBPs in novel regions can be facilitated by modern transportation carrying infected hosts and/or vectors, while the circulation of both novel and endemic VBPs relies on host and vector population dynamics that are regulated by environmental changes (Figure 1). Ultimately, the transmission of VBPs from an infected host to a new one depends on the blood-sucking behavior of vectors, and mosquitoes serve as primary vectors of many VBPs, such as avian *Plasmodium* and WNV (16, 17). Some VBPs circulate between humans, but others mainly infect animals, with humans and livestock acting as incidental hosts.

As a bridge between VBPs and their vertebrate hosts, mosquitoes play a central role in the transmission of VBPs. And those invasive mosquitoes become a research focus because they have the potential to become competent vectors of both novel and endemic VBPs and hence, significantly contribute to the expansion of VBPs. This review will focus on invasive mosquitoes, their introduction pathways, and the ecological factors that limit their establishment and spread. It will also examine the role these mosquitoes play in the transmission of VBPs during their introduction, establishment and spread, with particular attention to how the addition of an invasive mosquito can alter transmission intensity or pathways.

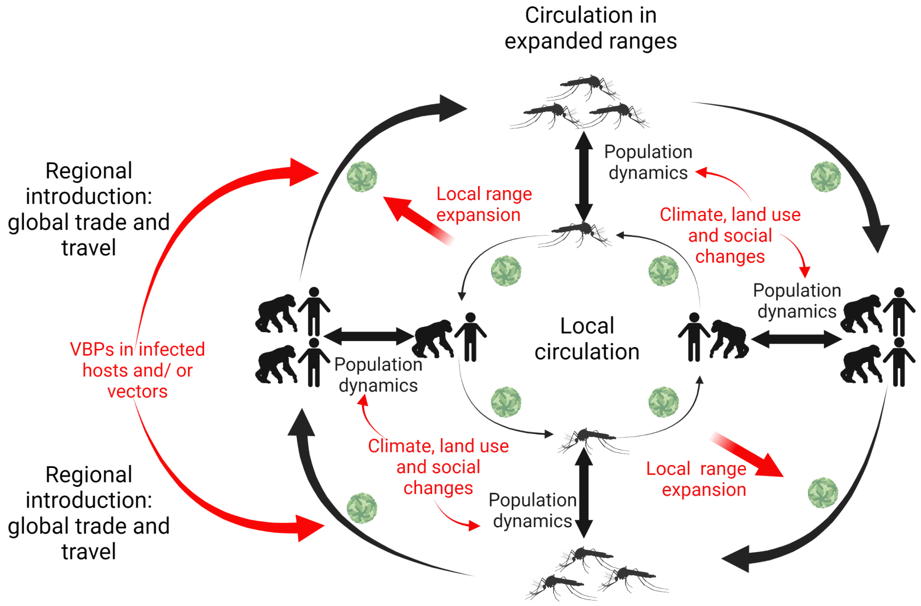

FIGURE 1
Drivers for the introduction and expansion of vector-borne pathogens (VBPs) at local and regional scales.

## Invasive mosquito species

A common definition of invasive alien species are animals, plants or microorganisms that are introduced to a non-native ecosystem as a direct or indirect consequence of human actions, where they cause harm by threatening economic development, public health, food security or biodiversity (18–20). A number of mosquitoes that were introduced to new regions meet this definition and can be defined as invasive mosquitoes. For example, the southern house mosquito *Culex quinquefasciatus*, which is a native species of Africa, has been introduced to most of the world (see Table 1). The introduction of this species along with pathogens (such as avian malaria and poxvirus) they are able to spread to Hawaii has been regarded as the major driver for the decline and extinction of native avifauna (71). *Anopheles stephensi*, another invasive species whose native regions are Southern Asia and Arabian Peninsula, has been introduced to the Horn of Africa in recent years and has been tied to an increase in malaria cases in Djibouti following its introduction in 2012 (64). There is considerable concern about the range expansion of this malaria vector that relate to how its presence could alter the previously established transmission patterns. Particularly, this species is well adapted to urban environments and uses man-made containers as oviposition and larval development sites. This differs from the primary sub-Saharan African malaria vectors that tend to be associated with ephemeral larval habitats in rural environments. There is thus concern that the spread of this invasive mosquito could lead to a surge in urban malaria in the African continent. Further, it has been found that due to the use of man-made containers, this species appears to be capable of persisting and remaining active and abundant throughout the dry season, which poses the threat of year-round malaria (72). Its role in spreading drug-resistant malaria has recently been documented (73). Due to these threats, an initiative to mitigate the further spread of this vector has been initiated by the World Health Organization (74). We provide a table to summarize the native and invaded regions, primary hosts and vectors as well as the recent outbreak of VBPs associated with several major invasive mosquitoes from the genus of *Aedes*, *Culex* and *Anopheles* in Table 1.

## Introduction pathways of invasive mosquitoes

The record of mosquito invasion dates back to the 16th century, when *Ae. aegypti* hitchhiked in the bilges of slave ships or in casks of drinking water from West Africa to the Americas (75, 76). Transoceanic ships were the major introduction pathway of invasive mosquitoes at that time. With the growth and development of the global economy and international transportation networks, modern trade and carriers have grown in importance as unintended pathways for mosquito invasion in new regions and even new continents. These pathways include two major trades via sea transportation (trades of used tires and Lucky bamboo), as well as air and ground transportation ((77) and references therein). In addition, natural dispersal of mosquitoes across terrestrial borders of adjacent countries may also be involved in range expansions (78).

### Trade of used tires

The global trade of used tires has been considered as a major introduction pathway of invasive mosquitoes, especially container-inhabiting *Aedes* species. Used tires that contain stagnant water and organic matter (e.g., rotten leaves) can serve as ideal incubators for container-breeding mosquitoes like *Aedes aegypti and Ae. albopictus*. Juliano & Lounibos (21) found that mosquito species that produced desiccation-resistant eggs were more likely to become established in non-native environments than species that did not. This is a likely reason for the successful transport of viable eggs through the used tire trade for such species. It has been found that the darker the egg color of mosquito species is as a result of increased eggshell melanization, the more resistant to desiccation, which enables their eggs to survive for several months outside water (79). In the United States, the first established population of *Ae. albopictus* was documented in Houston, Texas in 1985, thought to be introduced from its native range in Asia via the transportation of used tires (80). Since then, this invasive species has continued to spread throughout the southern and eastern United States, with 40 states reporting occurrence of this species by 2016 (81). In Europe, trade and transportation of used tires has also been recognized as the pathway for the introduction of *Ae. albopictus* in Italy (82), France (83), Croatia (84), Belgium (85), the Netherlands (86), and Portugal (87). Similarly, *Ae. japonicus* and *Ae. atropalpus* were also introduced in France, Belgium, The Netherlands and Italy through the import of used tires ( (77) and references therein).

### Trade of Lucky bamboo (*Dracaena sp*)

Lucky bamboo, an ornamental plant species, usually contains 5-8 cm of water during long-distance transport and can serve as a suitable development site for mosquito eggs and larvae. The importation of Lucky bamboo into Europe and the United States has caused repeated introductions of *Ae. albopictus* from its native range (88, 89). For example, the introductions of *Ae. albopictus* into southern California in 2001 and 2002 and the Netherlands in 2013 were reportedly associated with the shipment of Lucky bamboo from southern China (77, 90, 91).

### Airplanes

Modern air transportation provides the potential of global transit in a single day for goods and passengers, possibly on some occasions including hitchhiking mosquitoes. Although no direct evidence for the introduction of invasive mosquitoes by air transport has been reported in any continent so far, airplanes

TABLE 1 Distribution, primary hosts and pathogens of invasive mosquitoes.

| Species | Native region (NR) | Invaded region (IR) | Preferred host | Primary vectoring pathogens | Recent disease outbreak in NR | Recent disease outbreak in IR | Ref. |
|---|---|---|---|---|---|---|---|
| *Ae. albopictus* | East, Southeast and South Asia | Europe, Americas, Africa, Oceania | Mammals including humans | CHIKV, DENV, ZIKV | Chikungunya in South Asia | Chikungunya and dengue in Italy, France and Spain | (21–25) |
| *Ae. aegypti* | Sub-Saharan Africa | Americas, Europe, Asia, Oceania | Humans | DENV, ZIKV, YFV, CHIKV | Dengue in Tanzania | Dengue in Americas and Southeast Asia | (26–31) |
| *Ae. japonicus japonicus* | East Asia, Southeast Siberia | North America, Europe, Hawaii | Mammals Including humans, birds | WNV, JEV, SLEV JEV, | No report | No report | (31–33) |
| *Ae. koreicus* | East Asia Eastern Russia | Europe | Humans | CHIKV, *D. immitis* | No report | No report | (34–37) |
| *Ae. atropalpus* | Eastern North America | Western North America, Europe | Mammals including humans | WNV, LACV, JEV | No report | No report | (21, 31, 37) |
| *Ae. notoscriptus* | Australia, Tasmania | New Zealand, Torres Strait Islands. New Guinea, New Caledonia, Indonesia, USA | Mammals, Birds | RRV, BFV | RRV in Australia (primary urban vector) | No report | (38–40) |
| *Ae. togoi* | East Asia | North America, Southeast Asia | Mammals, birds | JEV, *D. immitis*, *B. malayi* | No report | No report | (41–43) |
| *Ae. scapularis* | Neotropics | USA | Mammals, birds | Multiple arboviruses and parasites | No report | No report | (44–46) |
| *Ae. vittatus* | Africa, Asia, western Mediterranean region | Cuba, Dominican Republic | Mammals including humans | YFV, DENV, CHIKV, ZIKV | YFV in Senegal, ZIKV in Senegal | No report | (47–53) |
| *Cx. coronator* | Trinidad and Tobago | Americas | Mammals, birds | SLEV, WNV | | | (54–56) |
| *Cx. quinquefaciastus* | Africa | Americas, Asia, New Zealand, Southern Europe | Mammals including humans, birds | SLEV, WNV, *W. bancrofti* | No report | No report | (16, 21, 57, 58) |
| *Cx. tritaeniorhynchus* | Southeast Asia, Middle East, Africa | Europe, Australia | Large mammals | JEV | No report | No report | (59–61) |
| *An. darlingi* | Neotropics, especially eastern Amazonia | Peru | Mammals including humans | *Plasmodium* | Malaria in Africa | No report | (21, 62) |
| *An. gambiae* complex | Africa | Brazil, Mauritius | Humans | *Plasmodium* | Malaria in Africa | No report | (21, 63) |
| *An. stephensi* | Southern Asia, Arabian Peninsula | Horn of Africa, Ghana, Republic of Sudan, Sri Lanka | Mammals including humans | *Plasmodium* | Malaria in Indian | Malaria in Djibouti | (64–70) |

BFV, Barmah Forest virus; CHIKV, chikungunya virus; DENV, dengue virus; ZIKV, Zika virus; YFV, yellow fever virus; WNV, West Nile virus; JEV, Japanese encephalitis virus; SLEV, St. Louis encephalitis virus; LACV, la Crosse virus; JCV, Jamestown Canyon virus; RRV, Ross River virus; *D. immitis*, *Dirofilaria immitis*; *B. malayi*, *Brugia malayi*; *W. bancrofti*, *Wuchereria bancrofti*.

have been identified as a highly likely pathway for the introduction of invasive mosquitoes in islands (92), and the recent establishment of *Cx. quinquefasciatus* in the Galápagos Islands was demonstrated to be ascribed to the regular air transport of mosquitoes from Ecuador (93). Similarly, 14 non-indigenous mosquito species were introduced to Guam following the second World War and this has been attributed to increased air traffic to the island (94). Further, the presence of invasive mosquitoes including *Ae. aegypti*, *Ae. albopictus* and *Ae. koreicus* at European airports have been reported (95, 96), and detections of *Ae. aegypti* at Australian airports have become increasingly common over recent years (97), indicating air transport of invasive mosquitoes is occurring and may prove a concern and/or require risk-based surveillance in more areas in the future (98, 99).

### Ground vehicles

The initial detection of *Ae. japonicus* in northern Germany was in towns adjacent to a highway, suggesting that this species was likely introduced by ground vehicles (100). Although direct evidence is rare, it has been demonstrated that mosquitoes can hitchhike with ground vehicles to spread to new areas (101). Egizi et al (102) showed a correlation between genetic distance and distance along roads for *Ae. japonicus* in the northeastern United States, suggesting their local dispersal was related to road transportation. An analysis of gene flow for *Ae. albopictus* likewise pointed to the importance of highways and human-aided transport for long-distance dispersal of this species (103). Other recent studies reported that the introduction of *Ae. albopictus* into European countries, such as Germany and Spain, has been facilitated by ground vehicles (101, 104). Therefore, ground vehicles may play an important role in the introduction of invasive mosquitoes, especially for a short-distance introduction. Railway transportation has been linked to the movement of mosquitoes, particularly in the first half of the 20th century, including observations of *Ae. notoscriptus* and *Ae. aegypti* larvae breeding in fire buckets in railway stations, which were common at stations when steam locomotives were used, as well as frequent reports of passengers being bitten on trains (105).

### Natural dispersal

Although the flight capacity for mosquitoes is very limited (106), natural active dispersal of invasive mosquitoes has been documented in some European countries (77). For example, the pathways for the introduction of *Ae. japonicus* from Austria to Italy and from Germany to Luxemburg have been identified as natural dispersal (78, 107). This pathway could be used by migratory mosquitoes to cross the borders of adjacent countries and over time allow them to expand their range. However, recent studies have also reported long-distance mosquito migration facilitated by wind, including the successful introduction of significant vector species (108, 109). For instance, the introduction of *An. stephensi* to Africa may have been driven by windborne dispersal over long distances (110).

## Limiting factors for the invasion of mosquitoes

### Temperature

Following introduction of propagules into a new environment, whether an invasive species will be able to establish and spread will determine on the suitability of the habitat in the new region. As such, temperature can be a major factor limiting the establishment and spread of invasive mosquitoes (111), and result in differences in distribution between invasive species, such as is seen for *Ae. albopictus* and *Ae. japonicus* in Europe (112). Low temperatures affect the survival of overwintering mosquito life stages and have been used to predict the northern distribution limits of invasive mosquitoes by comparison to the native range (113). Overwinter survival in species such as *Ae. albopictus* depends on photoperiod-induced egg diapause and cold tolerance of eggs, and species possessing these characteristics are therefore more likely to expand their range to temperate areas (114, 115). For example, Hawley et al (80) demonstrated that the eggs of invasive *Ae. albopictus* in the US had similar photoperiodic sensitivity and cold hardiness with those in their native range Northern Asia. These characteristics have been considered as an adaptation to cold environments in their native range, which may have laid the foundation for its invasion success in the temperate USA (114). In addition, this adaptation continues to evolve rapidly and divergently in the invaded ranges, with populations in the south reducing their diapause response, while populations at the northern range edge expressing enhanced diapause response, which may enable a continuing northward expansion (115–117).

### Dryness

Dryness is another important climatic factor that affects the survival of eggs and hence, the invasion success of mosquitoes. Juliano and Lounibos (21) demonstrated that nearly half of invasive or non-native mosquito species have desiccation-resistant eggs and that this characteristic was strongly associated with becoming an introduced alien species. However, desiccation resistance was not significantly related to invasive status (i.e., invasive or non-invasive). This may indicate that dryness may strongly affect the establishment of an introduced mosquitoes, but other factors may play a greater role in limiting the spread of introduced mosquitoes (i.e., becoming invasive). The combination of desiccation tolerance and temperature can also affect the establishment of invasive species. For instance, in Florida *Ae. albopictus* had greater occupancy in cooler sites without a significant dry season, while *Ae, aegypti* showed greater occupancy in hotter sites with a dry season, highlighting that these factors jointly can affect the establishment and coexistence of invasive species (118).

## Microhabitats

The presence of suitable microhabitats is important for the establishment of introduced mosquitoes. One way in which this can matter is if suitable microhabitats represent an ‘empty niche’ that can be filled by an introduced mosquito species, which could result in establishment while avoiding or limiting the extent of interspecific competition with native species. Many invasive and non-native mosquito species are able to develop in small natural and artificial containers (e.g., tree holes, man-made containers), which may indicate containers as a key for the successful introduction of non-native mosquitoes. However, the establishment and spread of introduced species was not significantly associated to their specific larval habitat types (i.e., container vs. non-container), rather success of invasive species was linked to their adaptation to non-natural microhabitats in urban, suburban, and domestic areas (21). This may indicate that human disturbance plays a role in the spread of introduced mosquitoes, e.g., by creating peridomestic underexploited habitats, or because invasion pathways for mosquitoes favor urbanized areas as a consequence of the associations with transportation nodes, and thereby anthropogenic environmental change could contribute to their invasiveness.

## Interspecific competition

Following the introduction into new regions, interspecific competition between introduced and native species can take place if they occupy overlapping habitats. Interspecific competition can affect mosquito population dynamics through the negative effects of resource competition and mating interference and play a role in determining the outcome of an introduction (119). If introduced species are superior competitors, they may exclude resident species and become invasive in the new areas. On the contrary, an introduced species may not spread out because of the stronger competition from residents and become non-native in a limited range. Both lab and field experiments often showed that *Ae. albopictus* was superior in competition to *Ae. aegypti* (120, 121), as a result, the distribution of *Ae. aegypti* has declined with the expansion of *Ae. albopictus* in the continental US, whereas in certain tropical cities exclusion of *Ae. albopictus* by *Ae. aegypti* has been noted (119).

## Predation and parasitism

Predation can have direct effect on population dynamics of introduced mosquitoes. Predators in the new areas for introduced mosquito species may help keep them from spreading out and becoming invasive. On the contrary, the absence of predators in the new areas for the introduced mosquitoes may facilitate the establishment and spread of the introduced species. This enemy release hypothesis while sometimes supported, is also frequently questioned (122). The extent to which it applies for different mosquito species is not entirely clear, but there are examples of both predation and parasitism affecting invasive mosquitoes. For example, the presence of *Toxorhynchites rutilus*, an efficient predator of *Ae. aegypti*, may have limited the invasion success of *Ae. aegypti* in wooded areas (123), while the absence of predators and competitors of *Cx. quinquefasciatus* in artificial container habitats have contributed to the invasion success of this species (124). Even when there are multiple exotic species coexisting, predation can severely lower their performance, especially the performance of the species that are less competitive, thus forming barriers for the spread of exotic species (125). Parasitism may have a similar effect on invasive species through pathogenic effects on development and performance (126). Parasitism by *Ascogregarina taiwanensis*, for example, has been demonstrated to reduce the competitive advantage of *Ae. albopictus* over a native species, *Ae. triseriatus*, which was thought to limit the establishment and spread of this invasive species (127, 128). However, such pathogenic effects are usually mild, depending on environmental conditions (126).

# Potential roles in the transmission of VBPs

Invasive mosquitoes may pose a great threat to wildlife and human health, for instance through the introduction of invasive mosquitoes that are capable of transmitting exotic pathogens to native host populations lacking herd immunity. The introduction of invasive mosquitoes may play varying roles in the transmission of vector-borne pathogens, depending on their competence for transmitting native or novel pathogens and the ways in which their introduction shifts vectorial capacity of the local mosquito community for different pathogens (see Box 1 for an example). Some mosquito vectors and pathogens may be associated in their native ranges but are introduced separately into new regions, which is considered as the most common cause of disease outbreak in the invaded regions (21). In other cases, some mosquito vectors and pathogens are introduced simultaneously into new regions, or introduced mosquitoes are already capable of transmitting endemic pathogens.

Separate introductions of novel vector and pathogens are likely to occur in introduction events as a consequence of mosquitoes and pathogens having different introduction pathways. For instance, the propagule pressure for mosquitoes could be greatest due to long distance travel of containers, and uninfected mosquitoes (e.g., transported in the egg stage) will arrive in a much greater volume than infected mosquitoes. At the same time, the pathogen might be introduced much less frequently through movement of the vector, compared to the movements of infected hosts such as humans, livestock, or migratory birds (5). Following establishment, introduced mosquitoes may acquire an association with separately introduced pathogens and create a new threat to susceptible hosts. For instance, the separate introductions of *Cx. quinquefasciatus* and avian *Plasmodium* in Hawaii have caused the outbreak of avian malaria and the decline of Hawaiian birds, particularly in those avian fauna at low elevations (149). Another example is the separate

**BOX 1** Role of *Ae. japonicus japonicus* as a disease vector in its native and invaded regions

The Asian bush or rock pool mosquito, *Ae. japonicus japonicus* (Theobald, 1901), originating from East Asia (northeastern Russian, Japan, Korea, Southern China), is a highly invasive species, which has spread throughout North American and later into Central Europe (32). Like the introduction of other invasive *Aedes* mosquitoes, transportation in used tires via international trade is presumably a major pathway for its invasion into novel regions. In 1993, the first record for its non-native range was reported in New Zealand, with larvae found in the used tires imported from Japan, although this introduction did not result in an established population (129, 130). In 1998, introduction of this species was first documented in Connecticut and then New York and New Jersey (131). Since then, *Ae. japonicus japonicus* has successfully established and was found in 33 states of the US by 2011 and southwestern Canada (31, 132). In 2000, this invasive species was first detected in France after which it spread to several central European countries including Belgium, Switzerland, Germany, Liechtenstein, Austria, The Netherlands, Croatia and Slovenia over the next decade (133).

In its native range, *Ae. japonicus japonicus* is not considered as an important disease vector (31). Only three arboviruses were tested on *Ae. japonicus japonicus* for its vectorial potential (Table 2). Japanese and Russian researchers demonstrated that this species was able to get infected both in the laboratory and field and transmit JEV in the laboratory (134, 135). It was also susceptible to ZIKV and GETV infection in the laboratory (147, 148). In its invaded areas, a number of arboviruses have been tested on *Ae. japonicus japonicus* (Table 2). It was susceptible to JEV, CHIKV and DENV infection in the laboratory, both infection and transmission in the laboratory for SLEV, EEEV, RVFV, UVSV, ZIKV, and infection and transmission in the laboratory and field infection for WNV and LACV (Table 2). However, no evidence from both its native and invaded regions has shown that it plays a major role in the field transmission of disease agents. Compared to its invaded regions, few experimental infections by arboviruses have been tested on *Ae. japonicus japonicus* in its native regions. As *Ae. japonicus japonicus* feeds on a variety of hosts and is capable of vectoring and/or transmitting an array of pathogens, it can be a potentially important bridge vector threatening humans, livestock and wildlife, especially in invaded novel regions where its enemies and competitors from its native region may be absent and it can pick up novel pathogens.

introduction of *Culex pipiens* complex and West Nile virus in North America where the pathogen was introduced long after the mosquito (150).

Simultaneous introductions of novel vectors and pathogens likely occurs much more rarely. However, it may still have the potential to cause large outbreaks of diseases, given native host populations are relatively naïve to novel pathogens. For example, the historical introductions of *Ae. aegypti* in North and South Americas have caused immediate outbreak of yellow fever and dengue, respectively, upon the arrival of slave ships from Africa that were presumably carrying yellow fever and dengue virus that were novel to these regions at that time (21).

Invasive mosquitoes can also be competent for existing native pathogens and modify local transmission cycles of vector-borne diseases. If the introduced vectors are highly competent, the disease transmission rates and risk to public health could be enhanced. But if the introduced vectors are less efficient or through competitive interactions lower the population densities or exclude existing primary vectors, the disease transmission rates could decrease. An example of this is *Ae. aegypti* which is an invasive species in Asia, originating in sub-Saharan Africa, and becomes a major vector of dengue in tropical Asia. Although it is possible that dengue originated in Africa, there is compelling evidence that dengue virus is native to Asia (151).

The introduction of invasive mosquitoes into local mosquito communities can significantly impact the transmission risk (e.g., potential exposure for humans) and intensity (e.g., the basic reproduction number of the pathogen) of VBPs in their invaded areas. Invasive species may compete with native mosquitoes for ecological niches, such as breeding sites and nectar, and disrupt the existing host-vector interaction networks. These changes can lead to alterations in native mosquito population densities and modify the

TABLE 2 Demonstrated role of *Aedes japonicus japonicus* in arbovirus transmission in native and invaded regions.

| | Native region | | | | Invaded region | | | | Ref |
|---|---|---|---|---|---|---|---|---|---|
| | Lab infection | Lab transmission | Field infection | Field transmission | Lab infection | Lab transmission | Field infection | Field transmission | |
| JEV | + | + | + | uc | + | uc | uc | uc | (134–136) |
| WNV | uc | uc | uc | uc | + | + | + | uc | (137, 138) |
| SLEV | uc | uc | uc | uc | + | + | uc | uc | (139) |
| EEEV | uc | uc | uc | uc | + | + | uc | uc | (140) |
| LACV | uc | uc | uc | uc | + | + | + | uc | (141, 142) |
| RVFV | uc | uc | uc | uc | + | + | uc | uc | (143) |
| CHIKV | uc | uc | uc | uc | + | uc | uc | uc | (144) |
| DENV | uc | uc | uc | uc | + | uc | uc | uc | (144) |
| USUV | uc | uc | uc | uc | + | + | uc | uc | (145) |
| ZIKV | + | uc | uc | uc | + | + | uc | uc | (146) |
| GETV | + | uc | uc | uc | uc | uc | uc | uc | (147) |

JEV, Japanese encephalitis virus; WNV, West Nile virus; SLEV, St. Louis encephalitis virus; EEEV, Eastern equine encephalitis virus; LACV, la Crosse virus; RVFV, Rift Valley fever virus; CHIKV, chikungunya virus; DENV, dengue virus; USUV, Usutu virus; ZIKV, Zika virus; GETV, Getah virus. “+”: confirmed; “uc”: uncertain.

rates at which pathogens are transmitted to native hosts and vectors. For instance, Box 2 provides a case study on how the invasive species *Ae. albopictus* and *Ae. j. japonicus* can alter the host-vector interaction network of the native species *Ae. triseriatus* in North America.

We reviewed the literature for studies in North America that investigated the blood feeding patterns of a native mosquito, *Ae. triseriatus*, considered the primary vector of La Crosse encephalitis virus, and two invasive species, *Ae. albopictus* and *Ae. j. japonicus*, both of which are competent vectors under laboratory conditions (168) and have been found to be infected in the field with this virus as well (169, 170) In areas where these three species co-occur, ignoring possible effects they may exert on each other's population density, the range of host species fed upon is considerably more diverse than in areas with only the native species. In the case of LACV, where the primary hosts are considered chipmunks and squirrels, the invasive species could potentially become exposed. The role of rabbits is less clear, although there have been suggestions, they may play a role as well (157). The larger impact of these invasive species however could be that rather than increasing $R_0$ in a meaningful way for a virus like LACV, they could however act as additional bridge vectors and increase the rate with which humans are bitten by infective mosquitoes. Theoretical models exploring these virus-vector-host networks, density-dependent interactions among vectors, and seasonal overlap, could shed light on exactly how VBP transmission would be altered by the introduction of one or more invasive species.

## Challenges and future directions

Current surveillance and control programs for invasive mosquitoes and vector-borne pathogens (VBPs) have shown

### BOX 2 Invasive mosquitoes alternative host-vector network in North America

The introduction of an invasive mosquito species can change transmission risk or intensity in a number of ways. Density-dependent competition can, as described above, lead to changes in the mosquito community with possible exclusion of certain native species, while if the niche differences are sufficiently large, coexistence can also occur. The exact outcome in terms of population densities of the various vector species relevant for the pathosystem in question will determine to a large extent what will occur. In the case of coexistence, the addition of another species to an assemblage of vectors can affect transmission in a number of ways. Increased vector diversity could take the form of temporal separation, and a result of this could potentially be that the effective transmission season of a given pathogen becomes extended (152). Another way in which transmission risk and intensity could shift with the addition of an invasive vector is through changes to the host-vector network. With different species having different preferences for host species, and different rates of blood feeding on those vertebrate hosts, it is possible that pathogens associated with a host that was initially not connected to other amplifying hosts or humans, now becomes so due to an invasive species. An example of such a network is provide in Figure 2.

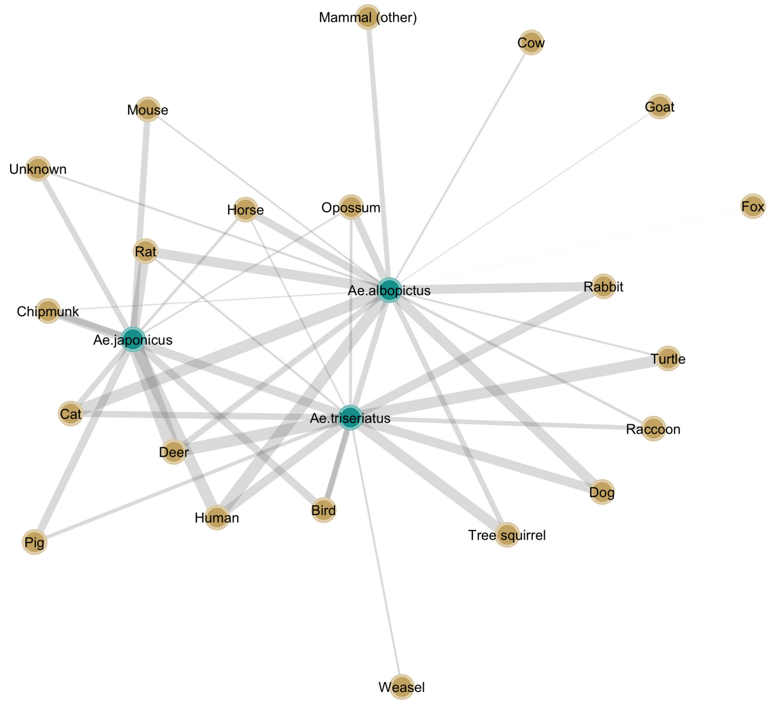

FIGURE 2
Bipartite graph highlighting the interactions between a native mosquito, *Ae. triseriatus*, and two invasive species, *Ae. albopictus* and *Ae. j. japonicus*, and vertebrate hosts used as blood meal sources. The connections between each vector and host species are weighted and represent average proportions of identified blood meals collated from studies in North America (153–167).

varying degrees of effectiveness across different regions (171, 172). This variability is influenced by key factors such as the scope and enforcement of national and intergovernmental regulatory policies enacted for preventing the introduction, establishment, and spread of alien species, public investment in vector control and surveillance capacity, as well as efforts to reduce the vectorial capacities of invasive mosquitoes. For instance, the increased movement of goods and tourists poses significant challenges for controlling the entry of alien mosquitoes and VBPs at points of entry (5). Integrated Vector Management (IVM) remains the most effective strategy for mosquito control (173). IVM combines chemical, biological, and physical control methods and typically requires the use of insecticides and significant resources, including trained technicians. However, resource limitations, environmental concerns, and the development of insecticide resistance can hinder the effectiveness of IVM (174). Additionally, the ecological mechanisms underlying the establishment and spread of invasive mosquitoes in new regions remain largely unknown (54), making ecological control a significant challenge.

These challenges underscore the need to develop and implement newer, safer, more effective, and sustainable tools for invasive mosquito control. To address these challenges and the process of mosquito invasion, we propose several priority research questions for future study and control of invasive mosquitoes and VBPs: 1) Integrating advanced techniques (e.g., artificial intelligence (AI), quantitative risk assessments) for predicting future invasion risks, identifying high risk routes of entry, and enhancing the detection sensitivity and control of imported mosquito adults and eggs at entry points; 2) innovating surveillance techniques (e.g., high-throughput molecular tools and rapid detection kits) for mosquito and VBP identification and screening; 3) unravelling the ecological mechanisms behind the success of invasive mosquitoes in invaded regions, from establishment to spread, particularly their interactions with native mosquito species, vertebrate hosts, and how they change vector-host-pathogen networks; 4) Incorporating advanced tools such as AI, sterile insect techniques, and gene drive into IVM to effectively monitor, suppress, or replace invasive mosquito populations and reduce their vectorial capacities; 5) Enhancing control options for invasive mosquitoes by exploiting a wider range of their life cycle and behaviors, such as novel baitstations based on plant-derived volatiles; 6) Enhancing community engagement and education, as well as public integration in mosquito surveillance and control programs, such as through citizen science initiatives aimed at early detection of novel vector introduction and spread.

## Conclusions

Mosquitoes can be introduced into novel regions by the transportations of used tires and lucky bamboo in global trade and by hitchhiking airplanes and ground vehicles in global travel. Local ecological factors including temperature, dryness, competition, predation, and parasitism may limit the establishment and spread of the introduced mosquitoes in novel regions. Invasive mosquitoes can play a critical role in the transmission of VBPs in their introduced regions, depending on whether they are introduced separately or simultaneously with already vectoring VBPs, or whether they can acquire the competence for novel pathogens in the invaded regions over generations. Management and control effort should be targeted at cutting off their introduction pathways as the frontline, limiting their establishment and spread using ecological measures and reducing their contact with local hosts and pathogens.

## Author contributions

JY: Conceptualization, Data curation, Investigation, Validation, Visualization, Writing – original draft, Writing – review & editing. AM: Data curation, Validation, Writing – review & editing. CS: Conceptualization, Funding acquisition, Visualization, Writing – original draft, Writing – review & editing.

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

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The author(s) declare that no Generative AI was used in the creation of this manuscript.

## Publisher's note

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