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The invasive mosquito species *Aedes albopictus*: current knowledge and future perspectives

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Abstract

One of the most dynamic events in public health is being mediated by the global spread of the invasive mosquito *Aedes albopictus*. Its rapid expansion and vectorial capacity for various arboviruses affect an increasingly larger proportion of the world population. Responses to the challenges of controlling this vector are expected to be enhanced by an increased knowledge of its biology, ecology, and vector competence. Details of population genetics and structure will allow following, and possibly predicting, the geographical and temporal dynamics of its expansion, and will inform the practical operations of control programs. Experts are coming together now to describe the history, characterize the present circumstances, and collaborate on future efforts to understand and mitigate this emerging public health threat.

Keywords

Aedes albopictus; public health; arboviruses; expansion; vector control

The Asian tiger mosquito: origin and spread

The Asian tiger mosquito, *Aedes albopictus* (Figure 1), is an aggressive, day-time biting insect that is emerging throughout the world as a public health threat following its primary role in recent dengue (DENV) and Chikungunya (CHIKV) outbreaks [1–3]. Part of its impact on human health is due to its quick and aggressive spread out of its native home range in East Asia and islands of the western Pacific and Indian Ocean [4]. *Ae. albopictus* has colonized every continent except Antarctica in the past 30–40 years (Figure 2) [4–5]. The first record of this species in Europe (Albania) was in 1979 [5]. Today, *Ae. albopictus* is present in all countries on the Mediterranean sea, including parts of Turkey and the Middle Eastern states of Lebanon, Israel, and Syria, and is gradually moving north [4,6]. Italy and

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southern France are the most infested regions [6], but *Ae. albopictus* also have limited local distribution in southern Switzerland, the Netherlands, Bulgaria, Russia, Belgium, and Germany, confirming predictions of expansions based on climate changes [4].

Ae. albopictus was introduced into the US at the end of the eighteenth century in Hawaii [7]. The first detection in the continental US was in 1985 in Texas, and *Ae. albopictus* is established currently in 866 counties of 26 states. A breeding population of *Ae. albopictus* was discovered recently in southern California [8,9], and this species also is detected sporadically in Washington and New Mexico (www.cdc.gov/ncidod/dvbid/arbor/albopic_new.htm).

The presence of *Ae. albopictus* in Central and South America has been documented since the 1980–1990s, primarily in Mexico and Brazil (www.cdc.gov/ncidod/dvbid/arbor/albopic_new.htm). Records of *Ae. albopictus* in Mexico reflect a widespread distribution starting from the north at the border with Texas in the 1990s, and moving south and east into neighboring countries of Guatemala and Belize [4,6]. The Caribbean islands of Barbados, the Dominican Republic, Trinidad, the Caymans, and Cuba, along with the Central and South American States of El Salvador, Honduras, Panama, Nicaragua, Venezuela, Colombia, and Bolivia also have documented detections of *Ae. albopictus* since the late 1990s [4,6]. Invasion of Brazil started with focal detection in Rio de Janeiro in 1986, and then in two neighboring states of Espirito Santo and Minas Gerais, and San Paulo the following year [7,10]. A rapid expansion followed with mosquitoes moving to northern, northeastern, and central regions, and reaching the Amazon basin by the early 2000s [11]. Breeding populations of *Ae. albopictus* have been identified since the late 1990s in the Misiones province of northern Argentina, at the border with Brazil [12]. The current distribution of this species in Argentina is limited to northeast provinces and includes the neighboring countries of Uruguay and Paraguay [4].

The first detection of *Ae. albopictus* in Africa was in 1989 when live larvae were detected in the port city of Cape Town, South Africa, in used tires imported from Japan; the infestation was immediately controlled [13,14]. Two years later, it was recorded in Nigeria and dispersed to Cameroon, Equatorial Guinea, and Gabon [1,14].

Once *Ae. albopictus* is established in an area, it is difficult to eradicate, and constant surveillance and appropriate control strategies are required [15]. The widespread distribution of *Ae. albopictus* outside its native home range is presumed to have been primarily human-mediated and accidental [16]. Low levels of mtDNA and limited phylogeographic genetic differentiation among populations are consistent with dispersal and invasion mediated by human activities, such as continued migration events, and commerce in used tires and live plants (lucky bamboo) and continued propagule pressure [9,17–19].

Public health impact of the Asian tiger mosquito

Retrospective studies of the incidence of DENV infections in regions with exclusive or prevalent presence of *Ae. albopictus* versus the main vector, *Aedes aegypti*, show the absence of explosive dengue outbreaks [20]. Meta-analysis of published laboratory-based experiments on the relative vector competence of *Ae. albopictus* versus *Ae. aegypti* for DENVs reveal that the former are more susceptible to midgut infection, but more resistant to virus dissemination [20]. These observations led to the conclusion that *Ae. albopictus* is currently a less efficient vector of DENVs than *Ae. aegypti* [1]. However, *Ae. albopictus* was the sole or primary vector of recent (2001–2010) DENV outbreaks in Hawaii, Indian Ocean islands, Central Africa, and southern China [1–2,21–22] and the first DENV (2010) autochthonous transmissions in Europe [3].

Ae. albopictus can transmit several other arboviruses of public health significance, including CHIKV and possibly West Nile virus (WNV) [1,24]. *Ae. albopictus* was responsible for recent CHIKV epidemics in several islands of the Indian Ocean, Central Africa, and Europe [3,24]. A total of 26 viruses from five different families, including Eastern equine encephalitis, La Crosse, Japanese encephalitis, and Venezuelan equine encephalitis, have been isolated from wild-caught *Ae. albopictus*, although their role in transmission is uncertain [1]. This species also vectors the filarial nematode *Dirofilaria*, with transmission occurring primarily between dogs and mosquitoes, but occasionally involving humans [6].

What makes *Ae. albopictus* a threat? The density of mosquito populations is an important element favoring epidemics in the presence of limited vector competence. This was shown during the yellow fever epidemic in Nigeria in 1987, which was vectored by a high density, sylvatic *Ae. aegypti*, that had low competence for the virus [23]. Moreover, vector competence is a dynamic status as evidenced by recent CHIKV outbreaks in the Indian Ocean islands of La Reunion, Mauritius, Madagascar, and Mayotte (2005–2007), as well as Central Africa (2006–2007) and Italy (2007) [24]. Phylogenetic analysis of full-length viral sequences of isolates from these outbreaks revealed an example of rapid (1–2 y), convergent evolution through the independent acquisition of a mutation from Ala to Val at position 226 (A226V) in the E1 gene of the polyprotein [24]. This convergent evolution results from a strong selective advantage of the A226V mutation [24], which is associated with improved CHIKV replication and transmission efficiency in *Ae. albopictus* [25–26]. *Ae. albopictus* is now the predominant or only CHIKV vector in La Reunion, Mauritius, Italy, Cameroon, and Gabon, supporting the conclusion that the A226V mutation is a viral adaptation to a previously atypical vector with aggressive and rapid dispersal efficiency [24].

The emergence of arboviruses is linked frequently to changes in vector or vertebrate hosts, or both [27]. This continuous evolutionary adaptation is particularly troubling considering *Ae. albopictus* competency for multiple arboviruses [1] and emphasizes the importance of understanding and monitoring the competence of geographic populations for different arboviruses (Box 1). In addition, *Ae. albopictus* shows ecological plasticity in different traits such as larval breeding sites, feeding behavior, and climatic adaptation that increase their potential for spread and adaptation to new environments, and influence their co-existence with other vector species. Increased global movements of goods and humans along with climate change are associated already with the expansion of its range and impact on human health [1,6,16].

Ecological variation

Breeding habitat choice and feeding behavior

Ae. albopictus originated at the edges of forests and bred in natural habitats (tree holes, bamboo stumps, and bromeliads) and consequently was considered previously to be a rural vector [28]. However, this species has adapted well to suburban and urban environments with larvae now breeding in artificial containers (tires, cemetery urns, and water storage containers) (Figure 3) and has become the most important and sometimes sole vector in urban areas (southern China and Italy) [21,29]. *Ae. albopictus* feeds aggressively and opportunistically during the day on a wide range of hosts dependent on their availability and the environment [30–32]. When offered a choice, this species prefers humans (anthropophilic behavior) [1,30–31], but it also can feed on a large variety of animals (cows, goats, dogs, birds, reptiles, and amphibians) (zoophilic behavior) [30–31]. The opportunistic zoophily enhances the spectrum of pathogens it can vector and the ecological niches it can occupy [1]. Most literature refers to this species as resting and feeding outdoors (exophilic and exophagous), but recent reports provide evidence of geographical variation in this behavior with gravid females captured indoors in Rome, Italy [32]. Whether this variation is

dependent on different capture methodologies needs further investigation because it is difficult to find *Ae. albopictus* resting in the wild [30,32].

Climatic adaptation

The ability of *Ae. albopictus* to colonize different ecological niches and hence expand its species range is related partly to its capacity to adapt to seasonal variations through photoperiodic diapause [33–34]. Diapause is an environmentally-dependent period of dormancy, characterized by changes in metabolic pathways, insulin signaling, cell-cycle arrest, and upregulation of stress-response genes [35–37]. When exposed to seasonal short-day length (as in winter time), *Ae. albopictus* adult females of temperate populations oviposit eggs in which pharate larvae enter into diapause inside the chorion of the egg until permissive conditions favor the resumption of development [33–34]. Rapid evolution in traits such as the critical photoperiod (seasonal timing of diapause) and diapause incidence has been shown in *Ae. albopictus* populations invading the US, and these data support the conclusion that these adaptive phenotypes are a critical element of the invasion potential [34,37].

Diapausing eggs are larger, contain more total lipid, and are more desiccation-resistant than non-diapause eggs [38–39]. In addition to enhancing overwinter survival, these traits are likely to favor passive dispersal and thereby contribute to invasion success [40]. Analyses of gene expression profiles during diapause identified two genes (*Pepck* and *PCNA*) in *Ae. albopictus* with diapause-related transcriptional profiles conserved across different insect taxa and support the conclusion that diapause and developmental programs are integrated tightly [36]. These results support the existence of a universal diapause gene set that could be disrupted, providing a basis for novel control strategies [36].

The observed ecological variation in the breeding habitat choices, the opportunistic feeding behavior, and the adaptation to different climates may be either the result of plasticity (i.e., one genotype is flexible in its phenotypes) or of local adaptation of different genotypes.

Competitive interactions among species

Competitive interactions of invasive *Ae. albopictus* depend on the environment and include both endemic species (primarily *Ae. triseriatus*, *Ae. atropalpus*, and *Ae. barberi* in the US and *Culex pipiens* in Italy) and other invasive species (*Ae. japonicus* in the US; *Ae. aegypti* throughout the American continents, Indian Ocean islands, Bermuda, and tropical Asian countries, and *Culex* species in Europe and the US) [40,41]. Most studies focus on competition and co-existence between the two dengue vectors, *Ae. albopictus* and *Ae. aegypti*, because of their public health relevance [41]. *Ae. aegypti* is native to sub-Saharan Africa, but has expanded its species range to most tropical and sub-tropical regions of the world where *Ae. albopictus* populations also breed [42]. Competition between the two species occurs primarily at the larval stage, although there is new evidence of adult mating interactions influencing the impact of *Ae. albopictus* on *Ae. aegypti* [43]. *Ae. albopictus* tends to be a superior larval competitor, displacing *Ae. aegypti* in suburban and rural sites [1,41]. Furthermore, competition among larvae appears to have asymmetrical effects on adult longevity [44]. Abiotic factors such as temperature, rainfall regime, spatial aggregation, and salinity, and biotic factors such as presence of predators, some aspects of detritus input, bacterial communities inhabiting the breeding site, and variation among geographically-distinct mosquito populations can influence both breeding-site choices and the outcome of competition [45–52]. Seasonality may contribute to coexistence by causing fluctuations in both climate and detritus inputs [50]. Patterns of exclusion and coexistence in Florida are observed in different areas and are correlated with climate and land use, with wetter and cooler conditions favoring *Ae. albopictus*, and *Ae. aegypti* remaining prevalent in

urban and southern areas of the state [40–41,45]. When *Ae. albopictus* was introduced to Reunion Island at the beginning of the 20th century, it became ubiquitous and displaced *Ae. aegypti*, which is now restricted to the drier western coast of the island [48]. *Ae. albopictus* populations in this island were shown to be more temperature-tolerant and superior larval competitors than *Ae. aegypti* [48].

***Aedes albopictus* microbiota**

Facultative and obligate symbiotic relationships between insects and microorganisms are widespread in nature, affect different insect phenotypes including their interaction with pathogens, digestion, protection against natural enemies, and also are exploited for control purposes [53–55]. *Ae. albopictus* natural populations are infected with *Wolbachia pipientis* (hereafter referred to as *Wolbachia*) [56]. Two *Wolbachia* strains (wAlbA and wAlbB) were identified and shown to differ in tissue-distribution and density [57-]. *Wolbachia* is the causative agent of cytoplasmic incompatibility (CI) and affects other host traits, including life span and vector competence [58–59]. These characteristics fostered the exploration of the use of *Wolbachia* to aid control of DENV transmission by *Ae. aegypti* and *Ae. albopictus* [55,60]. Naturally-occurring *Wolbachia* strains do not affect either CHIKV or DENV replication in *Ae. albopictus*, but reduce DENV infection of the salivary glands [58]. In addition, recent studies of wild-caught mosquitoes from Madagascar and North America showed the presence of members of the *Asaia*, *Acinetobacter*, and *Pantoea* genera. Members of these gram-negative bacteria genera are found in several mosquito species such as *Ae. aegypti*, *Ae. albopictus*, and *Anopheles stephensi*, where they reside primarily in the gut, can be cultured and genetically-transformed, and infection persists through generations; these characteristics suggest they are amenable candidates for paratransgenesis [61–63].

***Aedes albopictus* genome and phylogeny**

The sequencing and annotation of an arthropod genome generates an important tool for understanding its biology and improving its management. INFRAVEC in Europe (<http://www.infravec.eu/index.pl>) and the Southern Medical University of Guangzhou (China) have undertaken independently the task of sequencing *Ae. albopictus* genomes. The genome is organized into three linkage groups (chromosomes) and has a variable estimated haploid DNA content of 0.62–1.66 pg [7]. INFRAVEC is sequencing a strain isolated from an urban environment from the northern Italian city of Rimini. This strain was maintained in a laboratory for 40 generations before multiple rounds of isofemale selections were carried out to reduce heterozygosity prior to genome sequencing and assembly. The genome effort in China is concentrated on the Foshan strain, which was isolated in Guangdong and has been maintained in the laboratory since 1981. Genome annotations are expected by the end of 2013 (D. Lawson and X. Chen, unpublished data). The availability of genome sequences and annotations of two *Ae. albopictus* strains of different geographic origins and histories (the Foshan strain is from the native home range and the Rimini strain is from the 1990 invasion wave into Italy) is important with respect to reports of fluidity in the genome size of individual mosquitoes, most likely resulting from variation of the amount of highly-repetitive DNA [7,64]. The genome sequence also will facilitate phylogenetic assessment and allow direct comparisons with other sequenced mosquito vectors, including *Anopheles gambiae*, *Ae. aegypti* and *Culex quinquefasciatus*, and nine additional anophelinae genomes (vectorbase.org). Additionally, the genome will contribute to transcriptome analyses, which currently are limited to the salivary glands and eggs as well as the embryos prepared for studying diapause [35–36,65].

Vector control strategies

Control of vector populations is the only current strategy for preventing many arbovirus infections, including DENV and CHIKV, because there are no commercially-available vaccines nor treatments for these pathogens and their diseases. Vector control strategies can be classified broadly into four categories: (i) environmental modification; (ii) use of chemical compounds; (iii) biological control; and (iv) genetic-based strategies [60]. An integrated approach tailored to local environments and the socio-economic status of the targeted community is expected to result in the most success [66].

Environmental modification

The adoption of screens for windows and the systematic cleanup of water containers that could be exploited as breeding sites are measures proven effective to reduce *Ae. albopictus* larval populations and impact DENV transmission [60,67]. Community participation is critical to the success of these efforts.

Chemical compounds

Various chemical compounds are being used to control larval and adult *Ae. albopictus*. Insect growth regulators (methoprene, novaluron, and pyriproxifen) and the organophosphate, temephos, which has low mammalian toxicity, low odor, and is available in long-lasting formulations, are applied in different strategies to mosquito breeding sites to reduce larval populations [68–70]. One recent approach proposes the auto-dissemination by adult females attracted to resting spots containing the insecticides and subsequent spread to new breeding sites [29].

Treatment of public areas with high mosquito density with adulticides is a recommended protective measure [71]. Pyrethroids are the most commonly used adulticides because of their low mammalian toxicity and rapid mosquito knockdown [69–70]. Increased use of insecticides for agricultural pest control, for direct control of *Ae. albopictus*, or for control of sympatric vectors (such as other Anophelinae and Culicinae species) has imposed selection pressures on *Ae. albopictus* populations for increased resistance. Resistance to larvacides, primarily temephos, is documented in Asia (China, Pakistan, Malaysia, and Thailand), Central and South America (Caribbean islands and Brazil) and Europe (Italy and Greece) [7,69–70]. Resistance to DDT and pyrethroids is recognized in *Ae. albopictus* populations native to Asia, including China, Pakistan, Malaysia and Thailand, and emerging in Africa (Cameroon) [7,69–70,72–75]. The monitoring of insecticide resistance, adoption of standardized procedure for resistance assessment, publication of results through a centralized database (i.e., IRbase available via vectorbase.org), and characterization of biomarkers for understanding resistance would be of great benefit to rational design of control programs [69–70].

Biological control

Emerging control measures include the use of toxins produced by *Bacillus thuringiensis israelensis* (Bti) as larvacides, the exploitation of endosymbionts such as representatives of the *Asaia*, *Acinetobacter*, and *Pantoea* genera for paratransgenesis or *Wolbachia* and the use of predators [61–63,76].

Bti toxins differ from other chemical compounds in that they are specific against mosquitoes and black flies. This specificity makes Bti the most widely-used biological insecticide in the US, and it is commercialized in various formulations with different lasting/releasing properties [77]. Recently, Bti application was shown to have a negative impact on DENV transmission by *Ae. albopictus* and *Ae. aegypti* in Malaysia [78]. However, the European

Food Safety Authority identified gaps in the knowledge of the safety of Bti, primarily in relation to potential horizontal transfer of genetic material from Bti to other organisms and Bti interference with the analytical systems for quality control of drinking water [79].

A number of *Wolbachia* strains, including *w*Ri, *w*MelPop, *w*Pip, and *w*Mel, were transferred successfully into *Ae. albopictus* through embryonic microinjection [80–85]. *w*Ri, originally from *Drosophila simulans*, induces either unidirectional or bidirectional CI toward the wild-type superinfection (i.e., *Ae. albopictus* is naturally co-infected with two *Wolbachia* types) [80–81]. The *w*Mel strain of *Wolbachia*, found naturally in *D. melanogaster*, reduces susceptibility to DENV and CHIKV, induces immune gene upregulation and produces bidirectional CI when transinfected into *Ae. albopictus* [84–85]. Strong CI and anti-dengue resistance also were observed in *Ae. albopictus* transinfected with *w*Pip, originally from *C. pipiens*. These promising results led scientists of the Sun Yat-sen University, the Guangzhou Center for Disease Control and Prevention, and Michigan State University to prepare a field trial in Southern China for the implementation of a vector control strategy based on mosquitoes infected with *w*Pip (Z. Xi, unpublished data). *Wolbachia*-based strategies focused on *Ae. aegypti* are being implemented already in Australia and are under development in Vietnam, Indonesia, and Brazil (Eliminate Dengue Program, <http://www.eliminatedengue.com/>). The long-term sustainability of a *Wolbachia*-based strategy against *Ae. albopictus* depends on further studies aimed at understanding the: (i) fitness effect of novel *Wolbachia* strains the mosquitoes; (ii) interaction between the novel strains and the two naturally-occurring *w*AlbA and *w*AlbB strains; and (iii) mechanism of DENV/CHIKV blocking [57,85].

The use of predators, such as larvivorous fishes, copepods, or the elephant mosquito *Toxorhynchites splendens*, is an alternative strategy of biological control suited for breeding containers like *Ae. albopictus*. Successful application of this strategy was proven against *Ae. aegypti* [76]. Several laboratory and field-trials support the feasibility of this approach for *Ae. albopictus* [86–88].

Genetic-based strategies

Two main approaches have been proposed that result in either population reduction (decrease or eliminate target mosquito population) or population replacement (replace the target population with mosquitoes genetically-modified in their vector competence) [89]. So far, most progress has been made in population-reduction strategies, which include both the production of genetically-engineered mosquito strains impaired in their ability to fly or the use of sterilizing chemicals or γ -irradiation to induce random mutations leading to sterility in mosquitoes before their release in the wild (Sterile insect technique, SIT) [57, 90–91]. Population replacement strategies for *Ae. albopictus* are still in their infancy with the main issues being to: (i) generate mosquitoes with zero viral particles in the salivary glands; (ii) assess the epidemiological impact of these genetically-engineered mosquitoes; and (iii) identify methodologies for introgression of the transgene into the target population. Extensive progress has been made in acquiring knowledge in fitness, mating, and quality control of mass-rearing of genetically-engineered mosquitoes and in addressing issues related to their safety and community acceptance [92–97]. First releases of *Ae. albopictus* males sterilized through irradiation were undertaken from 2005 to 2009 in urban and sub-urban areas of Italy, and these resulted in suppression of the local *Ae. albopictus* population [91].

Concluding remarks

Ae. albopictus is ranked as one of the world's 100-most invasive species and is being recognized as an increasingly important vector. We estimate that from 1990 to today, the

number of people living in countries with documented detections of *Ae. albopictus* increased from 3.2 to 5.1 billion (http://www.nationmaster.com/graph/peo_pop-people-population&date=2011). During the last ten years, this species was the sole or primary vector for a number of DENV and CHIKV outbreaks in Hawaii, Indian Ocean islands, Central Africa, and southern China, and the first DENV autochthonous transmissions in Europe, emphasizing its public health impact. The public health relevance of this vector mosquito results from its: (i) invasiveness and ecological adaptability; (ii) competence for multiple pathogens; (iii) potential as a bridge vector as a consequence of its opportunistic feeding behavior; and (iv) breeding adaptability to urban, rural, and forest areas. The increase of dengue risk in endemic areas is related primarily to urbanization. The widespread distribution of this species in temperate regions fosters concerns for the introduction of DENV, CHIKV, or other pathogens through travel of a viremic person. Additionally, the presence of invasive *Ae. albopictus* can increase transmission of competent native pathogens, as is happening with *Dirofilaria* in Italy [3].

We summarize here the current knowledge on the species distribution, vector competence status, ecological adaptability, and available control strategies. Perspectives for novel vector control strategies and future research needs also are highlighted based on current data gaps. One of the challenges is how to integrate current knowledge and translate it into control approaches. The release of the *Ae. albopictus* genome annotation is expected to facilitate discovery of molecular markers to characterize the genetic diversity of the species, including geographic and temporal variation and variability among populations in biologically relevant traits (i.e., vector competence, insecticide resistance, breeding preferences, climatic adaptation, and competitive ability). A genome-wide approach is suited to provide a comprehensive view of the genetic basis of a complex phenotype and potentially identify its markers as shown by studies on diapause [36]. Additionally, the availability of the genome sequence will facilitate comparative studies across mosquito species. This will result in deeper knowledge and in species-to-species transfer of methodologies and experimental procedures (i.e., transgenesis and SIT) [90–91]. Given the wide-spread and rapid distribution of *Ae. albopictus* into regions colonized by indigenous and other invasive vectors, studies of competitive interactions and/or co-existence among species are needed to assess the impact of each species on public health, identify the cross-species impact of broadly-targeted control strategies, and prioritize resources for control. For example, insecticide applications to control *Ae. aegypti* or *Culex* species could result in selection for resistance in sympatric *Ae. albopictus*.

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Glossary

Abiotic factor	a non-living or physical component of an ecosystem, such as climate or habitat
Anthropophilic	preferring humans as a blood source
Arbovirus	animal virus dependent on arthropod vectors for transmission
Biotic factor	any living component of an ecosystem
Cytoplasmic incompatibility (CI)	inability to produce viable offspring as a result of gamete infection by intracellular parasites. In the case of <i>Wolbachia</i> , CI occurs when an infected male mates with an un-infected female (unidirectional CI) or a female infected with a different <i>Wolbachia</i> type (bi-directional CI). When an infected female mates with an infected male, no CI is observed, but the progeny are infected with <i>Wolbachia</i>
Critical photoperiod	the number of hours of daylight that results in diapause entrance for 50% of the insect population, excluding those that do not enter diapause under unambiguous short-day lengths
Detritus	particulate matter originating from the disintegration of biological materials such as microbiota and tissues
Diapause incidence	proportion of the insect population entering diapause under unambiguous short-day lengths
Endophagous	preferring to feed indoors
Endophilic	preferring to rest indoors
Exophagous	preferring to feed outdoors
Exophilic	preferring to rest outdoors
Isofemale selection	selection strategy whereby progeny are derived by mating single females
Paratransgenesis	genetic modification of a symbiont to affect the vector competence of its host. Symbionts need to be easily transformed without affecting their fitness, they need to spread across host populations, and they need to reside in host organs affected by pathogens

Polyprotein	a single peptide chain that is the primary product of peptide synthesis and is cleaved into different functional proteins. The genomes of Flaviviruses, which include DENV and CHIKV, encode a polyprotein that contains 3 structural and 8 non-structural proteins
Sterile insect technique (SIT)	insect control technique based on the generation of random mutations through chemicals or γ -irradiations that lead to sterility, and release of these insects in the wild to suppress local populations
Vector competence	the ability of an arthropod to acquire, maintain, and transmit pathogens
Zoophilic	preferring animals to humans as a blood source

Highlights

The Asian tiger mosquito *Aedes albopictus* is currently the most invasive vector species world-wide

Aedes albopictus are competent vectors for different arboviruses, including Dengue and Chikungunya

The public health relevance of this species is increasing in geographic extent and number of people affected

We present a brief summary of the current knowledge of the biology, ecology, vector competence, and vector control strategies

Future research perspective on this species were derived from a panel discussion among world-wide experts

Box 1. Future perspectives

This review summarizes the present knowledge of the Asian tiger mosquito *Aedes albopictus*. Research is needed to enhance the understanding of *Ae. albopictus* biology and contribute to the development of efficient and sustainable strategies for population control. An important aspect of future research activities is the definition and adoption of standardized procedures that allow comparisons of results from different studies and the availability and sharing of wild-caught mosquitoes among the research community.

Phylogeny/taxonomy/genomics and population genetics

- Identification of molecular markers
- Characterize the genetic diversity of the species including geographical and temporal aspects and variability in biological important traits (i.e. vector competence, insecticide resistance, breeding preferences, climatic adaptation and competitive ability)
- Taxonomic status of *Ae. albopictus*
- Comparative genomics

Biology and ecology of *Aedes albopictus*

- Projected species range
- Microbiota
- Ecological influences on competition – impact/effects on vector control strategies
- Diapause, cold- and drought-tolerance
- Species range expansion

Vector competence/vectorial capacity

- Collection of epidemiological data
- Pathogen-resistance phenotypes; identification of markers for vector competence
- Characterization of arboviruses infecting geographically-different populations and their interaction with arboviruses of public health importance

Vector control strategies

- Insecticide resistance in *Ae. albopictus* worldwide populations
- Biology of *Wolbachia* in *Ae. albopictus*: distribution/physiology of endogenous strains and their interaction with strains transferred into *Ae. albopictus* from other insect species
- Genetic engineering of *Ae. albopictus*: population suppression and population replacement strategies
- Mass breeding and quality control

A



B



Figure 1.
Aedes albopictus adult male (A) and female (B). Courtesy of Centro Agricoltura Ambiente, Crevalcore, Italy.

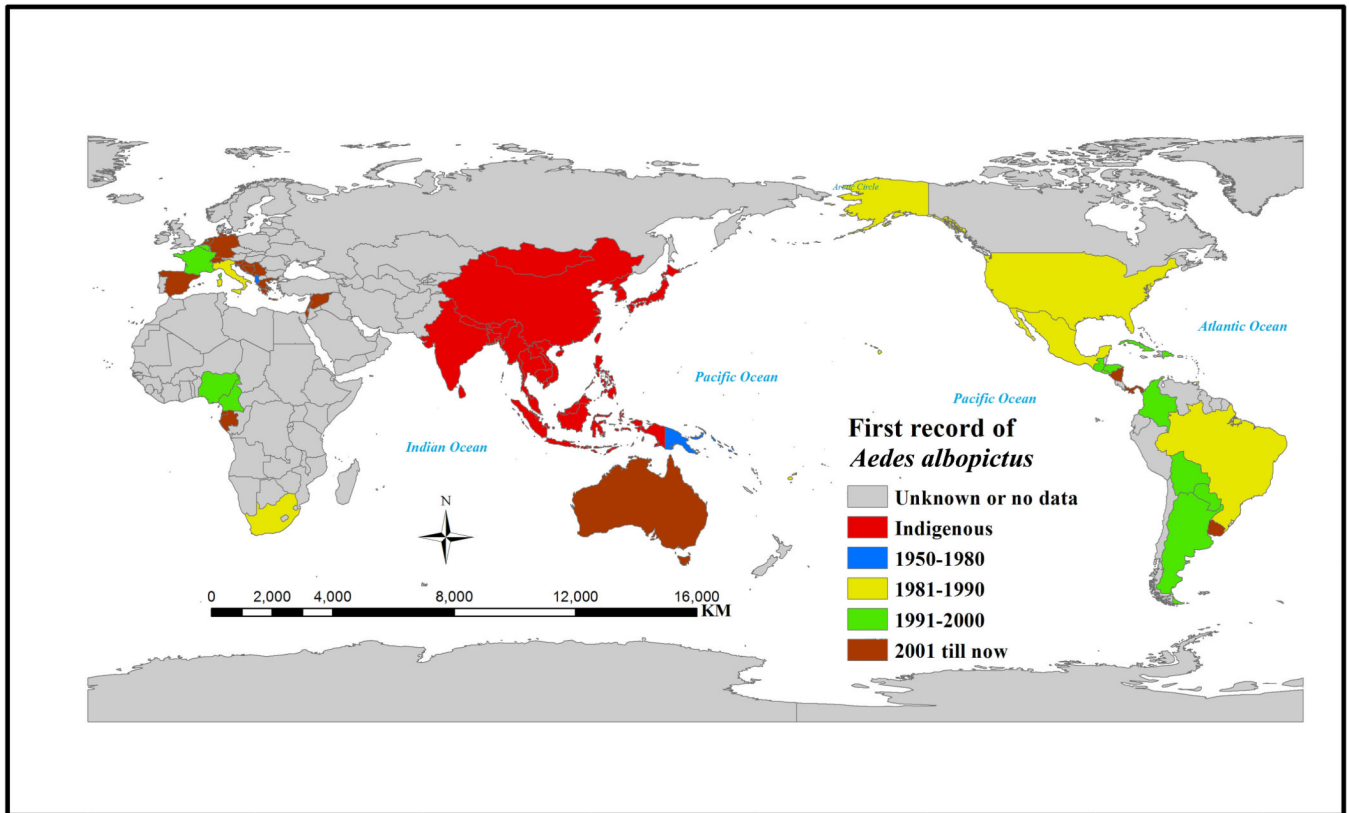


Figure 2. *Aedes albopictus* distribution range. Map indicating the first reports (interception on imports, local captures, and documented endemic populations) of *Ae. albopictus* by country (political boundaries). Record data are based on published literature [4,6]. In Madagascar, La Reunion, and Hawaii, *Ae. albopictus* was introduced in the 18th–19th or early 20th centuries.

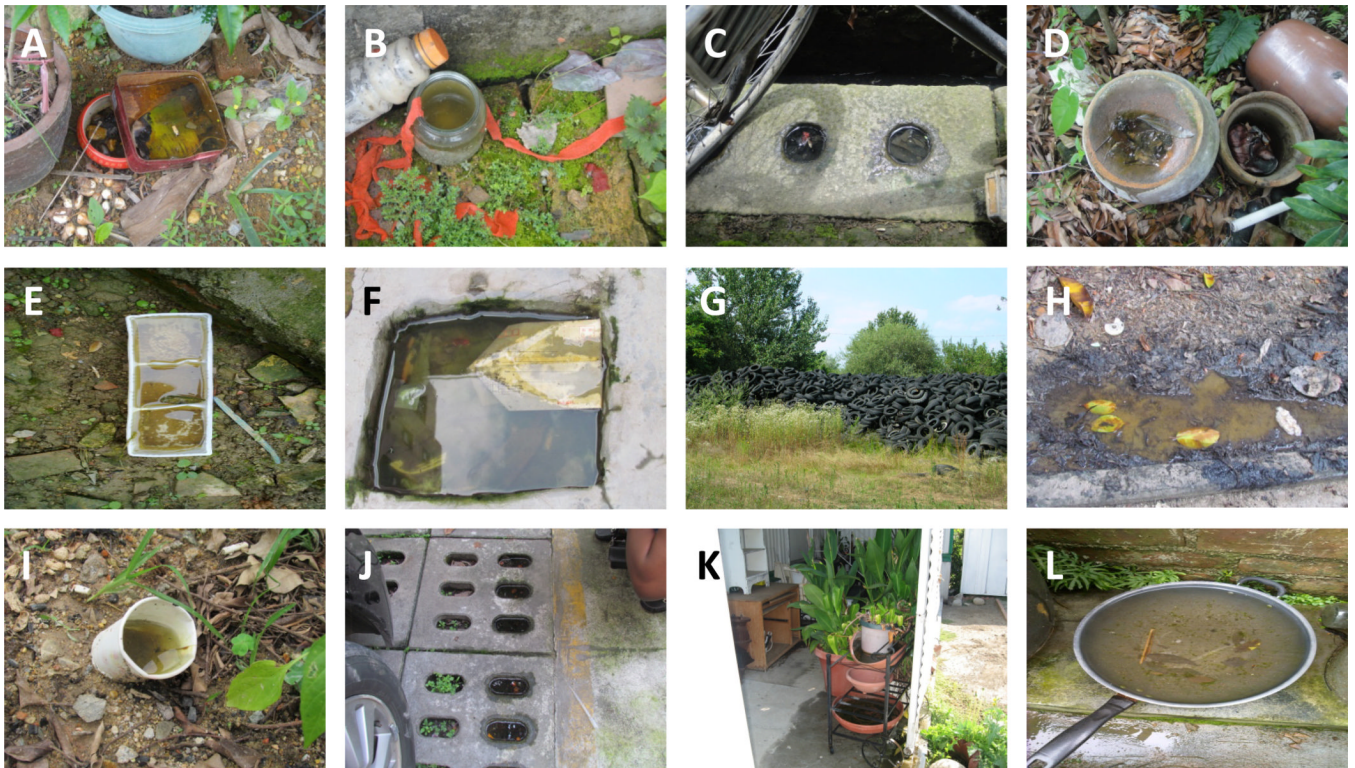


Figure 3. *Aedes albopictus* breeding sites. Examples include (A) metal containers, (B) terrarium, (C) stone holes, (D) ceramic vessels, (E) plastic containers, (F) gutters, (G) used tire dumps, (H) surface accumulated water, (I) disposable containers, (J) parking poundings, (K) flower pot trays, and (L) metal containers. Images courtesy of Romeo Bellini (Centro Agricoltura Ambiente, Crevalcore, Italy), Marco E. Metzger (California Department of Public Health, USA), and Xiaoguang Chen (Southern Medical University, Guangzhou, China).