

Review

Dengue Vectors and their Spatial Distribution

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Abstract: The distribution of dengue vectors, *Ae. aegypti* and *Ae. albopictus*, is affected by climatic factors. In addition, since their life cycles are well adapted to the human environment, environmental changes resulting from human activity such as urbanization exert a great impact on vector distribution. The different responses of *Ae. aegypti* and *Ae. albopictus* to various environments result in a difference in spatial distribution along north-south and urban-rural gradients, and between the indoors and outdoors. In the north-south gradient, climate associated with survival is an important factor in spatial distribution. In the urban-rural gradient, different distribution reflects a difference in adult niches and is modified by geographic and human factors. The direct response of the two species to the environment around houses is related to different spatial distribution indoors and outdoors. Dengue viruses circulate mainly between human and vector mosquitoes, and the vector presence is a limiting factor of transmission. Therefore, spatial distribution of dengue vectors is a significant concern in the epidemiology of the disease. Current technologies such as GIS, satellite imagery and statistical models allow researchers to predict the spatial distribution of vectors in the changing environment. Although it is difficult to confirm the actual effect of environmental and climate changes on vector abundance and vector-borne diseases, environmental changes caused by humans and human behavioral changes due to climate change can be expected to exert an impact on dengue vectors. Longitudinal monitoring of dengue vectors and viruses is therefore necessary.

Key words: *Aedes aegypti*, *Aedes albopictus*, spatial, distribution, environment, dengue

INTRODUCTION

Humans have experienced dengue fever (DF) since ancient times. Dengue-like illness was already described in Chinese literature in 992 [1]. Since the early 20th century when experiments showed that dengue virus was transmitted by *Aedes aegypti* (L.), a great number of studies on the relationship between *Ae. aegypti* and DF have been conducted [2]. Although there are several potential dengue vectors, the field isolation of viruses and epidemiological evidence clearly show that *Ae. aegypti* and *Ae. albopictus* are responsible for the majority of dengue transmission [1].

Aedes albopictus (Skuse), better known as the “Asian tiger mosquito”, originates in Orient and serves as a secondary vector of DF [2]. This species feeds on humans in gardens, parks and bushes around human dwellings in the daytime and is very common in Japan and other Asian countries. After *Ae. albopictus* was recognized to be a vector of DF in 1931 and dengue virus was isolated from *Ae. albopictus* caught in the wild, many scientists have taken an interest in this species as well as *Ae. aegypti* [2].

There is a wealth of studies on the distribution, morphology, genetics, biology and ecology of these two major dengue vectors due to their great medical importance. However, the dengue vector situation has completely changed since the 1980's. World geographic distribution of *Ae. albopictus* has dramatically shifted as a result of introduction of the species from Orient to New World, Europe and Africa by frequent used tire transportations [3]. In addition, recent uncontrolled urbanization in developing countries and global warming, which influence vector mosquitoes and exert an impact on vector-borne diseases, have become topics of concern among scientists. Frequent movement of people by aircraft has resulted in a further introduction of vector mosquitoes to new places. *Ae. aegypti* and *Ae. albopictus* were collected from aircraft arriving at Changi International Airport in Singapore [4]. Such vector movement will increase the risk of newly emerging vector-borne diseases. Not only the expansion of dengue vector distribution but also behavioral changes of *Ae. aegypti* and *Ae. albopictus* are currently reported. *Ae. aegypti*, which usually breeds in artificial containers in houses, was found

from subterranean breeding sites such as wells and manholes in a dengue epidemic area, Australia, and a direct epidemiological association between subterranean breeding sites and dengue virus infection was demonstrated [5]. In Japan, the density of *Ae. albopictus* was very high in catch basins which now provide important breeding sites for the species in the country [6].

Dengue viruses circulate between humans and vector mosquitoes and there is no intermediate host. Thus, spatial distribution of the vectors highly affects the epidemiology of the disease. Since DF/DHF (dengue fever/dengue hemorrhagic fever) vaccine is unavailable for practical use, transmission can be prevented only by reducing human-vector contact. Therefore, many dengue control programs are conducted targeting vector mosquitoes. However, most of the programs have not achieved successful levels [7]. Case studies attribute this lack of success to (1) a shortage of personnel (entomologists, social scientists, operational vector-control staff); (2) a lack of technical expertise at decentralized levels of service; (3) insufficient budgets; (4) inadequate geographical coverage; (5) interventions relying mostly on insecticides; (6) difficulties in engaging communities; (7) little capacity building; (8) almost no monitoring and evaluation. From the entomological viewpoint, the lack of appropriate understanding regarding the difference in vector mosquitoes, *Ae. aegypti* and *Ae. albopictus*, is one of the major reasons for the current difficulty of control. It is well known that *Ae. aegypti* and *Ae. albopictus* have their own ecological niches and show different spatial distribution. The different spatial distribution and different ecological zones indicate that the response of the vectors to the environment is different, that environmental factors influence the distribution, that infestation of *Ae. aegypti* and *Ae. albopictus* are often modified in various environments. Therefore, an understanding of the environmental factors which determine vector distribution is essential for dengue control. In the frontline of dengue control, however, measures are usually taken without critical estimation of the difference in ecology and biology between *Ae. aegypti* and *Ae. albopictus* in a given area. In spite of the co-existence of *Ae. aegypti* and *Ae. albopictus* in an area, the former species is usually targeted for control. Moreover, there have been few quantitative studies to elucidate how environmental and climate changes actually affect the infestation, ecology and biology of vector mosquitoes in endemic areas.

In this paper, we focus on the spatial distribution of *Ae. aegypti* and *Ae. albopictus* and environmental and climate changes and review the ecological and biological difference of vectors as well as its relation to environmental factors and DF/DHF. This information will be useful for future dengue control.

VECTOR BIOLOGY

In order to understand how dengue vectors are influenced by the environment, the general biology and ecology of *Ae. aegypti* and *Ae. albopictus* are described as follows.

Aedes aegypti

Although *Ae. aegypti* is currently distributed in urban areas throughout the tropical regions of Africa, Asia, Australia, South Pacific, Americas and some parts of the Middle East, the origin of the species is considered to be Africa [8]. According to Mattingly (1957), two subspecies are recognized morphologically. *Aedes aegypti formosus* has a dark body color and no pale scales on the abdominal tergite, breeds from natural habitats such as tree holes in African forests, and feeds on wild animals. This subspecies is ancestral and not anthropophilic. On the other hand, *Aedes aegypti aegypti* has pale scales at least on the first abdominal tergite and characteristically exhibits highly variable pale scale patterns through the first to seventh tergites. The latter is well domesticated and common around human dwellings. Sub-speciation between *formosus* and *aegypti* may have co-occurred along with domestication in the human habitat. Because of its adaptation to environments created by humans, the latter expanded its geographical distribution from the seventeenth to the nineteenth centuries via boats with water-holding vessels containing larvae. Recent genetic studies indicate that *aegypti* evolved from *formosus* in West Africa was introduced to world from that area [9]. Although their taxonomical status is still controversial, the domesticated form has been closely studied because of its intimate association with human and vector-borne diseases, and thus the *Ae. aegypti* discussed in the present paper constitutes the domesticated form.

Generally, mosquitoes spend the aquatic phase in immature stages and the terrestrial phase in the adult stage during which the events of mating, blood feeding and ovipositing take place (some species are autogenous, i. e. blood feeding is not required for egg maturation and oviposition). Among these events, larval breeding, blood feeding place, resting place, oviposition site and host animals differ among mosquito species. Because the biological and ecological characteristics described above are linked to degrees of human-vector contact and transmission of pathogens, studies on vector mosquitoes mainly focus on those characteristics. In the vector species, the events usually take place in the vicinity of human.

It may not be an exaggeration to say that the life cycle of *Ae. aegypti* is completely dependent on environments created by humans. Larvae breed from a variety of artificial containers such as jars, discarded cans, flower vases, cement

tanks, ant traps, used tires and plastic buckets around human dwellings [10–12]. Many domestic animals are also available for blood meals, a situation often seen in tropical countries, but *Ae. aegypti* is highly anthropophilic and feeds in the daytime. Its preference for humans as a host is an important factor for transmission [13, 14]. In addition, the species prefers dark places with moisture for blood feeding and resting [10]. The indoors and urban areas apparently provide environments which *Ae. aegypti* prefers over the outdoors and suburban/rural areas. Thus, the species is usually abundant in the indoors and urban areas in tropical countries [15, 16], and the close association with humans contributes largely to the effective transmission of dengue viruses.

Aedes albopictus

Ae. albopictus originates in the Orient and is distributed throughout tropical and temperate areas [2, 17]. Unlike *Ae. aegypti*, *Ae. albopictus* eggs have the ability to diapause during the winter season in temperate zone Asia [18, 19]. Larvae breed from a wide variety of natural and artificial habitats such as bamboo stumps, tree holes, discarded tires and flower vases [2, 3, 11, 20]. Since hosts of *Ae. albopictus* blood feeding include not only humans but also a wide range of amphibians, reptiles, birds and mammals in forests and domestic environments, the species has been regarded as a bridge vector of zoonosis pathogens [2, 3, 13, 21–24]. In fact, it has been reported that the species experimentally transmits many viruses and that medially important arboviruses were isolated from *Ae. albopictus* caught in the wild [2, 23]. Recently, it was reported that *Ae. albopictus* was involved in chikungunya epidemics in Italy, India and elsewhere [25–27]. In the domestic environment, *Ae. albopictus* prefers vegetation and feeds and rests outdoors [28–32]. Because of the preference for vegetation, the density of *Ae. albopictus* is usually high in rural and suburban areas [11, 33–39]. Biting usually takes place at dawn and dusk, although nighttime biting is sometimes observed [3, 40].

The geographic distribution of *Ae. aegypti* and *Ae. albopictus* overlaps in Asia, Americas, the South Pacific and some parts of Africa. However, the niche characteristics of the adult are somewhat different as described above. Recently, Lambrechts et al. (2009) reviewed the role of *Ae. albopictus* in past dengue epidemics and compared its dengue virus vector competence with that of *Ae. aegypti* [41]. They noted that although *Ae. albopictus* is overall more susceptible to dengue virus midgut infection, rates of virus dissemination from the midgut to other tissues are significantly lower in *Ae. albopictus* than in *Ae. aegypti*. With regard to biological and ecological characteristics and rates of virus dissemination, vectorial capacity is much higher for *Ae. aegypti* than for *Ae. albopictus*. Although *Ae. albopictus*

is definitely responsible for epidemics of DF in Japan and other countries [23, 42], *Ae. aegypti* is a primary vector of DF/DHF worldwide.

SPATIAL DISTRIBUTION OF DENGUE VECTORS

Distribution along the north-south gradient

The fact that *Ae. aegypti* is distributed in tropical regions and *Ae. albopictus* from tropical to temperate regions shows that the geographical distribution of the two species differs along the north-south gradient. In Vietnam, where the climate is both tropical and subtropical, the difference is very clear. Higa et al. (2010) showed the pronounced effect of the north-south gradient on the spatial distribution of *Ae. aegypti* and *Ae. albopictus* in Vietnam, and they indicated that the distribution and survival of these mosquitoes was strongly affected by climatic factors such as temperature, humidity, and precipitation [43]. *Ae. albopictus* was highly abundant in northern Vietnam, while *Ae. aegypti* was abundant in the south. In the central part of the country, the two species co-existed. The change of response to climatic conditions was possibly one of the factors in the sequential change of infestation of *Ae. aegypti* and *Ae. albopictus* along the north-south environmental gradient in Vietnam [43]. In Japan, like Vietnam, *Ae. aegypti* was previously established in the Ryukyu Archipelago where the climate is subtropical, while *Ae. albopictus* was very common on the mainland where the climate is temperate [17].

The ecological mechanisms of dengue vectors along the north-south gradient can be defined as follows. In a region where one species dominates over the other, climatic conditions highly favor the former species. For example, *Ae. albopictus* is distributed in temperate regions as well as tropical regions, and thus it is more adaptive to cooler climates than *Ae. aegypti*. Moreover, the eggs and adults of *Ae. aegypti* are resistant to desiccation which makes *Ae. aegypti* more adaptive to a hot and dry environment than *Ae. albopictus* [3, 43–46]. In such regions, the distribution of the less adaptive species is marginal or seasonal, and the adaptive species is superior to the other in all stages. Therefore, the adaptive species dominates over the other and expands its distribution. On the other hand, in the region where *Ae. aegypti* and *Ae. albopictus* co-exist, the climate may be moderate for both species and one species does not dominate over the other in all the stages. In such regions, habitat heterogeneity along the urban-rural gradient and interspecific competition may be more important than climate as a factor in spatial distribution [36, 46].

In Vietnam, the number of reported cases of DF/DHF is associated with the distribution of *Ae. aegypti*, indicating that this species plays a significant role in the country [47].

Distribution along the urban-rural gradient

Generally, *Ae. aegypti* is highly adapted to the domestic environment and therefore the abundance is positively correlated with increasing urbanization. On the other hand, the distribution of *Ae. albopictus* is associated with vegetation throughout rural and urban areas and the abundance is adversely affected by urbanization [3, 11, 33–39]. This difference in distribution along the urban-rural gradient is associated with the behavior related to blood feeding, resting, host preference and preference for vegetation. It was reported that habitat segregation in an environment where *Ae. aegypti* and *Ae. albopictus* have different niches plays an important role in the co-existence of dengue vectors even if the larvae have similar habitat requirements [3, 11, 39]. These studies suggest that the former species may be abundant in urban areas because the urban environment favors it, while the latter species may be abundant in rural areas because this environments usually has more vegetation than urban areas and therefore favors the latter species.

Since the distribution of *Ae. aegypti* and *Ae. albopictus* is highly influenced by climate, the response of the two species to environmental heterogeneity may be modified according to geographically different areas. Infestation of the two species along the urban-rural gradient may differ among areas. Therefore, it is hypothesized that, in *Ae. albopictus* (or *Ae. aegypti*) dominant regions, one of the species may be able to occupy a niche if it is unoccupied, even in urban (or rural) areas, because the population of *Ae. aegypti* (or *Ae. albopictus*) would be small. In regions where the two species co-exist, habitat segregation in which *Ae. aegypti* is abundant in urban areas and *Ae. albopictus* in rural areas would be conducive to co-existence. The infestation of *Ae. aegypti* and *Ae. albopictus* along the urban-rural gradient in northern, central and southern in Vietnam was examined [43]. In the north, *Ae. aegypti* was mainly collected from transition areas, while *Ae. albopictus* was collected throughout urban and rural areas. In the south, *Ae. aegypti* was dominant throughout urban and rural areas. In the central part of the country, *Ae. aegypti* was dominant throughout urban and rural areas while *Ae. albopictus* was observed in urban areas. These findings indicated that the infestation of *Ae. aegypti* and *Ae. albopictus* along the urban-rural gradient differed among geographic areas. In the central part of the country, however, the typical habitat segregation of the two species between urban and rural areas as hypothesized was not observed. A limitation of the study was that larvae were collected from used tires only [43]. The results of other studies revealed a variety of larval habitats throughout urban and rural and north to south gradients in Vietnam [12, 48–50]. The way in which People stored water affected mosquito larval occurrence. Moreover,

Ae. aegypti and *Ae. albopictus* exhibited a different preference for containers [2, 3]. In Indonesia, differing coverage of piped water in urban and rural areas affected the infestation of *Ae. aegypti* and *Ae. albopictus* [51]. The distribution in urban and rural areas differed among countries in which dengue control targeting a certain species affected the infestation [36]. These studies suggest that environmental factors created by humans as well as climatic factors greatly influence local distribution of dengue vectors. The distribution along the urban-rural gradient can be regarded as a consequence of those factors.

Since *Ae. aegypti* with a higher dissemination rate of dengue viruses than *Ae. albopictus* is abundant in urban areas, DF/DHF is referred to as an urban disease. The difference in the infestation of *Ae. aegypti* and *Ae. albopictus* along the urban-rural gradient has been extensively studied in view of the ecological and epidemiological importance [11, 33, 34, 36, 37, 39, 43, 52, 53]. Thus, it is worthwhile to study the relationship between the distribution of *Ae. aegypti* and *Ae. albopictus* and the environment related to urbanization in order to understand population trends in changing environments and the ecological basis of the spatial distribution as well as to develop effective mosquito control measures [3, 33, 34, 36–38, 43, 54]. It will also be helpful to assess high-risk areas with high vector densities.

It is difficult to describe the environment quantitatively. Categories such as urban, suburban and rural are subjective, but the recent development of remote sensing technology with satellite imagery and the geographical information system (GIS) in which an environment is visible and can be estimated by indices such as the normalized difference vegetation index (NDVI) has opened new windows for analyses related to mosquito control strategy [34, 55–58]. The quantitative estimation of an environment by freely accessible satellite imagery and meteorological data is applicable to various countries and regions. Although it is still difficult to estimate the degree of urbanization/domestication quantitatively, Tun-Lin et al. (1995) proposed “the premise condition index” reflecting the house condition, yard condition and degree of shade, and they successfully related this to the presence of *Ae. aegypti* [59]. Studies such as this help to streamline dengue vector surveillance. Quantitative estimation is considered significant especially for dengue epidemic countries experiencing uncontrolled urbanization.

Recently, some studies have reported that *Ae. albopictus* is increasing in the indoors and urban cities [43, 60, 61]. Although the reasons remain unclear, it is likely that, when a society develops to some extent, parks with vegetation are constructed and people cultivate gardens at home. Since *Ae. albopictus* can breed from a wide range of habitats and feed

on various animals, parks and gardens in urban cities are suitable for the species.

Distribution around houses

When human-vector contact is estimated, a house is the smallest spatial unit. Therefore, studies to examine the blood feeding/resting place of vector mosquitoes, indoors or outdoors, is essential for the control of vector-borne diseases. There have been many studies on the feeding/resting place of dengue vectors. The density of *Ae. aegypti* is high indoors (endo-phagy/phily), while that of *Ae. albopictus* is high outdoors (exo-phagy/phily) [3, 38]. Why are *Ae. aegypti* and *Ae. albopictus* distributed in such way? As described above, high *Ae. aegypti* density in the indoor environment may be associated with the preference of the species for dark and moist places and for humans as a blood source. However, although the degree of preference may be differ between *Ae. aegypti* and *Ae. albopictus*, the latter species also prefers shaded and moist places in vegetation and has blood meals from humans. This indicates that the response of the two species is extremely different in the domestic environment.

What is a house/building for *Ae. aegypti* and *Ae. albopictus*? In Thailand, the indoor and outdoor density of *Ae. albopictus* was examined using an experimental bamboo hut $2 \times 2 \times 3$ m in size [32]. The wall of the hut was removable, and three types of wall were prepared, that is, walls with 25, 50 and 75% of the surface area open to the outside. In the experiment, there was no significant difference between the indoor and outdoor densities of *Ae. albopictus* with 50 and 75% opening walls. On the other hand, the outdoor density was significantly higher than indoor density with the 25% opening wall. The experiment clearly showed that walls were physical barriers impeding the entry of *Ae. albopictus* to a building.

Higa et al. (2001) conducted the second experiment on *Ae. albopictus* in Nagasaki, Japan [32]. Net-walled buildings ($2 \times 2 \times 2$ m) were built in an area with vegetation. In the buildings, the physical barrier was present, but the microclimate was similar indoors and outdoors due to the exchange of air through the net. Indoor and outdoor densities were examined, and temperature, relative humidity and light intensity were measured both indoors and outdoors. In addition, the density outdoors without vegetation was also examined. As a result, there was no significant difference in density between indoors and outdoors (with vegetation) or microclimate. However, density outdoor without vegetation was significantly low. The results indicated that the presence of vegetation was highly important for *Ae. albopictus*. Thus, we clarified that the lower density of *Ae. albopictus* indoors than outdoors is due to vegetation located outdoors and the

physical barrier presented by the walls of buildings. It was interesting to note that when a building was located in a vegetation area and microclimate indoors and outdoors did not significantly differ, some *Ae. albopictus* entered into the building [32].

At least three factors, i. e. physical barriers, presence of vegetation and microclimate, are associated with the exophagy/phily of *Ae. albopictus*. The degree of significance of each factor may depend on location, and the density seems to be an integrated consequence of the three factors.

The behavior of *Ae. aegypti* and *Ae. albopictus* around houses/domestic environment is of special interest to the medical entomologist. The mark-release-recapture method is frequently used to understand this behavior. In this method, wild caught or laboratory-reared mosquitoes are marked with dye or material which can be traced, released in the field and recaptured at several sites over certain time intervals. Using this method, movement, dispersal and survival rate can be estimated. Previous studies have shown that the flight range of *Ae. aegypti* and *Ae. albopictus* is relatively small, usually within 100 m [3, 15]. However, it was also reported that the dispersal of dengue vectors was highly affected by the environment. In Puerto Rico, Reiter (1995) developed a method for marking *Ae. aegypti* eggs with a rare alkali metal (rubidium) and showed that the dispersal in urban areas was influenced by habitat availability [62]. More marked eggs were detected from places distant from the release site when breeding sites were cleared. This study suggested that source reduction may enhance dissemination of virus-infected mosquitoes by reducing the number of available ovipositing sites. Horizontal and vertical dispersal of *Ae. aegypti* and *Ae. albopictus* was studied in apartment blocks in semi-rural and urbanized parts of Singapore [63]. From the results, it was concluded that females of both *Ae. aegypti* and *Ae. albopictus* could disperse easily and quickly throughout a radius of 320 m in search of oviposition sites. Releases on level 12 of a 21-storey apartment block, with ovitraps on each storey, showed a similar easy and rapid dispersal to the top and bottom of the building. The results contrasted with the general belief that *Ae. aegypti* seldom flies more than 50 m and that control operations can safely be based on such an assumption. In a village in China, Tsuda et al. (2001) released marked *Ae. aegypti* from different sites in the center and marginal area of a village and found that the distribution pattern of houses around the release site affected dispersal [64]. When marked females were released from a house in the center of the village, more females were recaptured inside the village, indicating that the females tended to remain in the village. In Thailand and Puerto Rico, Harrington et al. (2005) conducted 21 mark-release

recapture experiments and examined the *Ae. aegypti* flight range and dispersal patterns [65]. Throughout these extensive experiments, the majority of mosquitoes were collected from their release house or the adjacent house. Adult *Ae. aegypti* disperse over relatively short distances, and inter-village movement was detected only rarely. The authors (2005) therefore suggested that people rather than mosquitoes are the primary mode of dengue virus dissemination within and among communities [65].

For *Ae. albopictus*, several mark-release-recapture experiments were conducted to examine the movement of the species in the domestic environment in Nagasaki, Japan. Takagi et al. [29–31] showed that trivial movement of *Ae. albopictus* occurred among sites and that the distribution of the released females overlapped with that of wild mosquitoes after a few days of release through trivial movement. Even among vegetation sites, there was a site with a high density of *Ae. albopictus* as compared to the other vegetation sites. Dispersal was influenced by larval rearing conditions as well. *Ae. albopictus* females emerging from high larval densities dispersed more often over a considerable distance than those from low larval densities [66].

These studies suggest that dispersal and movement of *Ae. aegypti* and *Ae. albopictus* around houses is largely influenced by larval breeding sites, buildings and vegetation in the domestic environment. Microclimate and the availability of hosts also affected dispersal and distribution of dengue vectors [67, 68]. From the entomological viewpoint, the epidemiology of DF/DHF may vary depending on locality because of modified distribution and movement of vector mosquitoes among localities. Thus, environmental assessment at the household level is necessary for dengue control [69].

It was observed that the density of *Ae. aegypti* varied among houses. In a temple in Thailand, *Ae. aegypti* and *Ae. albopictus* were collected from five different buildings used as bedrooms, kitchen, pray room, bell-ringing room and sermon room at four intervals. The movement of people was also observed and estimated as a score calculated as follows: the number of people \times time spent in a building in a day \times number of days in a week. This score was considered to represent the degree of human presence. Density of *Ae. aegypti* was positively correlated with the scores derived from each building (Higa et al., unpublished data). For *Ae. albopictus*, the presence of vegetation around buildings was more important than the human presence. The human presence in a building seems highly important for *Ae. aegypti* and influences the density among houses.

CURRENT DISTRIBUTION BY CLIMATE CHANGE, TRANSPORTATION AND TRADE ON A CONTINENTAL SCALE

Climate change

For vector-borne diseases, a higher temperature within a range of survival of vectors will enhance reproduction of vector mosquitoes and elongate the yearly period of reproductivity [3, 70]. The incubation period of viruses meanwhile will be shortened [71]. The recent enhancement of DF/DHF transmission and expansion of the geographic range of the diseases and vector mosquitoes are matters of great concern in that they may be influenced by the global warming trend associated with climate change [72].

Since DF/DHF vaccine is unavailable for practical use and the viruses circulate mainly between human and vector mosquitoes, vector presence is a limiting factor of transmission. Since vector-borne diseases are usually tropical diseases, medical entomologists are keenly interested in the effects of global warming on vector distributions at higher latitudes. Kobayashi et al. (2002) clearly showed the relationship between the expansion of *Ae. albopictus* northward and temperature increases including the annual mean temperature above 11°C, January mean temperature, number of days above 11°C per year, and the total accumulated temperature in Japan using Geographical Information Systems (GIS) [55].

Although it is not so easy to demonstrate how the current spread of DF/DHF is related to the geographic expansion of mosquito vectors by climate change, recent computer and remote sensing technologies have allowed researchers to analyze enormous datasets with satellite pictures, GIS and distribution-modeling software easily affordable [73]. These tools have made it possible to predict vector distribution in changing environments. The results of related studies suggest that human behavioral change exerts a more significant impact than climate change on the geographical expansion of dengue vectors [58, 74, 75]. Beebe et al. (2009) analyzed past *Ae. aegypti* collection data and temperature in Australia and concluded that the increased risk of an *Ae. aegypti* range expansion in Australia is due not directly to climate change but rather to human adaptation to current and forecasted regional drying through the installation of large domestic water storage containers [58]. Global warming enhances the usage of air conditioners, which means that windows are closed and people are less vulnerable to mosquito bites, but frequent use of drinking cans and bottles which can be larval breeding sites may result in increased vulnerability.

Events caused by climate change are dynamic and subsequent impacts on vector mosquitoes by unknown factors

may occur. It is necessary to monitor the distribution of *Ae. aegypti* and *Ae. albopictus*, as well as climate parameters over the long term.

Transportation and trade

The flight range of *Ae. aegypti* and *Ae. albopictus* is relatively small, approximately 50–500 m [3, 10, 15]. In spite of small active movements, both species have spread across continents from their origins. This is associated with resistance of eggs to desiccation. Even when the water in a container dries up, eggs laid on the container wall can survive for several months. When containers with eggs are carried to a new place and rain falls, the eggs hatch. If there are host animals and climate is suitable, a population will be established there. Water-holding containers with larvae have also contributed to the movement of mosquitoes. From the 17 to 19th centuries, *Ae. aegypti* hidden in vessels on boats traveled from Africa to other continents [1, 2], while *Ae. albopictus* started to spread to the Pacific islands in the early 20th century. However, it was not until the 1970's that the geographic distribution dramatically changed. *Ae. albopictus* larvae were found in Albania in 1979 and then in the U.S. in the 1980's [71, 72]. The establishment of *Ae. albopictus* was first confirmed in Texas in 1986 [76]. Although there are some records of *Ae. albopictus* in the U.S., the species was not established in other states before 1986 [77, 78]. After that, however, *Ae. albopictus* expanded quickly over the country and has been recorded from 26 states at present [79]. All of the *Ae. albopictus* in the U.S. were collected from water-holding used tires. Therefore, it was speculated that *Ae. albopictus* eggs laid on the inside wall of used tires were carried and a population established [80]. In order to determine the origin of the *Ae. albopictus* population in the U.S., Hawley et al. (1987) examined the presence of egg diapause and found that North American strains of *Ae. albopictus* exhibit characteristics of photoperiodic sensitivity and cold-hardiness similar to strains originating from temperate zone Asia [19]. A careful investigation of *Ae. albopictus*-infested tire-exporting countries and the tire imports of newly infested countries revealed that more than 90% of used tires imported to the U.S. were from Japan [81]. Similarly, *Ae. albopictus* was recorded from Brazil and the Dominican Republic where 81.5% and 97.4% of tires, respectively, were from Japan. Reiter (1998) concluded that infestations of *Ae. albopictus* in the U.S., Brazil and the Dominican Republic were probably primary infestations derived directly from Japan [81]. The large size of the *Ae. albopictus* population carried to the U.S. facilitated the further spread of the species to other countries. *Ae. albopictus* was collected from tire piles in Italy in 1990 and the population was established by the following year [82,

83]. After 1990, Mexico, Guatemala and Nigeria were also found to be infested. These infestations were probably secondary, derived from the U. S. which exports 55.4–99.4% of the used tires to the above countries. The same was probably true for Italy. The Cuban infestation may have been derived from Mexico, from which 90.8% of used tires were imported [81]. Due to the global trade in tires, *Ae. albopictus* was introduced through many countries and continued to be recorded from parts of Europe and Africa after 2000 [84–87]. Since most of the current records are from human dwellings, therefore *Ae. albopictus* was probably introduced earlier without being noticed, and some authors considered the species to have been carried by used tires. Unfortunately, *Ae. albopictus* has become a vector of infectious diseases in the places it has newly invaded. In the U.S., West Nile virus was isolated from field-collected *Ae. albopictus* [88]. In the 2007 outbreak of chikungunya fever in Italy, *Ae. albopictus* was incriminated as the principal vector [27]. Chikungunya virus was also isolated from adult *Ae. albopictus* derived from larvae collected during a chikungunya outbreak in Kerala, south India in 2009 [26].

CONCLUSION

The differing in spatical distribution of *Ae. aegypti* and *Ae. albopictus* reflects the difference in the niches of the two species in an environment. However, the spatial distribution of *Ae. aegypti* and *Ae. albopictus* sometimes does not conform to preconceptions as high abundance of *Ae. aegypti* in urban areas and *Ae. albopictus* in rural areas. This is attributable to the dependence of the vector mosquitoes on environments created by humans. Since the lifestyle and customs of people vary among countries and regions, the environments for *Ae. aegypti* and *Ae. albopictus*, such as larval breeding sites which are usually artificial containers, housing structures, gardens etc., also vary. As suggested by studies predicting changes in the distribution of dengue vectors, global warming and other aspects of climate change caused by the consumption of fossil fuels will undoubtedly have a great impact on spatial distribution of the vectors. The expansion of *Ae. albopictus* northward due to the influence of global warming on vector distribution provides actual evidence. In conclusion, however, environmental changes caused by human activities and human behavioral changes caused by climate change exert a greater impact on spatial distribution of *Ae. aegypti* and *Ae. albopictus* than direct climate changes. Uncontrolled urbanization and the construction of buildings without proper environmental management may create slums favorable to *Ae. aegypti*. In slums, houses are built close to each

other and the human population density is high, environmental conditions are more suitable for *Ae. aegypti*. Parks and gardens in developing countries may enhance the breeding of *Ae. albopictus* even in urban areas. Water storage behavior at times of drought may produce more breeding sites for dengue vectors. The difference in water storage customs among localities may modify the infestation of *Ae. aegypti* and *Ae. albopictus* because habitat preference differs between the two species. Furthermore, the expansion of *Ae. albopictus* by the trade in tires may continue in the future.

The impact of human activities on vector mosquitoes is considered to be larger for *Ae. aegypti* than for *Ae. albopictus* in view of the ecology and biology of the two species. However, the increasing abundance of *Ae. albopictus* in urban areas should be of particular concern. There are many reports showing that *Ae. aegypti* populations in the U. S. are being replaced by *Ae. albopictus* populations newly introduced by the trade in used tires [3]. *Ae. albopictus* has a wider range of activity than *Ae. aegypti*, feeds on wild animals as well as humans, and therefore is more adaptive to a variety of environments. Increased contact between humans and wild animals because of deforestation may enhance human-*Ae. albopictus* contact as well, and the role of *Ae. albopictus* in arbovirus transmission may become more crucial than ever. It has already been reported that *Ae. albopictus* contributes largely to chikungunya transmission both in tropical countries where dengue epidemic occurs and in Europe. This implies that the co-occurrence of dengue and chikungunya epidemics is highly possible. In such a situation, vector-borne disease control will be ever complicated, because the vector mosquitoes targeted will be both *Ae. aegypti* and *Ae. albopictus* with equivalent priority. Events caused by environmental and climate change are dynamic, and unknown factors may exert a subsequent impact on vector mosquitoes. Longitudinal monitoring of the distribution, the infestation and the abundance of *Ae. aegypti* and *Ae. albopictus*, along with environmental and climate change and virus activity, is necessary.

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