The Climate Range Expansion of *Aedes albopictus* (Diptera: Culicidae) in Asia Inferred From the Distribution of *Albopictus* Subgroup Species of *Aedes* (Stegomyia)

著者	Mogi Motoyoshi, Armbruster Peter A., Tuno Nobuko, Aranda Carles, Yong Hoi Sen
著者別表示	都野 展子
journal or publication title	Journal of medical entomology
volume	54
number	6
page range	1615-1625
year	2017-11-07
URL	http://doi.org/10.24517/00050494

doi: 10.1093/jme/tjx156

Motoyoshi Mogi
Takagise-higashi 3-3-23
Saga 849-0922
Japan
Tel: +81-952-30-9709
e-mail: motomogi@festa.ocn.ne.jp

Adaptation of *Aedes albopictus* (Diptera: Culicidae) to human habitats contributed to
establishment of the broad climatic range in Asia through ecological and eco-evolutionary
impacts

Mogi, M.,^{1,2} P. A. Armbruster,³ N. Tuno,⁴ C. Aranda,⁵ and H. S. Yong⁶

Footnotes to the first page

¹Division of Parasitology, Faculty of Medicine, Saga University, Nabeshima 5-1-1, Saga,
849-8501, Japan (retired)

²Corresponding author, e-mail: motomogi@festa.ocn.ne.jp

³Department of Biology, Georgetown University, 37th and O sts. NW, Washington, DC 20057

⁴Laboratory of Ecology, Graduate School of Natural Science and Technology, Kanazawa
University, Kanazawa, 920-1192, Japan

⁵Mosquito Control Service, Baix Llobregat Council, Barcelona, Spain

⁶Institute of Biological Sciences, University of Malaya, Kuala Lumpur, Malaysia

ABSTRACT We examine the hypotheses that (1) *Ae. albopictus* (Skuse) originated in continental Asia under monsoon climate, and (2) the broad climatic range in Asia was attained in part by adaptation to human habitats. We compared climatic distribution ranges between *Ae. albopictus* and the five closely-related but wild (non-domesticated) species in southern Asia. Distribution sites of the wild species concentrate in seasonal forest and savannah climate zones in India, Indochina, and southern China, supporting the first hypothesis. The distribution of *Ae. albopictus* is broader than the wild species under (1) tropical rain-forest climate, (2) steppe and temperate savannah climate, and (3) continental climate (large seasonal temperature variation, hot summer and cold winter) at temperate lowlands (northernmost sites 40°N in *Ae. albopictus* vs. 32°N in the wild species). However, the distribution of *Ae. albopictus* is more limited at tropical and subtropical highlands where climate is oceanic (small seasonal variation, mild summer and winter). The broader ranges of *Ae. albopictus* can be explained as ecological or eco-evolutionary consequences of adaptation to human habitats where reproduction is facilitated primarily by higher accessibility to water-holding containers relatively free from competitors and predators. We propose a hypothesis that the adaptation of *Ae. albopictus* to human habitats contributed to establishment of the climatically broad distribution. We also submit a general scenario for the origin, dispersal, and adaptation of *Ae. albopictus* in Asia as a hypothesis for future research.

KEY WORDS Culicidae, *Aedes albopictus*, origin, human habitat, adaptation

Aedes albopictus (Skuse), a vector of important viral diseases, has expanded globally since the end of the 20th century. The origin, dispersal, and adaptation of *Ae. albopictus* in its invasive ranges have attracted much attention since Hawley et al. (1987). In contrast, the biogeographic history in native Asia was discussed only by Porretta et al. (2012) who presented a hypothesis that *Ae. albopictus* maintained genetic cohesion during the last glaciation despite forest fragmentation in expanding drier environments.

The unusually broad climatic range of *Ae. albopictus* across tropical and temperate Asia was well established before the worldwide invasion over the last 30 years. How did *Ae. albopictus* establish such a broad Asian range? Artificial containers where it breeds are transported by humans, but movement may simply result in expansion within the same climate range. Theoretical models suggest that gene flow to species' range margins may constrain the adaptation and range expansion, but this effect can be ameliorated by environmental changes facilitating population growth (Kirkpatrick and Barton 1997). Human habitats (lands primarily for human residence and activities without natural vegetation) facilitate *Ae. albopictus* reproduction primarily by higher accessibility to water-holding containers relatively free from competitors and predators (full explanation in Discussion). Did human habitats contribute to the climate niche expansion of *Ae. albopictus*? This issue has not been considered, despite its importance for prediction and prevention of further expansion in both native and invasive ranges subjected to anthropogenic climate change and other environmental modifications.

Analyzing the climate conditions at *Ae. albopictus* distribution sites in the range from the easternmost Hawaii through westernmost Madagascar (before the start of worldwide invasions in 1980's), we hypothesized that (1) *Ae. albopictus* evolved on the Asian continent under monsoon climate with hot, wet and distinct dry seasons, and (2) the broad climatic range in native Asia was attained in part by using human habitats (Mogi et al. 2015).

As a way to pursue further the origin and adaptation of *Ae. albopictus* in Asia, we considered the wild (non-domesticated) species belonging to the *albopictus* subgroup of the *scutellaris* group of *Stegomyia* in southern Asia. Because these wild species primarily inhabit forests (Huang 1972), their distributions could indicate the distribution of the *albopictus* subgroup species before adaptation to human habitats.

In this paper, we compare the climatic niche of *Ae. albopictus* with that of the wild species. The goals of our analyses are three-fold. First, we examine whether the distribution of the wild species supports a hypothesis of *Ae. albopictus* origin under the monsoon climate in the Asian continent. Second, we elucidate the differences in climate ranges between *Ae. albopictus* and the wild species. Third, we consider how those differences are related to the adaptation of *Ae. albopictus* to human habitats. Combining all of these results, we present a hypothesis that adaptation to human habitats contributed to the establishment of the broad climatic range of *Ae. albopictus*. We also submit a general scenario for the origin, dispersal, and adaptation of *Ae. albopictus* in Asia as a hypothesis for future research.

Materials and Methods

Rationale for comparison. In most mosquito taxa, species richness is highest in the tropics, with a few species extending or endemic to the temperate region, justifying the assumption that tropical populations or species are ancestral to temperate ones with winter diapause (Ross 1964, Bradshaw and Lounibos 1977). This assumption is applicable to the subgenus *Stegomyia* where a few among ≈ 130 species extend their range or are endemic to the temperate region. Most *Stegomyia* species primarily breed in wild-plant containers such as tree holes, but a few depend on artificial containers in human habitats, a trait derived following the development of human settlements.

The *albopictus* subgroup (Huang 1972) includes 11 Asian species (Table 1). Of species other than *Ae. albopictus*, five have lost the ancestral tropical distribution. *Aedes flavopictus* Yamada covers the subtopics through the cool-temperate region up to 45°N (Tanaka et al. 1979). The three morphological subspecies (*Ae. f. flavopictus* of the temperate region and two subtropical ones, each of the northern and southern Ryukyu Islands) are genetically well differentiated (Toma et al. 2002). Similarly, three geographical (temperate, northern and southern Ryukyus) subspecies in *Aedes japonicus* (Theobald) (Tanaka et al. 1979) are also genetically distinct (Cameron et al. 2010). This differentiation pattern is consistent with separation of the three geographical regions since the middle Pleistocene, ≈1 million years ago (Mya), at the latest (Ota 1998). The remaining four species, tentatively called as the *galloisi* complex (*Aedes galloisi* Yamada, *Aedes sibiricus* Danilov and Filippova, *Aedes galloisioides* Liu and Lu, and *Aedes neogalloisi* Chen and Chen) are distributed from highlands of western and central China to the southern sub-polar region up to 55°N (Danilov and Filippova 1978, Lei 1989, Dong et al. 2010). A phylogenetic study suggests *A. galloisi* to be a distinct lineage as ancient as the *scutellaris* group (Sota and Mogi 2006).

Among species of the *scutellaris* group, only *Ae. f. flavopictus*, *Ae. galloisi*, and *Ae. sibiricus*, occur widely in the cool-temperate region, with eggs more cold-hardy than *Ae. albopictus* (Mogi 2011). These three species primarily breed in tree holes (Tanaka et al. 1979, Gutsevich and Dubitskiy 1987) in forests having persisted during the Quaternary in eastern Asia (Harrison et al. 2001). Altogether, these three species (1) or their ancestors appeared in eastern Asia before the middle Pleistocene, (2) must have acquired and strengthened winter diapause during the glacial cycles independently each in *Ae. flavopictus* and the *galloisi* complex, and (3) indicate the potential for diapause evolution in the *albopictus* subgroup species.

In contrast to the above five species, *Ae. albopictus* has maintained the ancestral tropical distribution and also extends to the temperate region without geographic morphological

differentiation (Huang 1972, Tanaka et al. 1979, Lu et al. 1997). The tropical populations are fully inter-fertile with temperate populations that overwinter as diapause eggs (pharate larvae) (O'Donnell and Armbruster 2009). These facts indicate that winter diapause in *Ae. albopictus* evolved independently and later than the species discussed above. In the *albopictus* subgroup, only *Ae. albopictus* is well adapted to artificial containers in human habitats.

The remaining five *albopictus* subgroup species, *Aedes novalbopictus* Barraud, *Aedes patriciae* Mattingly, *Aedes pseudalbopictus* (Borel), *Aedes seatoi* Huang, and *Aedes subalbopictus* Barraud, have maintained their ancestral tropical distribution (Huang 1972). They breed primarily in tree holes and bamboo stumps and bite humans in forests (Harrison et al. 1972, Amerasinghe and Munasingha 1988a, Rajavel and Natarajan 2008, Dong et al. 2010). In Thailand, *Ae. seatoi* is said to be semi-domestic due to occurrence in bamboo stumps around rural villages, but rarely breeds in jars near houses (Harrison et al. 1972). For convenience, we call these five non-domesticated species collectively “the wild species”.

Phylogenetic relations among *Ae. albopictus* and the wild species are unknown. However, the *albopictus* subgroup is well defined based on adult morphology (Huang 1972). In genetic analyses including other *Stegomyia* species, *Ae. albopictus* forms a clade with *Ae. pseudalbopictus* and *Ae. subalbopictus* (Wang et al. 2012) and with *Ae. seatoi* (Pashley and Rai 1983), indicating their evolutionary affinity. Ecologically, *Ae. albopictus* shares an ancestral tropical distribution with the others but has unique derived traits (widespread temperate distribution and human dependence). The comparison between *Ae. albopictus* and the wild species could provide insights into the impact of domestication on climatic niches.

Distribution data. To characterize the whole distribution range of the wild species, we assembled distribution data regardless of information on population density. Distribution records span ≈ 90 years (since 1928 when *Ae. pseudalbopictus* was described), during which administrative systems, place names, and English expressions have been changed extensively.

We identified the distribution sites mainly on Google Earth Pro. To use climate data from weather stations, each distribution site must be identified generally at county or lower levels. Distribution data only at upper administrative levels (state, province, etc.) were listed as “site unspecified”. Sites with information at lower levels that could not be located on maps were treated as “site unidentified”. Some publications describe altitudes or coordinates in sufficient detail to pinpoint altitudes. Otherwise, county or village altitudes were represented by administration centers. All the distribution data (≈ 400), including references, original descriptions and our interpretations, are compiled in Table S1.

The whole geographical range of the wild species extends from the Indian subcontinent to China, including several islands on the continental shelf (Table 2). Except *Ae. seatoi*, each species also ranges from India through China via Indochina; *Ae. pseudalbopictus* has the broadest geographical distribution reaching Jiangsu, eastern China to the north and western Java to the south. *Aedes seatoi* is known only from Thailand and one site in China, but is distributed throughout Thailand (Rattanakul et al. 2010), and, in rural areas, is the most common *Stegomyia* next to morphologically similar *Ae. albopictus* (Harrison et al. 1972). Thus, the distribution of *Ae. seatoi* may be broader than our present knowledge.

All of the wild species were recorded from lowlands through highlands (Table 2). Altitudinal ranges in particular regions are also wide; for *Ae. pseudalbopictus*, 100-2,400 m in Taiwan (Lien 1978), 320-1,790 m in Sichuan Province, China (Song et al. 1981, see Table S1), and 50-1,250 m in eastern Java (Ramalingam 1974).

Climate data. In contrast to *Ae. albopictus* which is associated with humans, the distribution sites of the wild species may be far apart from weather stations. As each species occupies wide geographical and altitudinal ranges (Table 2), we used climate data from weather stations within 200 km and 200 m (higher or lower) in altitude. In total, climate data at 116 stations were included, covering coasts through highlands and also western India through

Taiwan. Of 116 stations, 20 (17%) and 45 (39%) were related to 2-4 species and 2-8 sites (all species inclusive), respectively. For convenience, weather station names and locations were used as a representative of the distribution sites. The nearest distribution site was within 10, 30, 50, 70, 100, and 169 km for 42 (36%), 61 (53%), 82 (71%), 98 (85%), 110 (95%), and 116 (100%) stations, respectively. The station data, including coordinates, altitudes, distance from each distribution site, and data sources, are also in Table S1.

Analyses. Climate conditions were analyzed by using a thermal index, WI_{10} , and an aridity-humidity index, PE (Mogi et al. 2015). Briefly, $WI_{10} = \sum (t - 10)$ where summation is made for n months in which monthly mean temperature $t > 10^{\circ}\text{C}$. Thus, WI_{10} is a simple indicator of cumulative warmth above 10°C . WI_{10} is a modification of Kira's warmth index (WI) for the analysis of plant distribution and is related to the thermal series of climate and vegetation types (Table 3). Thornthwaite's PE is an indicator of year-round biological effectiveness of precipitation as the sum of monthly PE incorporating precipitation and temperature (a determinant of evaporation); $PE = 1.645 \sum \{p / (t + 12.2)\}^{10/9}$ where p = monthly total precipitation (mm), t = monthly mean temperature ($^{\circ}\text{C}$), and summation is made across 12 months. PE values, expressed as integers, are related to the aridity-humidity series of climate and vegetation types (Table 3).

Besides warmth and wetness, thermal continentality (the degree of seasonal temperature variation) influences dynamics of mosquito populations. Even if the annual mean temperature is the same (for example, 15°C), seasonal variation can either be large (the hottest month 25°C , the coldest month 5°C , the difference 20°C) or small (corresponding values, 20, 10, and 10°C). Thermal continentality was expressed by Conrad's continentality index (CCI); $CCI = 1.7R/\sin(A + 10) - 14$, where R = difference between means of hottest and coldest months, A = latitude. CCI takes smaller values with increasing oceanity.

Temperature, precipitation, WI_{10} , PE, and CCI at each weather station are presented in Table

S2.

Summary of *Ae. albopictus* distribution. As depicted on Fig. 1, the distribution sites of *Ae. albopictus* range from the per-humid, rain-forest climate zone through the semiarid, steppe climate zone, and throughout the temperature gradient from the tropics through the temperate zone (Mogi et al. 2015). Northernmost, lowland (altitudes ≤ 200 m) distribution sites in eastern Asia reach the border with the cool-temperate region ($\approx 40^\circ\text{N}$, $\text{WI}_{10} \approx 45$), and CCI values in temperate China and Korea are 45-60 (highly continental, hottest months 25-28°C, coldest months often $< 0^\circ\text{C}$, the differences usually $> 25^\circ\text{C}$) (Mogi et al. 2012 and its Appendix).

Results

The distribution sites of the wild species were concentrated into forest and savannah climate zones at 86% (68/79) for *Ae. pseudalbopictus* (Fig. 1A), 78% (43/55) for the other four species (Fig. 1B), and 84% (97/116) for all the species. Those sites were within the climate range of *Ae. albopictus*, except three cool, wet sites (Fig. 1A, B, one site was shared by *Ae. pseudalbopictus* and *Ae. subalbopictus*) and one hot, dry site (Fig. 1B, shared by *Ae. novalbopictus* and *Ae. subalbopictus*). There were only a few distribution sites in the subtropical rain-forest zone for both *Ae. albopictus* (4 sites) and the wild species (5) within a similar PE range. The differences in the distribution features between *Ae. albopictus* and the wild species were recognized in three (tropical rain-forest, driest, and temperate) climate zones.

In the tropical rain-forest zone, the distribution sites of *Ae. albopictus* ranged widely up to PE 260, while the sites of the wild species were limited to a few coastal sites and small islands with the maximum PE 156 (Table 4). PE values of 128-156, as well as 1-6 dry months

at four sites, indicates the conditions at these sites are close to the drier forest zone.

The driest distribution sites ($PE < 50$, 3-6 dry months) of the wild species were limited to the tropical and subtropical savannah zones except Anantapur (slightly out of the *Ae. albopictus* range but see Discussion, an arrow in Fig. 1B) and Coimbatore in the tropical steppe zone (Table 5). The Indian sites, other than Kanyakumari near the southernmost coast, were on the Deccan Plateau. In the temperate zone, the minimum PE was 56 in the upper savannah zone close to the forest zone.

The thermally temperate sites (cumulative summer warmth $WI_{10} < 120$) of the wild species were mainly tropical and subtropical highlands, and all the sites where $WI_{10} < 80$ were >500 m (Fig. 1A, B). Of coolest ($WI_{10} < 70$) and northernmost ($>30^\circ N$) sites, three (No. 4, 5, 7) at the foot of the western Himalayas fit both categories (Table 6). These data indicate that (1) coolest sites (No. 1-12) were all highlands (1,100-2,500 m) and south of $30^\circ N$ except the above-mentioned three (No. 4, 5, 7) at $31-34^\circ N$, (2) local warmth in the western Himalayas is also evident from the lower sites (No. 20, 21, 680-1,200 m) which were warmer than the lower Chinese sites (No. 13-19, 40-670 m) at equivalent latitudes ($30-32^\circ N$), (3) at the coolest sites, annual and hottest-month temperatures were also lower than the northernmost sites (No. 13-21), (4) the climate at highland sites ($>1,500$ m) is oceanic ($CCI < 30$), especially three sites out of the *Ae. albopictus* range (No. 1-3) and one additional Himalayan site (No. 10) were extremely oceanic ($CCI \approx 12-18$, with hottest months $\approx 15-20^\circ C$, coldest months $\approx 6-8^\circ C$, differences $\approx 8-12^\circ C$), and (5) in contrast, two northernmost lowland sites (No. 14, 17, $30-32^\circ N$, <100 m) (two arrows in Fig. 1A) in eastern China were most continental ($CCI \approx 50$, hottest months $\approx 27-28^\circ C$, coldest months $\approx 2-4^\circ C$, differences $\approx 24-25^\circ C$).

In summary, 84% of the distribution sites of the wild species concentrate in forest and savannah climate zones. The distribution of *Ae. albopictus* is broader than the wild species in (1) the tropical rain-forest zone, (2) the steppe and temperate-savannah zones, and (3)

temperate lowlands where climate is continental (up to 40°N vs. 32°N of *Ae. pseudalbopictus*). In contrast, the distribution of *Ae. albopictus* is more limited at tropical and subtropical highlands where climate is cool but oceanic.

Discussion

Adequacy of analyses. Some differences in climate between weather stations and distribution sites are unavoidable for the wild species. Nevertheless, we think the climate represents their living conditions, because (1) 39% of the stations were related to multiple distribution sites, (2) 95% of the stations were within 100 km from the nearest sites, (3) the stations covered western India through Taiwan and also coasts through highlands, and (4) the wild species' distribution ranges are broad in terms of latitude, longitude, and altitude.

We used warmth and wetness indices with criteria that delineate both climate and natural vegetation. Natural vegetation is characteristic of broad climate zones but also influenced by other factors such as soil characteristics (Begon et al. 1986). In our analyses, PE values at Anantapur and Coimbatore on the Deccan Plateau fell in the steppe climate zone, but the natural vegetation in central India is primarily tropical deciduous forests intermixed with savannahs (Roy et al. 2015). Breckle (2002) recognized only two climate categories with regard to tropical vegetation, namely, equatorial humid climate (yielding evergreen rain-forests) and humido-arid, tropical summer-rain climate where vegetation can be either deciduous forests, savannahs or grasslands. Recognizing the complexity and diversity of conditions experienced in nature, we propose that simple climate indices can be a tool to analyze the relation between climate and mosquito distribution.

Origin and adaptation to human habitats: an ecological perspective. Concentration of the five wild species in forest and savannah climate zones in southern Asia is consistent with

our hypothesis that *Ae. albopictus* originated in continental Asia under a monsoon climate with a dry season often spanning several months. These conditions could have selected for traits in *Ae. albopictus* that enabled adaptation to wider climate ranges. Transcriptional profiling of diapause and nondiapause eggs of temperate *Ae. albopictus* indicates that transcriptional differences are primarily due to the quantitative differences in expression levels of genes common to both conditions, rather than the unique expression of specific genes under one condition (Armbruster 2016). For example, higher expression of a fatty acyl coA elongase gene is related to greater desiccation resistance of diapause relative to non-diapause eggs, but this gene is expressed both under non-diapause conditions and in tropical populations (Urbanski et al. 2010). Egg dormancy under extended drought in southern Asia could have selected for increased egg desiccation resistance, which might have facilitated colonization of sub-tropical or temperate regions where a more fully-elaborated diapause response was then selected for.

The Asian monsoon system has persisted during the Quaternary (Wang et al. 2005). Did *Ae. albopictus* originate before the last glaciation (Porretta et al. 2012), or in the postglacial age as a human inquiline like the domestic form of *Ae. aegypti* (Brown et al. 2014, Crawford et al. 2017)? Pre-mating ethological isolation (choice of conspecifics) between *Ae. albopictus* and the wild species (*Ae. pseudalbopictus*, *Ae. seatoi*) and between the wild species (McLain and Rai 1986) supports the former. Similar levels of pre-mating isolation (high, but not perfect) resulted from geographical isolation since 2-10 Mya (based on estimates of island separation) among the *scutellaris* subgroup species (distributed from Indochina through western Pacific islands) (McLain et al. 1985), and 0.15-6 Mya (based on estimates from genetic divergence) between two *Drosophila* flies (Jennings and Etges 2010). These estimates do not indicate the minimum duration for establishment of pre-mating isolation but favor allopatric divergence among the *albopictus* subgroup species preceding to the postglacial sympatry.

Opportunities of allopatry probably existed during the Pleistocene due to (1) forest reduction under drier glacial environments, (2) the complex topography and geological features in southern Asia that produce local climate and vegetation diversity, and (3) an ability of wild *Aedes* (*Stegomyia*) populations to persist in small, isolated natural forests on uninhabited islets or those persisting in areas protected for shrines (Mogi 1990).

Wild (ancestral) populations of *Ae. albopictus* coexist with the wild species in reserve forests on the Deccan Plateau (Thenmozhi et al. 2012) and along the coast (Rajavel and Natarajan 2008) in India, and in pre-development forests in Sri Lanka (Amerasinghe and Munasingha 1988b). Information from subtropical southern China is variable. It is said to be dominant at wild and cultivated bamboo forests in Yunnan Province (Dong et al. 2010), but Lu et al. (1997) regard it as a semi-wild species inferior to *Ae. pseudalbopictus* at forests far from houses. In Guizhou Province, it is absent from forests >2 km apart from houses (Chen 1987). In a nature reserve of Guizhou Province, *Ae. albopictus* was recorded together with the two wild species (Wang et al. 2012), but this reserve includes agro-ecosystems supporting >4,000 residents. In the subtropical Ryukyu Islands, Japan, *Ae. albopictus* is absent from natural forests that are separated from developed sites (Miyagi and Toma 1980, Toma and Miyagi 1981). Altogether, *Ae. albopictus* occurs more often in forested habitats with wild species in tropical rather than subtropical localities. Thus, available information reinforces the tropical origin of *Ae. albopictus*.

Adaptation to human habitats was an event that occurred within several millennia following the appearance of villages cultivating wet rice over a wide range from tropical India through subtropical China (Fuller 2011). The initial adaptation to human habitats in the tropics is the simplest scenario, but the spread from the subtropics cannot be ruled out.

Possible impacts of human habitats on the climatic distribution range of *Ae. albopictus*.

Hawley et al. (1989) estimated the overwintering range of *Ae. albopictus* in the U. S. by

considering the compensation of winter mortality by summer reproduction. Mogi et al. (2012) also assumed that the northern limit depends on the balance between summer reproduction and winter mortality instead of simple abiotic thresholds (for example, coldest-month temperature). This approach is common in analyzing the relation between climate and insect distribution under a seasonal climate. For example, R_y (year-long replacement rate) of Bradshaw et al. (2004) and λ (annual population growth rate) of Crozier and Dwyer (2006) both imply the distribution limits may be affected by biotic as well as abiotic factors influencing summer reproduction or winter mortality. More generally, the classical niche concept distinguishes between a fundamental niche (a range delineated by physical conditions, including climate, and essential resources but excluding biotic interactions) and a realized niche (a narrower range under the presence of competitors and natural enemies) (Hutchinson 1978, Begon et al. 1986). Therefore, even if climate remains unchanged, apparent climatic limits can either advance or retreat following habitat shifts or environmental changes that increase or decrease the availability of essential resources and the magnitude of species interactions, and thereby disturb an existing balance between reproduction and mortality. Indeed, insect populations around northern limits persist in particular habitats more suitable for population growth than the other habitats (Oliver et al. 2009), implying the changing northern limits following the acquisition or loss of favorable habitats.

Water-holding containers and blood-meal hosts are essential resources for *Ae. albopictus* and are abundant in human habitats. Although the impact of these resources has not been quantitatively compared between natural and human habitats, it could be very large, especially under historical conditions before the development of water services and mosquito-proof houses. This view is well illustrated by persistence of *Aedes aegypti* (L.) at a small port in central Kyushu during 1944-1952 under abundant concrete tanks for fire prevention spread during the war (Kurihara 2003).

336 Competition and predation affect adversely *Ae. albopictus* larvae in forests with rich
337 mosquito faunas. After inundation, the larvae hatch and develop quickly using detritus
338 accumulated during drying, but become inferior competitors in durable water occupied by
339 more specialized container-mosquitoes resistant to starvation and accumulated wastes
340 (Sunahara and Mogi 1997, 2002). Also, larvae of *Ae. albopictus* are more vulnerable to
341 predators than other mosquitoes (Yasuda and Mitsui 1992, Nyamah et al. 2011). In a forest of
342 Sri Lanka, the larvae shared each plant-container with a maximum of four other species; in
343 bamboo stumps, the density was one third of *Aedes (Stegomyia) krombeini* Huang (a species
344 outside the *scutellaris* group), and prey mosquito density was reduced to one quarter by
345 predatory *Toxorhynchites* (Amerasinghe 1982).

346 Larval competition and predation are alleviated in artificial containers in human habitats.
347 *Aedes aegypti*, a primary competitor in human habitats, was absent before its invasion into
348 Asia presumably in the 20th century (Brown et al. 2014). In laboratory competition using
349 sympatric Asian populations, *Ae. aegypti* showed some competitive advantages over *Ae.*
350 *albopictus* under certain conditions (Chan et al. 1971, Sucharit et al. 1978). However, field
351 observations reported segregation between these species at regional, habitat, and container
352 levels (for example, Kalra et al. 1997, Chan et al. 1971, Preechaporn et al. 2006). Control
353 trials of mosquitoes in artificial containers by the introduction of poeciliid fish, copepods, or
354 *Toxorhynchites* mosquitoes (Chang et al. 2008, Nam et al. 2005, Annis et al. 1989) in southern
355 Asia indicate the paucity of predators in human habitats. In the temperate region, *Ae. aegypti*
356 is absent, and aquatic predators are rare in small containers (Sunahara et al. 2002).
357 Consequently, human habitats facilitate *Ae. albopictus* reproduction by higher survival and
358 faster development (due to higher water temperature) of the larvae (Li et al. 2014).

359 Below, we refer to the impacts of human habitats on the distribution of *Ae. albopictus* as
360 either ecological or eco-evolutionary. We use ecological impact to mean the range expansion

of *Ae. albopictus* following the expansion of human habitats under the same general climate when species interactions are the primary limiting factors. We use eco-evolutionary impact to mean (1) expansion into more severe climatic ranges, and (2) genetic changes under new climate conditions.

Impacts under tropical per-humid climate. Broader occurrence of *Ae. albopictus* than the wild species in the tropical rain-forest zone is attributable to the ecological impact. The region from Peninsular Malaysia through New Guinea is the Old World center of mosquito evolution (Belkin 1962), where plant containers in rain forests are occupied by diverse competitors and predators. In this region, *Ae. albopictus* is always associated with humans (Macdonald 1957, Mogi et al. 1996a, Cooper et al. 1994). Further expansion to eastern islands resulted from increasing urbanization (Guillaumot et al. 2012).

Impacts under semiarid climate. Although Anantapur was slightly out of the *Ae. albopictus* range, this is due to arbitrary selection of distribution sites (>200 km apart from each other) from vast records from Hawaii through Madagascar (Mogi et al. 2015). Indeed, *Ae. albopictus* occurs widely on the Deccan Plateau (Kaul 2003), and was collected at Anantapur and Coimbatore together with the wild species (Kanojia and Jamgaonkar 2008, Thenmozhi et al. 2012). As stated above, natural vegetation of these sites is deciduous forests. Therefore, distribution at originally treeless sites was not confirmed for the wild species.

Occurrence of *Ae. albopictus* in the steppe climate zone from tropical through temperate zones probably resulted from the eco-evolutionary impact. In semiarid northwestern India where natural vegetation is open shrubs (Roy et al. 2015), *Ae. albopictus* breeds in tree holes at urban sites (Joshi et al. 2006, Angel and Joshi 2008). Planting of trees for comfort or production must have enabled its persistence at originally treeless sites. Desiccation resistance of *Ae. albopictus* increases in response to selection on the egg (Sota 1993) and varies by habitats in the adult (Mogi et al. 1996b), so genetic changes under semiarid climate are likely.

Impacts under northern temperate climate. The wild species occur widely at tropical and subtropical highlands, and some species appear adapted to the highland climate better than *Ae. albopictus*. In Taiwan, *Ae. pseudalbopictus* reaches higher (2,400 m) than *Ae. albopictus* (1,000 m) (Lien 1978), while lowland northern limits in China are 32 and 40°N, respectively. This discrepancy indicates that adaptation to cool, oceanic climate at southern highlands is not enough for the expansion deep into temperate lowlands under continental climate. This is consistent with (1) the difference of northern-temperate climate from oceanic southern-temperate and tropical-highland climate (Troll 1960, Darlington 1965), and (2) the hemispherical (northern vs. southern) difference in primary overwintering strategies of insects (Chown et al. 2004).

Seasonal dynamics and diapause potential of *Ae. pseudalbopictus* around the northern limit are unknown as well as factors preventing the expansion further north. For mosquitoes, 32°N in eastern China is an approximate border between Sino-Indian and Northeast China subregions (Lu et al. 1997). Probably, this species indicates the northern limit under continental climate for the wild species that maintain the ancestral tropical distribution.

How could *Ae. albopictus* overcome this constraint? Did only *Ae. albopictus* harbor unique genetic variation that enabled adaptation to temperate continental climate? We can say nothing at present. Ecologically, however, *Ae. albopictus* had a great advantage. We propose that enhanced reproduction in human habitats enabled it to colonize further north. The present distribution shows the expansion to the temperate region as a human inquiline. In Beijing, temperate China, it was recorded as early as 1931, but was absent from tree holes where four species, including *Aedes (Stegomyia) chemulpoensis* Yamada (a species outside the *scutellaris* group), are common (Feng 1938a, b). In temperate Japan, it is absent from natural forests apart from developed sites (Eshita and Kurihara 1979) or on uninhabited islets (Mogi 1990). This pattern is consistent with the higher habitat specificity (restriction to habitats enabling

higher population growth) around the northern distribution margin observed in other insects (Oliver et al. 2009).

An immediate response to cooler climate in *Ae. albopictus* is cold acclimation in diapause and nondiapause eggs (Hawley et al. 1989, Hanson and Craig 1994). The earliest genetic adaptation is changes in photoperiodism as demonstrated by evolution after its invasion into the Americas (Armbruster 2016 for review). Changes in critical photoperiods for diapause induction not only adjust seasonal dynamics to the latitudinal temperature gradient but involve enhanced cold hardiness that is higher in diapause than nondiapause and northern than southern eggs (Hawley et al. 1987, Hawley et al. 1989, Hanson and Craig 1994).

Where did photoperiodic diapause appear? This species overwinters as diapause eggs in southernmost-temperate Kagoshima (31°N, annual mean temperature $\approx 18^{\circ}\text{C}$) (Makiya 1968) and Yixing (31°N, $\approx 16\text{--}17^{\circ}\text{C}$) (Yang 1988). In subtropical Okinawa (26°N, $\approx 22^{\circ}\text{C}$), it reproduces year-round (Toma et al. 1982), but some eggs enter diapause under short day-lengths (Toma and Miyagi 1990). A subtropical Foshan (23°N, $\approx 24^{\circ}\text{C}$) population has diapause-related genes (Chen et al. 2015), but photoperiodic diapause is absent in Yonakuni and Ishigaki islands (24°N, $\approx 24^{\circ}\text{C}$) (Higa et al. 2007) as well as in Hainan Island (20°N, $\approx 24^{\circ}\text{C}$) (Yang 1988). These facts indicate that egg diapause appeared at least in the northern subtropics and was reinforced following the expansion to the temperate region with humans.

Expansion as a human inquiline to a new climate range followed by genetic reinforcement of diapause is a typical example of the eco-evolutionary impact of human habitats.

Synthesis. A hypothetical scenario for the origin, dispersal, and adaption of *Ae. albopictus* in Asia is; (1) allopatric speciation as a wild species under the monsoon climate during the Pleistocene, (2) appearance of photoperiodic diapause in the subtropics, (3) adaptation to human habitats within several millennia in the tropical or the subtropical region, (4) expansion as a human inquiline to the temperate region where photoperiodic diapause is

essential for persistence, (5) formation of geographic variation in photoperiodic diapause and cold-hardiness, and (6) expansion to per-humid tropics and originally treeless dry regions following urbanization.

Although the real sequence of events may be more complex (for example, involving reinforcement of ethological isolation by sympatry, McLain and Rai 1985), we submit this scenario as an initial hypothesis that needs to and can be verified for improvement. Molecular phylogenetic analyses including *Ae. albopictus* and the wild species from broad geographical and habitat ranges are necessary as well as field, laboratory, and theoretical studies focusing on this issue.

The hypothesis that adaptation to human habitats enabled *Ae. albopictus* to expand not only under the suitable climate but by producing opportunities for adapting to more severe climate is of practical importance in view of growing anthropogenic environmental changes and transportation that favor *Ae. albopictus* and other arthropods of medical importance.

Acknowledgments

We thank T. Sunahara for his comments on the earlier version of the manuscript.

References Cited

- Amerasinghe, F. P. 1982.** Observations of the mosquitoes (Diptera: Culicidae) of Udawattakele Forest, Sri Lanka. J. Natl. Sci. Counc. Sri Lanka 10(1): 81-97.
- Amerasinghe, F. P., and N. B. Munasingha. 1988a.** A predevelopment mosquito survey in the Mahaweli Development Project Area, Sri Lanka: adults. J. Med. Entomol. 25: 276-285.
- Amerasinghe, F. P., and N. B. Munasingha. 1988b.** A predevelopment mosquito survey in

the Mahaweli Development Project Area, Sri Lanka: J. Med. Entomol. 25: 286-294.

Angel, B., and V. Joshi. 2008. Distribution and seasonality of vertically transmitted dengue viruses in *Aedes* mosquitoes in arid and semi-arid areas of Rajasthan, Indian J. Vector Borne Dis. 45: 56–59.

Annis, B., S. Krisnowardojo, S. Atmosoedjono, and P. Supardi. 1989. Suppression of larval *Aedes aegypti* populations in household water storage containers in Jakarta, Indonesia, through releases of first-instar *Toxorhynchites splendens* larvae. J. Am. Mosq. Control Assoc. 5: 235-238.

Armbruster, P. A. 2016. Photoperiodic diapause and the establishment of *Aedes albopictus* (Diptera: Culicidae) in North America. J. Med. Entomol. 53:1013-23.

Begon, M., J. L. Harper, and C. R. Townsend. 1986. Ecology. Blackwell, Oxford, U. K.

Belkin, J. N. 1962. The mosquitoes of the South Pacific (Diptera, Culicidae). University of California Press, Berkeley.

Bradshaw, W. E., and L. P. Lounibos 1977. Evolution of dormancy and its photoperiodic control in pitcher-plant mosquitoes. Evolution 31: 546-567.

Bradshaw, W. E., P. A. Zani, and C. M. Holzapfel. 2004. Adaptation to temperate climates. Evolution 58: 1748–1762.

Breckle, S.-W. 2002. Walter’s vegetation of the earth: the ecological systems of the geo-biosphere 4th ed. Springer-Verlag, Berlin, Germany.

Brown, J. F., B. R. Evans, W. Zheng, V. Obas, L. Barrera-Martinez, A. Egizi, H. Zhao, A. Caccone, and J. R. Powell. 2014. Human impacts have shaped historical and recent evolution in *Aedes aegypti*, the dengue and yellow fever mosquito. Evolution 68: 514–525.

Cameron, E. C., R. C. Wilkerson, M. Mogi, I. Miyagi, T. Toma, H. Kim, and D. M. Fonseca. 2010. Molecular phylogenetics of *Aedes japonicus*, a disease vector that recently invaded Western Europe, North America, and the Hawaiian Islands. J. Med. Entomol. 47:

486 527-35.

487 **Chan, K.L., Y. C. Chan, and B. C. Ho. 1971.** *Aedes aegypti* (L.) and *Aedes albopictus*
488 (Skuse) in Singapore City. 4. Competition between species. Bull. WHO 44: 643–649.

489 **Chang, M. S., T. Seta, J. Nealon, D. Socheat, N. Chantha, and M. B. Nathan. 2008.**
490 Community-based use of the larvivorous fish *Poecilia reticulata* to control the dengue
491 vector *Aedes aegypti* in domestic water storage containers in rural Cambodia. J. Vector Ecol.
492 33: 139-144.

493 **Chen, H. 1987.** The mosquito fauna of Guizhou Vol. 1. Guizhou People’s Publishing House,
494 Guiyang, Guizhou, China.

495 **Chen, X., X. T. Jiang, J. Gu, M. Xu, Y. Wu, Y. Deng, C. Zhang, M. Bonizzoni, W.**
496 **Dermauw, J. Vontas, et al. 2015.** Genome sequence of the Asian tiger mosquito, *Aedes*
497 *albopictus*, reveals insights into its biology, genetics, and evolution. Proc. Natl. Acad. Sci.
498 USA. 112: E5907–E5915.

499 **Chown, S. L., B. J. Sinclair, H. P. Leinaas, and K. J. Gaston. 2004.** Hemispheric
500 asymmetries in biodiversity - a serious matter for ecology. PLoS Biol. 2 (11): e406. (DOI:
501 10.1371/journal.pbio.0020406).

502 **Cooper, R. D., D. G. E. Waterson, M. Kupo M, and A. W. Sweeney. 1994.** *Aedes*
503 *albopictus* (Skuse) (Diptera: Culicidae) in the Western Province of Papua New Guinea and
504 the threat of its introduction to Australia. J. Aust. Entomol. Assoc. 33: 115-116.

505 **Crawford, J. E., J. M. Alves, W. J. Palmer, J. P. Day, M. Sylla, R. Ramasamy,**
506 **S. N. Surendran, W. C. BlackIV, A. Pain, and F. M. . Jiggins. 2017.** Population genomics
507 reveals that an anthropophilic population of *Aedes aegypti* mosquitoes in West Africa
508 recently gave rise to American and Asian populations of this major disease vector. BMC
509 Biol. 15:16. (DOI: 10.1186/s12915-017-0351-0).

510 **Crozier, L., and G. Dwyer. 2006.** Combining population-dynamic and ecophysiological

511 models to predict climate-induced insect range shifts. *Am. Nat.* 167: 853-866.

512 **Danilov, V. N., and V. V. Filippova. 1978.** New species of mosquito, *Aedes (Stegomyia)*
513 *sibiricus* sp. n. (Culicidae). *Parazitologiya* 12:170-176.

514 **Darlington, P. J. 1965.** Biogeography of the southern end of the world. Harvard University
515 Press, Cambridge, MA.

516 **Dong, X., H. Zhou, and Z. Gong. 2010.** The mosquito fauna of Yunnan China Vol. 2. Yunnan
517 Science and Technology Press, Kunming, Yunnan, China.

518 **Eshita, Y., and T. Kurihara. 1979.** Studies on the habitats of *Aedes albopictus* and *Aedes*
519 *riversi* in the southwestern part of Japan. *Jpn. J. Sanit. Zool.* 30: 181-185.

520 **Feng, L. 1938a.** A critical review of literature regarding the records of mosquitoes in China.
521 Part II. Subfamily Culicinae, tribes Megarhinini and Culicini. *Peking Nat. Hist. Bull.* 12:
522 285-318.

523 **Feng, L. 1938b.** The tree hole species of mosquitoes of Peiping, China. *Chin. Med. J., Suppl.*
524 2: 503-525.

525 **Fuller, D. Q. 2011.** Pathways to Asian civilizations: tracing the origins and spread of rice and
526 rice cultures. *Rice* 4:78-92.

527 **Guillaumot, L., R. Ofanoa, L. Swillen, N. Singh, H. C. Bossin, and F. Schaffner. 2012.**
528 Distribution of *Aedes albopictus* (Diptera, Culicidae) in southwestern Pacific countries,
529 with a first report from the Kingdom of Tonga. *Parasit. Vectors* 5:247
530 (<http://www.parasitesandvectors.com/content/5/1/247>)

531 **Gutsevich, A. V., and A. M. Dubitskiy. 1987.** New species of mosquitoes in the fauna of the
532 USSR. *Mosq. Syst.* 19:1-92.

533 **Hanson, S. M., and G. B. Craig Jr. 1994.** Cold acclimation, diapause, and geographic origin
534 affect cold hardiness in eggs of *Aedes albopictus* (Diptera: Culicidae). *J. Med. Entomol.*
535 3:192-201.

536 **Harrison, B. A., P. Boonyakanist, and K. Mongkolpanya. 1972.** Biological observations on
537 *Aedes seatoi* Huang in Thailand with notes on rural *Aedes aegypti* (L.) and other *Stegomyia*
538 populations. J. Med. Entomol. 9: 1-6.

539 **Harrison, S. P., G. Yu, H. Takahara, and I. C. Prentice. 2001.** Diversity of temperate plants
540 in east Asia. Nature 413: 129-130.

541 **Hawley, W. A., C. B. Pumpuni, R. H. Brady, G. B. Jr. 1989.** Overwintering survival of
542 *Aedes albopictus* (Diptera: Culicidae) eggs in Indiana. J. Med. Entomol. 26:122-129.

543 **Hawley, W. A., P. Reiter, R. S. Copeland, C. B. Pumpuni, and G. B. Craig, Jr. 1987.** *Aedes*
544 *albopictus* in North America: probable introduction in used tires from northern Asia.
545 Science 236: 1114-1116.

546 **Higa, Y. T. Toma, Y. Araki, I. Onodera, and I. Miyagi. 2007.** Seasonal changes in
547 oviposition activity, hatching and embryonation rates of eggs of *Aedes albopictus* (Diptera:
548 Culicidae) on three islands of Ryukyu Archipelago, Japan. Med. Entomol. Zool. 58:1-10,

549 **Huang, Y. M. 1972.** Contributions to the mosquito fauna of Southeast Asia. XIV. The
550 subgenus *Stegomyia* of *Aedes* in Southeast Asia. I. The *scuterallis* group of species. Contrib.
551 Am. Entomol. Inst. 9: 1-109.

552 **Hutchinson, G. E. 1978.** An introduction to population ecology. Yale University Press, New
553 Haven, CT.

554 **Jennings, J. H., and W. J. Etges. 2010.** Species hybrids in the laboratory but not in nature: a
555 reanalysis of premating isolation between *Drosophila arizonae* and *D. mojavensis*.
556 Evolution 64: 587-598.

557 **Joshi, V., R. C. Sharma, Y. Sharma, S. Adha, K. Sharma, H. Singh, A. Purohit, and M.**
558 **Singhi. 2006.** Importance of socioeconomic status and tree holes in distribution of *Aedes*
559 mosquitoes (Diptera: Culicidae) in Jodhpur, Rajasthan, Indian J. Med. Entomol. 43:
560 330-336.

561 **Kalra, N. L., S. M. Kaul, and R. M. Rastogi. 1997.** Prevalence of *Aedes aegypti* and *Aedes*
562 *albopictus*-Vectors of Dengue Haemorrhagic Fever in North, North-East and Central India.
563 Dengue Bull. 21: 84-92.

564 **Kanojia, P. C., and A. V. Jamgaonkar. 2008.** Mosquito records from a hot and dry climatic
565 area experiencing frequent outbreaks of Japanese encephalitis, Bellary District, Karnataka,
566 India. J. Am. Mosq. Control Assoc. 24: 6-10.

567 **Kaul, R. 2003.** An update on the distribution of mosquitoes of the tribe Aedini in India
568 (Diptera: Culicidae). Oriental Insects 37: 439–455.

569 **Kirkpatrick, M., and N. H. Barton. 1997.** Evolution of a species' range. Am. Nat. 150:1-23.

570 **Kurihara, T. 2003.** Review of dengue vector mosquitoes in Japan. Med. Entomol. Zool. 54:
571 135-154.

572 **Lei, X. 1989.** The mosquito fauna of Sichuan. Chengdu University of Science and Technology,
573 Chengdu, Sichuan, China.

574 **Li, Y., F. Kamara, G. Zhou, S. Puthiyakunnon, C. Li, Y. Liu, Y. Zhou, L. Yao, G. Yan,**
575 **and X. Chen. 2014.** Urbanization increases *Aedes albopictus* larval habitats and accelerates
576 mosquito development and survivorship. PLoS Negl. Trop. Dis. 8(11): e3301
577 (doi:10.1371/journal.pntd.0003301).

578 **Lien, J. C. 1978.** Ecology and control of mosquitoes in Taiwan. Special Publ. Inst. Zool.,
579 Academia Sinica, 3: 37-69.

580 **Lu, B., B. Li, S. Ji, H. Chen, Q. Meng, L. Su, F. Qu, Z. Geng, and Z. Zhang. 1997.** Fauna
581 Sinica, Insecta, vol. 8, Diptera: Culicidae 1. Science Press, Beijing, China.

582 **Macdonald, W. W. 1957.** An interim review of the non-anopheline mosquitoes of Malaya.
583 Studies Inst. Med. Res. 28:1-34.

584 **Makiya, K. 1968.** Population dynamics of mosquito larvae overwintering in southern Japan.
585 Jpn. J. Sanit. Zool. 19: 223-229.

586 **McLain, D. K., and K. S. Rai. 1986.** Reinforcement for ethological isolation in the southeast
587 Asian *Aedes albopictus* subgroup (Diptera: Culicidae). *Evolution* 40: 1346-1350.

588 **McLain, D. K., K. S. Rai., and P. N. Rao. 1985.** Ethological divergence in allopatry and
589 asymmetrical isolation in the South Pacific *Aedes scutellaris* subgroup. *Evolution* 39:
590 998-1008.

591 **Miyagi, I., and T. Toma. 1980.** Studies on the mosquitoes in Yaeyama Islands, Japan 5.
592 Notes on the mosquitoes collected in forest areas of Iriomotejima. *Jpn. J. Sanit. Zool.* 31:
593 81-91.

594 **Mogi, M. 1990.** Further notes on the northern distribution of *Aedes (Stegomyia) riversi*
595 (Diptera: Culicidae). *Mosq. Syst.* 22: 47-52.

596 **Mogi, M. 2011.** Variation in cold hardiness of nondiapausing eggs of nine *Aedes (Stegomyia)*
597 species (Diptera: Culicidae) from eastern Asia and Pacific islands ranging from the tropics
598 to the cool-temperate zone. *J. Med. Entomol.* 48: 212-222.

599 **Mogi, M., P. Armbruster, and D. M. Fonseca. 2012.** Analyses of the northern distributional
600 limit of *Aedes albopictus* (Diptera: Culicidae) with a simple thermal index. *J. Med.*
601 *Entomol.* 49: 1233-1243.

602 **Mogi, M., I. Miyagi, K. Abadi, and Syafruddin. 1996b.** Inter- and intra-specific variation in
603 resistance to desiccation by adult *Aedes (Stegomyia)* spp. (Diptera: Culicidae) from
604 Indonesia. *J. Med. Entomol.* 33: 53–57.

605 **Mogi, M., P. Armbruster, N. Tuno, R. Campos, and R. Eritja. 2015.** Simple indices
606 provide insight to climate attributes delineating the geographic range of *Aedes albopictus*
607 (Diptera: Culicidae) prior to worldwide invasion. *J. Med. Entomol.* 52: 647–657.

608 **Mogi, M., I. Miyagi, T. Toma, M. Hasan, K. Abadi, and Syafruddin. 1996a.** Occurrence of
609 *Aedes (Stegomyia)* spp. mosquitoes (Diptera: Culicidae) in Halmahela villages, Indonesia. *J.*
610 *Med. Entomol.* 33: 169-172.

611 **Nam, V. S., N. T. Yen, T. V. Phong, T. U. Ninh, L. Q. Mai, L. V. Lo, L. T. Nghia, A. Bektas,**
612 **A. Briscoombe, J. G. Aaskov, et al. 2005.** Elimination of dengue by community programs
613 using *Mesocyclops* (Copepoda) against *Aedes aegypti* in central Vietnam. Am. J. Trop. Med.
614 Hyg. 72: 79-85.

615 **Nyamah, M. A., S. Sulaiman, and B. Omar. 2011.** Field observation on the efficacy of
616 *Toxorhynchites splendens* (Wiedemann) as a biocontrol agent against *Aedes albopictus*
617 (Skuse) larvae in a cemetery. Trop. Biomed. 28: 312-9.

618 **O'Donnell, D. and P. Armbruster. 2009.** Evolutionary differentiation of fitness traits across
619 multiple geographic scales in *Aedes albopictus* (Diptera: Culicidae). Ann. Entomol. Soc.
620 Am. 102:1135-1144.

621 **Oliver, T., J. K. Hill, C. D. Thomas, T. Brereton, and D. B. Roy. 2009.** Changes in habitat
622 specificity of species at their climatic range boundaries. Ecol. Letters 12:1091-1102.

623 **Ota, H. 1998.** Geographic patterns of endemism and speciation in amphibians and reptiles of
624 the Ryukyu Archipelago, Japan, with special reference to their paleogeographical
625 implications. Res. Popul. Ecol. 40: 189-204.

626 **Pashley, D. P., and K. S. Rai. 1983.** Comparison of allozyme and morphological
627 relationships in some *Aedes* (*Stegomyia*) mosquitoes (Diptera: Culicidae). Ann. Entomol.
628 Soc. Am. 76: 388-394.

629 **Porretta, D., V. Mastrantonio, R. Bellini, P. Somboon, and S. Urbanelli. 2012.** Glacial
630 history of a modern invader: Phylogeography and species distribution modelling of the
631 Asian tiger mosquito *Aedes albopictus*. PLoS ONE 7: e44515.
632 (doi:10.1371/journal.pone.0044515).

633 **Preechaporn, W., M. Jaroensutasinee, K. Jaroensutasinee. 2006.** The larval ecology of
634 *Aedes aegypti* and *Ae. albopictus* in three topographical areas of southern Thailand. Dengue
635 Bull. 30:204-213.

636 **Rajavel, A. R., and R. Natarajan. 2008.** Mosquitoes of the mangrove forests of India: Part
637 7-an overview. J. Am. Mosq. Control Assoc. 24: 478-488.

638 **Ramalingam, S. 1974.** A brief mosquito survey of Java. WHO/VBC/74. WHO, Geneva.

639 **Rattanarithikul, R., R. E. Harbach, B. A. Harrison, P. Panthusiri, R. E. Coleman, and J.
640 H. Richardson. 2010.** Illustrated Keys to the mosquitoes of Thailand VI. Tribe Aedini.
641 Southeast Asian J. Trop. Med. Public Health 41, Suppl 1: 1-225.

642 **Ross, H. H. 1964.** The colonization of temperate North America by mosquitoes and man.
643 Mosq. News 24. 103-118.

644 **Roy, P. S., M. D. Behera, M. S. R. Murthy, A. Royd, S. Singh, S. P. S. Kushwahad, C. S.
645 Jha, S. Sudhakar, P. K. Joshi, Ch. Sudhakar Reddy, et al. 2015.** New vegetation type
646 map of India prepared using satellite remote sensing: Comparison with global vegetation
647 maps and utilities. Intern. J. Appl. Earth Observ. Geoinform. 39: 142-159.

648 **Song, J., Z. Li, X. Xiong, and K. Liu. 1981.** Mosquito species and their distribution in
649 Sichuan. Sichuan J. Zool. 1: 1-34.

650 **Sota, T. 1993.** Response to Selection for desiccation resistance in *Aedes albopictus* eggs
651 (Diptera: Culicidae). Appl. Entomol. Zool. 28: 161-168.

652 **Sota, T. and M. Mogi 2006.** Origin of pitcher plant mosquitoes in *Aedes (Stegomyia)*: A
653 molecular phylogenetic analysis using mitochondrial and nuclear gene sequences. J. Med.
654 Entomol. 43: 795-800.

655 **Sucharit, S., W. Tumrasvin, S. Vutikes, and S. Viraboonthai, S. 1978.** Interactions between
656 larvae of *Ae. aegypti* and *Ae. albopictus* in mixed experimental populations. Southeast
657 Asian J. Trop. Med. Publ. Health 9: 93–97.

658 **Sunahara, T., and M. Mogi. 1997.** Can the tortoise beat the hare? A possible mechanism for
659 the coexistence of competing mosquitoes in bamboo groves. Ecol. Res. 12: 63-70.

660 **Sunahara, T., and M. Mogi. 2002.** Priority effects of bamboo-stump mosquito larvae:

661 influences of water exchange and leaf litter input. Ecol. Entomol. 27: 346-354.

662 **Sunahara, T., K. Ishizaka, and M. Mogi. 2002.** Habitat size: a factor determining the

663 opportunity for encounters between mosquito larvae and aquatic predators. J. Vector Ecol.

664 27: 8-20.

665 **Tanaka, K., K. Mizusawa, and E. S. Saugstad. 1979.** A revision of the adult and larval

666 mosquitoes of Japan (including the Ryukyu Archipelago and the Ogasawara Islands) and

667 Korea (Diptera: Culicidae). Contrib. Am. Entomol. Inst. 16: 1-987.

668 **Thenmozhi, V., R. S. Pandian, and B. K. Tyagi. 2012.** Type of ecosystems: a determinant

669 factor for the enhancement of diversity and density of mosquito fauna. Proc. 5th Conf. Med.

670 Arthropodology: 69-74.

671 **Toma, T., and I. Miyagi. 1981.** Notes on the mosquitoes collected at forest areas in the

672 northern part of Okinawajima, Ryukyu Islands, Japan. Jpn. J. Sanit. Zool. 32: 271-279.

673 **Toma, T., and I. Miyagi. 1990.** Seasonal changes in the hatchability of *Aedes albopictus*

674 (Diptera: Culicidae) eggs in Okinawajima, Ryukyu Archipelago, Japan. Jpn. J. Sanit. Zool.

675 41: 195-204.

676 **Toma, T., S. Sakamoto, and I. Miyagi. 1982.** The seasonal appearance of *Aedes albopictus*

677 in Okinawajima, the Ryukyu Archipelago, Japan. Mosq. News 42: 179-183.

678 **Toma, T., I. Miyagi, M. B. Crabtree, and B. R. Miller. 2002.** Investigation of the *Aedes*

679 (*Stegomyia*) *flavopictus* complex (Diptera: Culicidae) in Japan by sequence analysis of the

680 internal transcribed spacers of ribosomal DNA. J. Med. Entomol. 39: 461-468.

681 **Troll, C. 1960.** The relationship between the climates, ecology and plant geography of the

682 southern cold temperate zone and of the tropical high mountains. Proc. Roy. Soc. London.

683 Ser. B, Biol. Sci. 152: 529-532.

684 **Urbanski, J. M., J. B. Benoit, M. R. Michaud, D. L. Denlinger, and P. Armbruster. 2010.**

685 The molecular basis of increased desiccation resistance during diapause in the Asian tiger

686 mosquito, *Aedes albopictus*. Proc. R. Soc. B 277: 2683-2692.

687 **Wang, P., S. Clemens, L. Beaufort, P. Braconnot, G. Ganssen, Z. Jian, P. Kershaw, and**
688 **M. Sarnthein. 2005.** Evolution and variability of the Asian monsoon system: state of the
689 art and outstanding issues. Quaternary Science Reviews 24: 595-629.

690 **Wang, G., C. Li, X. Guo, D. Xing, Y. Dong, Z. Wang, Y. Zhang, M. Liu, Z. Zheng, H.**
691 **Zhang, et al. 2012.** Identifying the main mosquito species in China based on DNA
692 barcoding. PLoS ONE 7: e47051. (DOI: 10.1371/journal.pone.0047051).

693 **Yang, Z. 1988.** Egg diapause in the mosquito *Aedes albopictus* (Skuse) (Diptera: Culicidae).
694 Acta Entomol. Sinica 31: 287-294.

695 **Yasuda, H., and T. Mitsui. 1992.** Laboratory observations of prey behaviour for prey
696 acquisition by a predator among three larval mosquitoes. Ecological Research 7: 179-182.

697

Figure legend

Fig. 1. Climate conditions at distribution sites of (A) *Ae. pseudalbopictus* and (B) the other wild species (*Ae. novalbopictus*, *A. patriciae*, *Ae. seatoi*, and *Ae. subalbopictus*). Dotted polygon, distribution range of *Ae. albopictus* before the worldwide invasion since 1980's (Mogi et al. 2015). Symbols of sites are distinguished by altitudes; circle, below 500 m, diamond, 500-1,000 m, and triangle, above 1,000 m. Conditions at sites encircled by solid lines are detailed in Tables 4-6. For Table 6, only 12 coolest sites were encircled. Two arrows in the temperate-forest zone of (A) indicate northernmost lowland sites in eastern China, and a single arrow in (B) indicates a unique driest site slightly out of the *Ae. albopictus* range.

Table legends

Table 1. Species of the *albopictus* subgroup of the *scutellaris* group of *Aedes* (*Stegomyia*) in Asia, arranged approximately from the ancestral tropical distribution to the derived northerly distribution.

Table 2. Geographical and altitudinal distributions of the five wild species.

Table 3. Thermal Index (WI_{10}) and aridity-humidity index (PE) criteria for climate classification.

Table 4. Distribution sites under tropical, per-humid, rain-forest climate ($WI_{10} > 180$, $PE \geq 128$).

Table 5. Driest distribution sites ($PE < 50$).

Table 6. Distribution sites where summer is coolest ($WI_{10} < 70$) and/or at highest latitudes ($>30^\circ\text{N}$) arranged by the increasing order of WI_1

Table 1. Species of the *albopictus* subgroup of the *scutellaris* group of *Aedes* (*Stegomyia*) in Asia, arranged approximately from the ancestral tropical distribution to the derived northerly distribution.

Species	Distribution ¹					Habitat
	T	ST	SWT	NWT	CT	
<i>Ae. novalbopictus</i>	+	+				Forest
<i>Ae. patriciae</i>	+	+				Forest
<i>Ae. seatoi</i>	+	+				Forest
<i>Ae. subalbopictus</i>	+	+				Forest
<i>Ae. pseudalbopictus</i>	+	+	+			Forest
<i>Ae. albopictus</i>	+	+	+	+		Human-made
<i>Ae. flavopictus</i>		+	+	+	+	Forest
<i>Ae. galloisioides</i>		+ ²				Forest
<i>Ae. neogalloisi</i>			+ ²			Forest
<i>Ae. galloisi</i>			+ ²	+	+	Forest
<i>Ae. sibiricus</i>					+	Forest

¹T, tropical; ST, subtropical; SWM, southern part of warm-temperate; NWT, northern part of warm-temperate; CT, cool-temperate.

²Highland; *Ae. galloisioides*, Yunnan and Sichuan Provinces, China; *Ae. neogalloisi*, Henan Province, China; *Ae. galloisi*, Kyushu, Japan.

Table 2. Geographical and altitudinal distributions of the five wild species.

Species	Region ¹	Altitude (m) ²	
		Described	Estimated
<i>Ae. noalbopictus</i>	India, Sri Lanka, Thailand, China (Yunnan), Hainan*	430-1,220	10-1,850
<i>Ae. patriciae</i>	Pakistan, India, Thailand, Vietnam, Peninsular Malaysia, China (Yunnan), Taiwan*	530-2,130	60-1,750
<i>Ae. pseudalbopictus</i>	India, Andaman, Nicobar, Nepal, Myanmar, Thailand, Lao, Peninsular Malaysia, Sumatra*, Java, China (South-Central) ³ , Hainan*, Taiwan	10-1,860	10-2,400
<i>Ae. seatoi</i>	Thailand, China (Sichuan)	20-60	10-1,250
<i>Ae. subalbopictus</i>	India, Andaman, Nepal, Thailand, Vietnam, China (Sichuan, Yunnan, Guizhou), Hainan*	80-2,480	10-1,840

¹India and China indicate the continental part, respectively. *, site unspecified within the region.

²Described, publications gave altitudes or detailed coordinates; Estimated, estimated on Google Earth Pro.

³Jiangsu*, Anhui, Zhejiang, Fujian, Jiangxi, Hunan*, Guizhou, Sichuan, Yunnan, Guangxi, Guangdong*

Table 3. Thermal Index (WI_{10}) and aridity-humidity index (PE) criteria for climate classification.

Index ¹	Value	Climate	Vegetation
WI_{10}	~120	Temperate	
	120~180	Subtropical	
	>180	Tropical	
PE	0~15	Arid	Desert ²
	16~31	Semiarid	Steppe
	32~63	Sub-humid ³	Savannah ³
	64~127	Humid	Forest ⁴
	≥128	Per-humid	Rain forest ⁴

¹See Mogi et al. 2015 for detailed explanations. Note that these indices are indicator of warmth and wetness integrating latitudinal and altitudinal gradients. Therefore, the temperate zone includes tropical and subtropical highland sites besides northern temperate sites.

²Deserts may have ephemeral forbs and shrubs but lack continuous vegetation.

³Naming of vegetation under sub-humid climate depends on whether emphasis is put on tall grass or trees. Although trees do not form continuous canopies, their presence separates this vegetation from steppes.

⁴In tropical and subtropical zones, seasonal forests under humid climate can be discriminated from evergreen rain forests. In temperate zones, the same forest types may occupy both humid and per-humid zones.

Table 4. Distribution sites under tropical, per-humid, rain-forest climate ($WI_{10} > 180$, $PE \geq 128$).

Region	Station	Latitude (°N)	Altitude (m)	PE ¹	WI ₁₀	AMT ² (°C)	ATP ³ (mm)	No. Dry Month ⁴	Species (No. sites) ⁵
Andaman Islands	Port Blair	11.67	79	156	194.1	26.2	2,872	2	pse, sub
Western India	Kozhikode	11.25	4	147	214.5	27.9	3,113	4	nov
	Goa	15.48	60	137	209.3	27.4	2,813	6	nov
Phuket Island	Phuket	8.12	10	128	208.7	27.4	2,503	1	pse (2)
Peninsular Malaysia	Kota Bharu	6.17	5	140	200.7	26.7	2,599	0	pse (4)

¹Aridity-humidity index.

²Annual mean temperature.

³Annual total precipitation.

⁴In dry months, monthly PE=0 or 1. At Kota Bharu, the minimum PE was 2.

⁵pse, *Ae. pseudalbopictus*; sub., *Ae. subalbopictus*; nov, *Ae. novalbopictus*; No. sites were shown when distribution sites ≥ 2 .

Table 5. Driest distribution sites (PE < 50).

Region ¹	Station ²	Latitude (°N)	Altitude (m)	PE ³	WI ₁₀ ⁴	AMT ⁵ (°C)	ATP ⁶ (mm)	No. Dry Mo ⁷	Species (No. sites) ⁸
C. and S. India	Anantapur*	14.58	364	S 24	T 216.2	28.0	560	5	nov (3), sub (3)
	Coimbatore	11.00	409	S 29	T 200.4	26.7	647	5	nov
	Kanyakumari	8.08	37	33	T 213.1	27.8	735	3	pse
	Pune	18.53	559	36	176.4	24.7	741	6	nov, sub
	Mysore	12.30	760	40	174.1	24.5	804	4	nov, pse
	Belgaum	15.85	747	49	171.4	24.3	947	4	nov, pse, sub
N. and C. Thailand	Phayao	19.13	397	45	T 182.0	25.2	942	4	nov, pse (3)
	Kanchanaburi	14.02	29	48	T 215.1	27.9	1,050	4	pse (3), sea
SW. China	Yuanmou	25.73	1,221	32	137.5	21.5	642	6	sub
	Yuanjiang	23.60	398	37	164.7	23.7	796	4	pse
	Panzhihua	26.58	1,191	45	129.3	20.8	849	6	pse (2), sea, sub

¹C, central; S, southern; N, northern; SW, southwestern.

²Stations with asterisks are out of the *Ae. albopictus* range.

³ Aridity-humidity index. “S” indicates semiarid, steppe climate, while others are sub-humid, savannah climate.

⁴ “T” indicates tropical climate, while others are subtropical climate.

⁵ Annual mean temperature.

⁶ Annual total precipitation.

⁷ In dry months, monthly PE=0 or 1.

⁸ nov, *Ae. novalbopictus*; sub., *Ae. subalbopictus*; pse, *Ae. pseudalbopictus*; sea, *Ae. seatoi*; No. sites were shown when distribution sites ≥ 2 .

Table 6. Distribution sites where summer is coolest ($WI_{10} < 70$) and/or at highest latitudes ($>30^{\circ}N$) arranged by the increasing order of WI_{10} .

No.	Category ¹	Region	Station ²	Latitude ($^{\circ}N$)	Altitude (m)	WI_{10}	AMT ³ ($^{\circ}C$)	Hottest Mo ($^{\circ}C$)	Coldest Mo ($^{\circ}C$)	Range ⁴ ($^{\circ}C$)	CCI ⁵	Species (No. sites) ⁶
1	C	Taiwan	Alishan*	23.51	2,413	29.1	11.8	15.2	6.8	8.4	11.9	pse
2	C	E. Himalaya	Darjeeling*	27.05	2,128	40.1	12.5	16.9	5.6	11.3	17.9	pse
3	C	W. Himalaya	Mukteshwar	29.47	2,311	48.0	13.3	18.3	6.4	11.9	17.8	sub
4	C, N	W. Himalaya	Murree	33.92	2,127	50.4	12.7	20.6	3.7	16.9	27.4	pat
5	C, N	W. Himalaya	Shimla	31.10	2,202	50.5	13.3	19.8	5.3	14.5	23.5	pat (2)
6	C	E. China	Lushan	29.58	1,165	50.9	11.6	22.2	0.3	21.9	44.4	pse
7	C, N	W. Himalaya	Manali	32.27	2,039	53.3	13.3	20.6	4.5	16.1	26.7	pse, sub
8	C	W. Himalaya	Nainital	29.40	1,953	57.2	14.1	20.0	6.2	13.8	23.0	sub (3)
9	C	SW. China	Xishui	28.32	1,181	57.6	13.1	22.7	2.7	20.0	40.8	pse, sub
10	C	E. Himalaya	Gangtok*	27.33	1,765	64.0	15.2	19.5	8.4	11.1	17.1	pse, sub (2)
11	C	SW. China	Tengchong	24.98	1,655	64.1	15.1	19.9	8.1	11.8	21.0	pat
12	C	SW. China	Huili	26.65	1,788	68.9	15.3	21.2	7.3	13.9	25.6	pse (2)
13	N	W. China	Wanyuan	32.07	674	71.7	14.7	24.8	3.9	20.9	39.0	pse

No.	Category ¹	Region	Station ²	Latitude (°N)	Altitude (m)	WI ₁₀	AMT ³ (°C)	Hottest Mo (°C)	Coldest Mo (°C)	Range ⁴ (°C)	CCI ⁵	Species ⁶
14	N	E. China	Huoshan	31.40	88	82.8	15.2	27.4	2.4	25.0	50.3	pse
15	N	W. China	Liangping	30.68	455	88.1	16.6	26.8	5.7	21.1	41.0	pse
16	N	W. China	Langzhong	31.58	385	90.2	16.8	26.6	6.1	20.5	38.5	pse
17	N	E. China	Hangzhou	30.23	43	91.2	16.5	28.4	4.3	24.1	49.4	pse
18	N	W. China	Dazhou	31.20	344	92.6	17.0	27.5	6.1	21.4	41.2	pse
19	N	W. China	Wanzhou	30.81	189	100.9	18.0	28.3	7.0	21.3	41.4	pse
20	N	W. Himalaya	Dharmasala	32.27	1,211	109.1	19.1	26.5	10.4	16.1	26.7	nov
21	N	W. Himalaya	Dehradun	30.32	682	139.8	21.7	28.9	12.7	16.2	28.6	nov

¹C, coolest distribution sites where WI₁₀ < 70; N, northernmost distribution sites >30°N.

² Stations with asterisks are out of the *Ae. albopictus* range.

³Annual mean temperature.

⁴Difference between hottest month mean and coldest month mean.

⁵Conrad's continentality index.

⁶pse, *Ae. pseudalbopictus*; sub., *Ae. subalbopictus*; pat, *Ae. patriciae*; nov, *Ae. novalbopictus*; No. sites were shown when distribution sites ≥ 2.

(A) *Ae. pseudalbopictus*

(B) Other four species