Simple Indices Provide Insight to Climate Attributes Delineating the Geographic Range of *Aedes albopictus* (Diptera: Culicidae) Prior to Worldwide Invasion

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ABSTRACT *Aedes albopictus* (Skuse) has expanded its distribution worldwide during the past decades. Despite attempts to explain and predict its geographic occurrence, analyses of the distribution of *Ae. albopictus* in the context of broad climatic regions (biomes) has not been performed. We analyzed climate conditions at its distribution sites in the range before the worldwide invasions (from the easternmost Hawaii through westernmost Madagascar) by using thermal and aridity–humidity indices descriptive of major biomes. A significant advantage of this approach is that it uses simple indices clearly related to the population dynamics of *Ae. albopictus*. Although *Ae. albopictus* has been regarded as a forest species preferring humid climate, in areas with significant human habitation, the distribution sites extended from the perhumid, rain forest zone to the semiarid, steppe zone. This pattern was common from the tropics through the temperate zone. Across the distribution range, there was no seasonal discordance between temperature and precipitation; at sites where winter prevents *Ae. albopictus* reproduction (monthly means <10°C), precipitation was concentrated in warm months (>10°C) under the Asian summer monsoon. Absence of the species in northern and eastern coastal Australia and eastern coastal Africa was not attributable solely to climate conditions. However, Asia west of the summer monsoon range was climatically unsuitable because of low precipitation throughout the year or in warm months favorable to reproduction (concentration of precipitation in winter). We hypothesized that *Ae. albopictus* originated in continental Asia under the monsoon climate with distinct dry seasons and hot, wet summer, enabling rapid population growth.

KEY WORDS Culicidae, *Aedes albopictus*, Distribution, Temperature, Precipitation

Aedes albopictus (Skuse), a vector of dengue and chikungunya, has been expanding its geographical range worldwide since the end of the 20th century. Following the rapid expansion in the New World, it has established in southern Europe, central Africa, and the Near East (Benedict et al. 2007, Paupy et al. 2010, Haddad et al. 2012).

Climatic niche models have been used to identify areas at risk of *Ae. albopictus* invasion worldwide now and in the future under changing climate conditions (Benedict et al. 2007, Medley 2010, Fischer et al. 2011). However, these analyses incorporate several or many inter-correlated variables, some of which may not be clearly related to the survivorship and reproduction of *Ae. albopictus* populations. As a result, these analyses may obscure regional differences in climate types that affect suitability for establishment (e.g., oceanic or continental, summer wet or winter wet) as well as the relation between climate and dynamics of *Ae. albopictus* populations (Mogi et al 2012). Sutherst's (1993) ecoclimatic index was unique in that climate suitability for *Ae. albopictus* was evaluated by the population performance under local climate conditions, but this composite index had the same shortcomings noted above. Simple methods that can evaluate local climate attributes with respect to *Ae. albopictus* population dynamics could provide a useful addition to the more complex models described above (Sutherst 1993, Benedict et al. 2007, Medley 2010, Fischer et al. 2011). For example, we previously proposed a simple thermal suitability index (TSI) to delineate the northern limit of *Ae. albopictus'* distribution. Analyses with TSI revealed that thermal conditions around the northern limits vary by thermal continentality, and that, in Asia and North America, the limiting factor is winter coldness, whereas in Europe, under oceanic climate, it is probably insufficient summer warmth (Mogi et al. 2012).

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In this article, we analyze climate conditions at *Ae. albopictus* distribution sites across the species range before the recent worldwide invasions using thermal and aridity–humidity indices descriptive of major natural vegetation types (biomes). Until the start of invasions in recent decades, the geographical range of *Ae. albopictus* (Hawley 1988, World Health Organization [WHO] 1989) remained relatively stable. Invasion into easternmost Hawaii probably occurred around 1900 (Winchester and Kapan 2013), and establishment in westernmost Madagascar occurred by the early 20th century (Mattingly 1953). Therefore, climate attributes in this range can provide a basis to determine whether recent major expansions have been, in part, because of the development of new climatic niches. We also compare climate conditions in the distribution range with those in the neighbor regions, northern and eastern Australia, Western Asia, and Eastern Africa; these regions still remain free from *Ae. albopictus*, despite its invasion into the New World, Europe, Central Africa, and the Near East.

Materials and Methods

Thermal Index. Kira (1976, 1991) created a warmth index (WI) that is highly correlated with thermal vegetation zonation (Table 1). It sums monthly mean temperature ($t°C$) $>5°C$ (a threshold for plant growth); $WI = \sum (t - 5)$, where summation is made over n months in which $t > 5°C$. For analyses of the thermal suitability for *Ae. albopictus* around the northern limit, WI was modified by adopting a threshold temperature of $10°C$ for its reproduction; $WI_{10} = \sum (t - 10)$, where summation is made for n months in which $t > 10°C$ (Mogi et al. 2012). To delineate major climatic zones and vegetation types (biomes) associated with *Ae. albopictus* distribution according to W_{10}, we adjusted the WI criteria for classification (Kira 1976, 1991) to W_{10} values. Since the subtropical zone delineated by WI has a coldest month mean $\geq10°C$, temperate–subtropical and subtropical–tropical

boundaries in WI_{10} were obtained by subtracting 60 ($= 5 \times 12$) from WI criteria (Table 1).

Aridity–humidity Index. The simplest index expressing wetness is annual total precipitation. However, biological effectiveness of precipitation varies by temperature because of faster evaporation at higher temperature. Köppen's climate classification relates annual total precipitation to biomes by values calculated from annual mean temperature using one of three formulae corresponding to three types of precipitation seasonality (summer wet, winter wet, and aseasonal; Kottek et al. 2006, Peel et al. 2007). In reality, however, seasonality of precipitation varies continuously. Therefore, we used the precipitation–effectiveness index (PE) of Thornthwaite (1931, 1933) because it uses all the monthly data without pre-categorization of precipitation seasonality, and can explain major vegetation types as well as Köppen's method (Kira 1976). Effectiveness of precipitation, defined as a precipitation/evaporation ratio, was expressed as a function of precipitation and temperature (as evaporation depends on temperature), and multiplied by 10 to avoid decimals. The original equation is $PE = 115 \sum \{p/(t - 10)\}^{10/9}$, where p = monthly total precipitation in inch, t = monthly mean temperature in Fahrenheit, and summation is made across 12 mo. For precipitation in mm and temperature in °C, it was converted to $PE = 1.645 \sum \{p/(t + 12.2)\}^{10/9}$. PE values, expressed as integers, are related to the aridity–humidity series of vegetation types (Table 1).

Following the methods described by Thornthwaite (1931), minimal t was set to $28.4°F$ ($-2°C$; below which precipitation effectiveness for plants remains the same until melting), and monthly maximal PE was set to 40 (precipitation effectiveness for plants remains the same above this value). Each of the limitations was applied only 4 (-4.6, -4.3, -3.1, and $-2.1°C$) and 3 (43, 42, and 41 monthly PE) times of the 1,932 cases (161 sites $\times$ 12 mo). Hereafter, PE indicates annual PE, unless explicitly designated as "monthly PE."

Table 1. Warmth index (WI and WI_{10}) and PE for climate classification

Index	Original usage[a]			Different usage in this article[b]
	Value	Climate zone	Vegetation	
WI	45–85	Cool temperate		
	85–180	Warm temperate		<120 in WI_{10}
	180–240	Subtropical		$120\sim180$ in WI_{10}
	>240	Tropical		>180 in WI_{10}
PE	0–15	Arid	Desert[c]	
	16–31	Semiarid	Steppe	
	32–63	Subhumid[d]	Savannah[d]	
	64–127	Humid	Forest[e]	
	≥128	Wet	Rain forest[e]	Zone: Perhumid[f]

[a] WI, Kira (1976, 1991) but omitting polar and subpolar zones; PE, Thornthwaite (1931).
[b] For WI_{10} and its range, see text.
[c] Deserts may have ephemeral forbs and short shrubs but lack continuous vegetation.
[d] Naming of vegetation under subhumid 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.
[e] In 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 perhumid zones.
[f] Followed Kira (1977), as it is clearer than "wet".

Northern Limits of *Ae. Albopictus*. Details of analysis of the northern distribution limits of *Ae. albopictus* can be found in the study by Mogi et al. (2012). Briefly, WI_{10} values around the northern limits vary by thermal continentality (the degree of seasonal temperature variations), whereas the TSI for *Ae. albopictus* is independent of continentality, and delineates the northern distribution limit; $TSI = WI_{10}/CI_{10}$, where the coldness index, $CI_{10} = \sum(10 - t)$ and summation is made over n months in which $t < 10°C$. Thus, TSI indicates warmth during the reproductive season (monthly means $> 10°C$) relative to the coldness during the overwintering season (means $< 10°C$). When $TSI < 1$, establishment is impossible. In Asia and North America, establishment is possible when $TSI > 1$. However, it remains unresolved whether $TSI > 1$ always assures thermal suitability under a highly oceanic climate (hottest monthly mean $< 20°C$) such as in part of Europe. Such a climate is absent from the lowlands of Asia and North America, and it is yet to be determined whether absence of established populations of *Ae. albopictus* north of the Alps, despite repeated introductions (European Centre for Disease Prevention and Control [ECDC] 2009, Becker et al. 2013), indicates climate limitation or presence of other suppressive factors.

For sites where WI_{10} is < 60, we examined thermal suitability with both TSI and thermal continentality. Thermal continentality was evaluated by Conrad's continentality index (CCI; Hela 1953); $CCI = 1.7R/\sin(A + 10) - 14$, where $R =$ difference between means of hottest and coldest months, $A =$ latitude. CCI takes smaller values with increasing oceanity (smaller seasonal variations due to milder summer and winter). At the *Ae. albopictus* distribution sites in the northern temperate zone, approximate CCI ranges were 45–60 in China, 35–50 in North America, 35–45 in Japan, and 25–35 in Europe.

Distribution Data. We included into the analyses sites with *Ae. albopictus* records spanning the range from Hawaii through Madagascar. Sites within this range with records only after the start of the worldwide invasion (insofar as we could find) were not excluded unless the occurrence was temporary without establishment. In the greater part of the native range, *Ae. albopictus* is a common pest. Therefore, its distribution is often described in general terms (e.g., "widely distributed") or by states or provinces without specific collection sites. Site-specific, chronological distribution records are rarely available. For example, the absence of records in northern Japan, until recently, was probably because of insufficient surveys (Mogi and Tuno 2014). Low-density persistence or temporary occurrence (especially when repeated introductions are frequent without geographical isolation) could not be distinguished from limited collection information at the periphery of the distribution. Even though recent records indicate new invasions (e.g., Tonga), they did not result from increased favorableness of climate but from increased opportunities of transportation and establishment following the dramatic increase in urbanization and international trade (Guillaumot et al. 2012).

The *Ae. albopictus* distribution maps by Hawley (1988) and WHO (1989) are identical except that the former includes Korea, central Japan, northern New Guinea, New Britain, and Solomon Islands. We followed Hawley (1988) with the addition of northern Japan, northern Pakistan, southern New Guinea, Fiji, and Tonga (supporting literature in Supp Table 1 [online only]). Shenyang and Chaoyang, northeast China, also outside Hawley's range but with distribution records, were excluded because temporary occurrence due to winter coldness was evident (Mogi et al. 2012).

To cover the whole range from Hawaii through Madagascar, we divided the earth's surface into sampling quadrats of 5° (the starting point 0°) in latitudes and longitudes. Although the quadrats vary in sizes (the arc at 40°N is ~77% of the arc along the equator) and land ratios (100% to a few oceanic islands), this partition served to cover the whole distribution range and minimize the bias due to regional differences in intensity of mosquito surveys and reports. For each quadrat, we tried to find at least two sites with *Ae. albopictus* records and climate data recorded at weather stations. Distances between sites were generally > 200 km both within and between quadrats, a distance above which climate may be a dominant factor explaining species distributions (Pearson and Dawson 2003). However, these rules were applied flexibly to include different climate conditions, e.g., due to altitudinal differences, despite short horizontal distances. In total, 161 sites were included in the analyses.

Ae. albopictus is common in habitats disturbed by humans, including secondary forests (Hawley 1988). However, it is absent or uncommon in undisturbed rain forests in Singapore (Colless 1957), Malaya (Macdonald 1957), the Ryukyus (Miyagi and Toma 1980), and temperate Japan (Eshita and Kurihara 1979) in eastern Asia, and there is no report for areas where its occurrence is limited to primary forests. Records from forests, either primary or secondary, indicate that *Ae. albopictus* occurs in nearby disturbed sites relative to weather station locations. Its occurrence together with humans was a major assumption underlying our analyses.

Climate Data. We used means for specified periods in the 20th century; means within 1951–1990 were available at 86% of sites. The primary data sources used were Climate Normals 1961–1990, World Data Center for Meteorology (http://gosic.org/wdcmet/climate-world, accessed 3 April 2015), National Astronomical Observatory (NAO; 1994), World Weather Information Services, World Meteorological Organization (http://worldweather.wmo.int/en/region.html?ra=2, accessed 3 April 2015), and Worldclimate (http://www.worldclimate.com, accessed 3 April 2015). When only monthly mean minimal and maximal temperatures were available, they were averaged (Arguez et al. 2012). Data periods were the same or overlapping between temperature and precipitation. Longitudes, latitudes, and altitudes of weather stations generally followed Global Historical Climatology Network (GHCN-
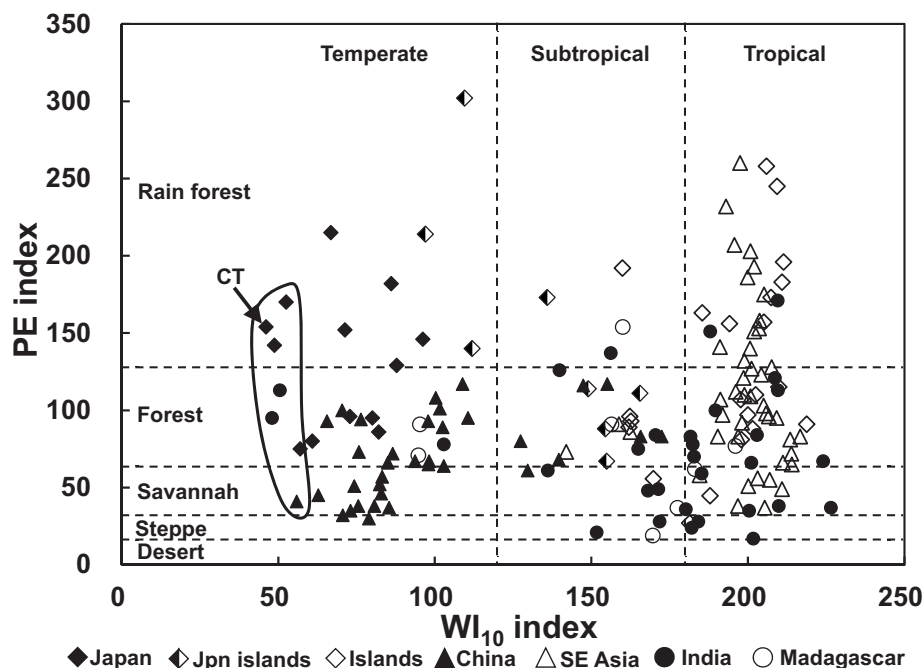
Fig. 1. Warmth index (WI_{10}) and PE at sites where *Ae. albopictus* was reported. For indices WI_{10} and PE and their zonation, see the text and Table 1. Temperate sites ($WI_{10} < 120$) are within the warm temperate zone except for Kamaishi, northern Japan (indicated with CT), which fell into the cool temperate zone (confirmed by WI). Seven sites with $WI_{10} < 60$ are enclosed by a line (detailed conditions in Table 2). Japan, temperate main islands; Japan islands, temperate and subtropical islands east or south of the main islands; Islands, islands from Hawaii through Réunion except for those otherwise stated; China, China, Korea, Taiwan, Hong Kong; SE Asia, from Myanmar through Papua New guinea including New Britain; India, India, Bangladesh, Nepal, Sri Lanka, and Pakistan. All names indicate regions.

Monthly) version 2 (http://www.ncdc.noaa.gov/ghcnm/v2.php, accessed 3 April 2015).

For the neighbor ranges without *Ae. albopictus* (the northern and eastern coasts of Australia, Western Asia, and the eastern coast of Africa), climate data were collected without assuming geographical quadrats.

Material Presentation. Distribution and climate data sources, monthly and annual mean temperature and precipitation, locations of weather stations (longitudes, latitudes, and altitudes), TSI, WI_{10}, and PE were presented in Supp Table 1 [online only] and Supp Table 2 [online only].

Results

Climates in the Distribution Range. The sites with *Ae. albopictus* covered diverse climates. In total, 161 populations of *Ae. albopictus* were confirmed as established at sites where the WI_{10} index ranged from 46.1 to 226.5, and the PE index ranged from 17 to 302 (Fig. 1, Supp Table 1 [online only]).

Along the temperature (W_{10}) gradient, the habitat ranged from the hottest part of tropics through the warmest part of the cool–temperate zone. WI_{10} was >220 in Madurai and Chennai, southern India, whereas it was <60 at a few sites in the Far East

temperate zone and also in Mukteshwar and Shimla, both the Indian highlands (western Himalaya; Table 2).

Along the aridity–humidity gradient, the habitat ranged from the perhumid, rain forest zone through the semiarid, steppe zone, but no sites fell into the arid, desert zone. This pattern was common from the tropics through the temperate zone. The maximal PE, 302, on Yakushima, a mountainous island (the peak 1,936 m) in the southernmost temperate zone, was followed by 260 (Lae, New Guinea), 258 (Pohmpei) and 245 (Kosrae), both Micronesian islands, and 232 (Kuching, Borneo). The lowest PE was 17 in Jodhpur, western India. The other sites in the semiarid, steppe zone (PE 16–31) were Ajmer (PE 24) and Jaipur (28) in western India, Peshawar (21) and Lahore (28) in northern Pakistan, Toliara (19) in southwestern Madagascar, Shijiazhuang (30) in central China, and Honolulu (27) in Hawaii.

Diverse climates were also evident from other climate indices. Annual mean temperature (Fig. 2A) ranged from 10.4°C in Dalian, northeast China, through 28.9°C in Madurai, southernmost India. Mean temperature of the hottest month (Fig. 2B) was lowest in the two Indian highland sites (Table 2), whereas it was highest in Kota (35.7°C) and Jodhpur (34.0°C), western India, and Raipur (35.0°C), central India. Mild summer and small WI_{10} at the Indian highland sites were attended by high oceanity (both summer and

Table 2. Thermal conditions at sites where $WI_{10} < 60$

Region	Site	Latitude (degree)	Altitude (m)	WI_{10}	TSI[a]	AMT[b] (°C)	No. months >10°C	Hottest month (°C)	Coldest month (°C)	Temp range[c] (°C)	CCI[d]
Within the distribution											
China	Dalian	38.90N	97	55.9	1.1	10.4	6	23.9	−4.6	28.5	50.3
Japan	Kamaishi	39.27N	5	46.1	1.2	10.7	6	22.9	−0.2	23.1	37.8
	Imaichi	36.73N	414	48.1	1.4	11.1	6	22.9	0.0	22.9	39.5
	Akita	39.72N	6	52.5	1.3	11.1	6	24.4	−0.4	24.8	41.3
	Nagano	36.67N	418	57.0	1.4	11.5	7	24.8	−1.2	26.0	46.8
Indian highland	Mukteshwar	29.47N	2,311	48.0	5.9	13.3	9	18.3	6.4	11.9	17.8
	Shimla	31.10N	2,202	50.5	4.6	13.3	9	19.8	2.4	17.4	31.0
Outside the distribution											
Australia	Bairnsdale	37.88S	50	48.5	28.5[e]	13.9	9	18.6	9.0	9.6	8.0
	Canberra	35.30S	577	48.6	4.0	13.0	7	20.4	0.5	19.9	33.6
Iranian highland	Oroomieh	37.53N	1,312	54.6	1.2	10.9	7	23.8	−3.3	27.1	48.5
	Hamedan	35.20N	1,602	57.9	1.2	10.8	7	25.3	−4.6	29.9	57.6

[a] Thermal suitability index.
[b] Annual mean temperature.
[c] Difference of the means between the hottest month and the coldest month.
[d] Conrad's continentality index.
[e] The large TSI value resulted from a small CI_{10} value (the coldest month temperature is close to 10°C).
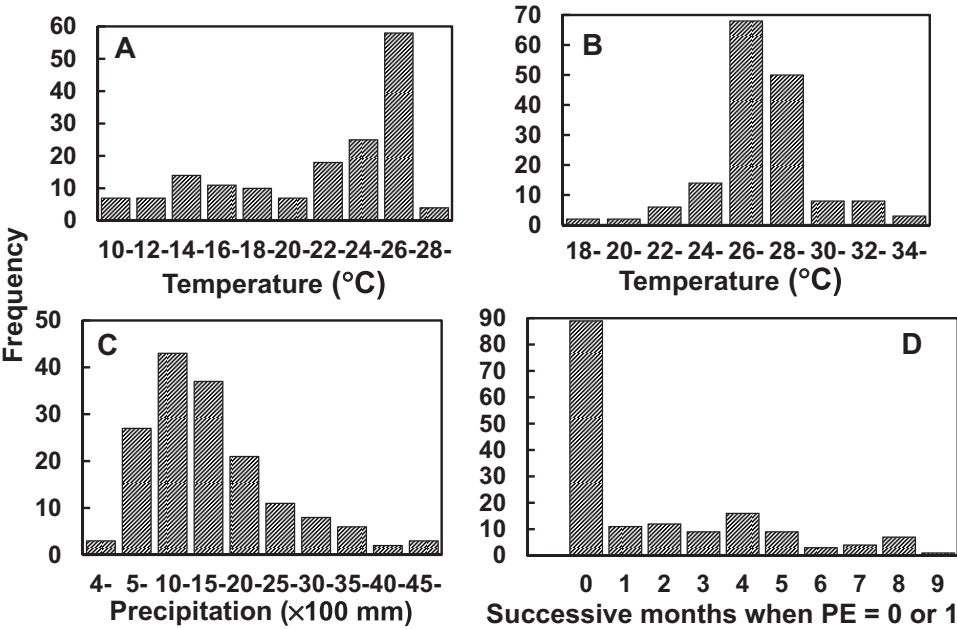

Fig. 2. Frequency distribution of selected climatic variables at sites where *Ae. albopictus* occurred. (A) Annual mean temperature; (B) Mean temperature of the hottest month; (C) Annual total precipitation; and (D) Successive months when PE = 0 or 1.

winter are mild; Table 2). Especially, Mukteshwar was extremely oceanic, with a continentality index value smaller than those observed at the distribution sites in the northern temperate zone worldwide (see Methods).

Annual total precipitation (Fig. 2C) was <500 mm in Peshawar (404 mm) in northwestern Pakistan, Jodhpur (409 mm) in western India, and Toliara (418 mm) in southwestern Madagascar, whereas it was >4,500 mm in Pohmpei (4,769 mm) and Kosrae (4,589 mm), both mountainous Micronesian islands, and Lae (4,688 mm) on the New Guinean coast surrounded by mountain ridges. These three sites were followed by Yakushima, (4,290 mm) with the largest PE (as stated above) because of lower temperature (annual mean 19.1°C) relative to the three tropical sites (26.6–27.5°C). Figure 2D shows the length of periods when monthly PE is successively 0 or 1. If monthly PE = 0 or 1 throughout the year, annual PE is ≤12, falling into the arid, desert zone. At 55% of the sites, monthly PE was ≥2 throughout the year (annual PE ≥24), whereas at
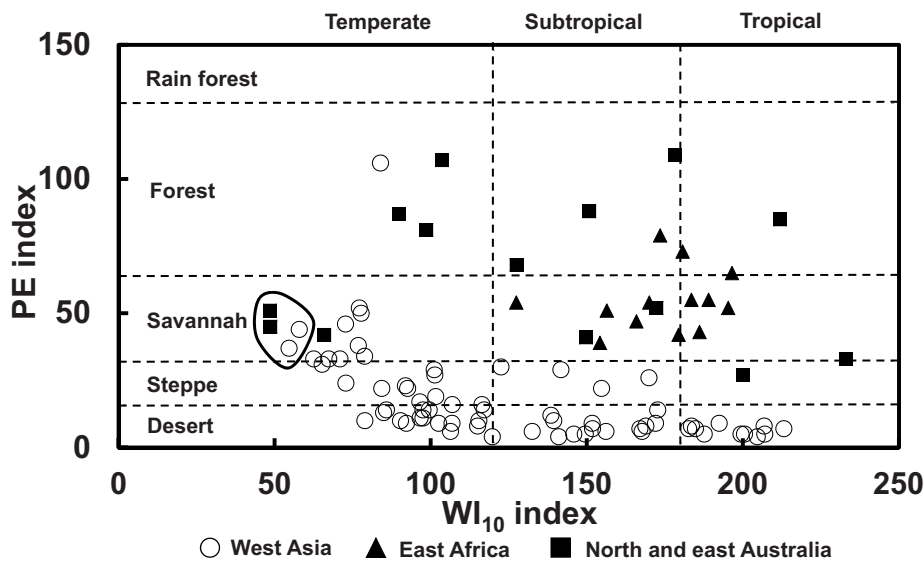
Fig. 3. Warmth index (WI_{10}) and PE at sites where *Ae. albopictus* was absent. For indices WI_{10} and PE and their zonation, see the text and Table 1. Four sites with WI_{10} <60 are enclosed by a line (detailed conditions in Table 2). West Asia, Pakistan excluding a few sites where the *Ae. albopictus* distribution was confirmed, Afghanistan, Iran, Iraq, Tajikistan, Uzbekistan, and Turkmenistan; East Africa, coastal sites from Kenya through South Africa; North and East Australia, coastal sites from Western Australia through Victoria.

Table 3. Climate conditions at sites in Western Asia where *Ae. albopictus* was absent

Group	No. sites	PE^a	Annual precipitation (mm)	No. cold months[b]	PE in warm months[a,c]	Establishment
1	41	8 (4–14)	51–252	0–5	6 (1–14)	Impossible
2	19	29 (16–40)	186–386	3–5	7 (4–12)	Impossible
3	3^d	50 (46–52)	479–568	5	13 (9–13)	Impossible
4	3^e	26 (22–29)	329–401	0–1	23 (18–26)	Barely possible
5	1^f	106	1,322	4	38	Possible

[a] Precipitation effectiveness index; median and range in parentheses.
[b] Cold month: monthly mean temperature <10°C.
[c] Warm month: monthly mean temperature >10°C.
[d] Faiz Abad (northern Afghanistan), Dushanbe (western Tajikistan), Kermanshah (western Iran).
[e] Dezful (westernmost Iran), Kanaqin and Kirkuk (easternmost Iraq).
[f] Rasht (northern Iran).

the remaining 45% of sites, the driest conditions continued for various lengths. The longest period of PE = 0 or 1 was 9 mo, which occurred in Jodhpur, western India, under a combination of high temperature and low precipitation; nevertheless, PE at this site remained in the steppe zone because the precipitation was concentrated in the three months after the hottest months (Supp Table 1 [online only]).

Throughout the distribution sites, there was no seasonal discordance between temperature and precipitation for *Ae. albopictus*. At 118 sites, including the three sites with the smallest precipitation (404–418 mm, see above), monthly mean temperatures remained >10°C, which allowed full exploitation of precipitation. At the remaining 43 sites, where, in winter, monthly means fell <10°C, precipitation was concentrated in summer. There was no site where precipitation was concentrated in cold months (means <10°C). At the three sites in temperate China with the least precipitation among

temperate sites in eastern Asia (Shijiazhuang, Xian, and Beijing; 554–577 mm, PE 30–35), 81–95% of annual precipitation occurred in warm months (>10°C), during which PE reached 25–29. At the other nine Chinese sites, where annual PE fell into the savannah zone, PE values during the warm months were 30–55. Temperate sites in Korea and Japan were wetter than those in China, none falling into the savannah zone.

Climates Outside the Distribution Range. Excluding a few highlands (altitude >2,000 m) where TSI < 1, the analyses included 94 sites where TSI > 1 and annual mean > 10°C.

All the sites were too dry to support rain forests (Fig. 3). Along the northern and eastern coasts of Australia and the eastern coast of Africa, none of the sites fell into the arid, desert zone. Therefore, absence of *Ae. albopictus* from these regions was not attributable to climate conditions alone. Climate conditions in Canberra and Bainsdale, temperate eastern Australia, were
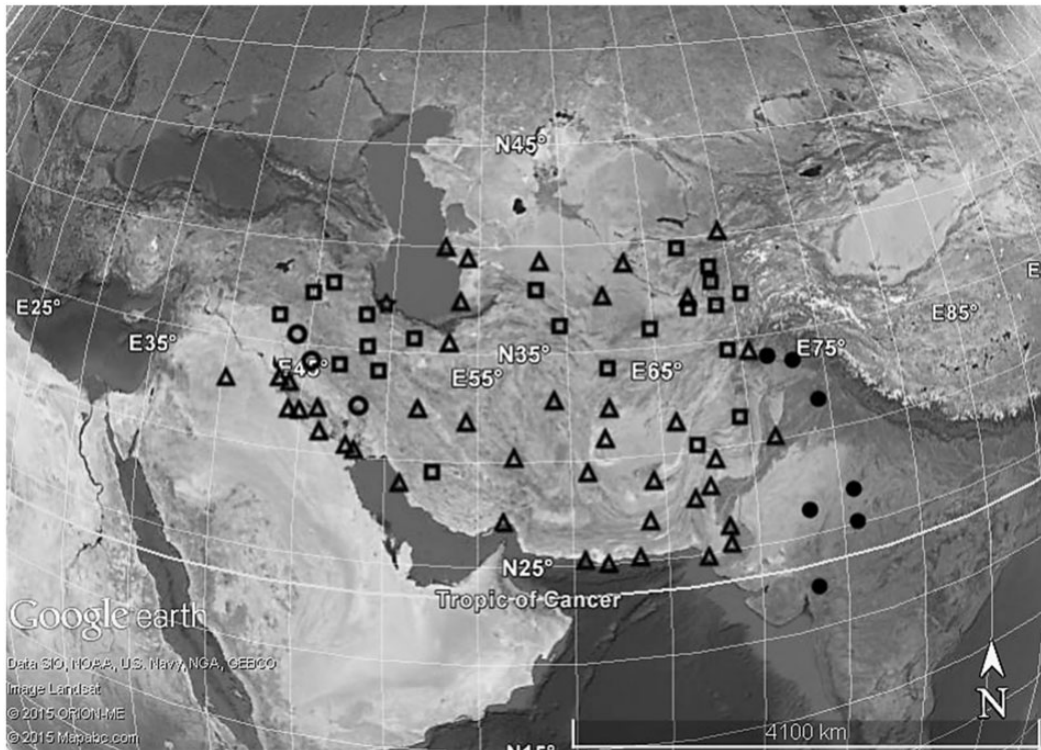
Fig. 4. Aridity–humidity conditions for *Ae. albopictus* in Western Asia. All sites are within the range where establishment is thermally possible (TSI > 1). Closed circle, westernmost distribution sites in India (Jodhpur, Jaipur, Kota, and Vadodara) and Pakistan (Peshawar, Rawalpindi, and Lahore); Open star, establishment is possible (Group 5 in Table 3); Open circle, establishment is barely possible (Group 4); Open square, establishment is impossible because of aridity in warm months (Groups 2 and 3); Open triangle: establishment is impossible because of aridity throughout the year (Group 1). The original color image is in online Supplementary Figure.

similar to those of the Indian highlands in mild summer, small WI_{10}, and high oceanity (Table 2). These sites were cooler than nearby temperate sites, Sydney and Melbourne (WI_{10} values 98.6 and 65.9, respectively, and monthly means >10°C throughout the year), which we regarded as suitable for establishment. The climate suitability of Canberra and Bainsdale will be discussed later.

In Western Asia outside the distribution range, WI_{10} was <60 at the two Iranian highlands where the climate was continental (Table 2). Many sites fell into the arid, desert zone, but wetter sites increased with decreasing warmth at higher latitudes and altitudes. In contrast to the distribution range, precipitation was concentrated in cold months (<10°C) at 69% of sites (46 of 67). Annual PE including cold months could lead to error in the evaluation of climate suitability, so we also calculated PE limited to warm months (>10°C) and recognized five groups with respect to *Ae. albopictus* reproduction (Table 3). At 61% (41 of 67) of sites (Group 1), *Ae. albopictus* establishment was unlikely because precipitation was <252 mm and PE was <14 (desert zone) even including cold months. At 19 sites (Group 2), <40 PE ≥16 (steppe or savannah zones), but PE during warm months was <15 because 42–80% of annual precipitation (<400 mm)

concentrated in cold months except one site with aseasonal precipitation. At these 19 sites from Group 2, *Ae. albopictus* establishment was also unlikely owing to aridity during warm months. The third group, three highlands (altitude 800–1,322 m) with long cold periods, had larger PE and precipitation >400 mm, but PE for warm months was <13 as 56–72% of precipitation was concentrated in cold months. At these sites, although annual PE and precipitation fulfilled the establishment criteria in the distribution range, climate conditions were regarded as being unsuitable owing to the aridity in warm months. The fourth group, three sites in the western foothill of the Zagros mountains, had PE >18 even for warm months because of no (monthly minimum 10.8°C) or only one slightly cold (9.9°C, 8.6°C) month. These sites were regarded as being barely suitable because the annual precipitation was below the minimum in the distribution range. The last site, Rasht (the Caspian Sea coast), had four cold months with 40% of annual precipitation, but PE in warm months was still 38 owing to high annual precipitation (1,322 mm), which was exceptional in Western Asia. This was the only site well-suited for *Ae. albopictus* establishment.

In Western Asia, there was a large area unsuitable for *Ae. albopictus* establishment (Fig. 4). This climate

barrier was attributable to aridity either throughout the year or in warm months owing to concentration of precipitation in cold months.

Discussion

Climate Conditions in the *Ae. albopictus* Distribution Range. The distribution range prior to the start of worldwide invasions covered a moisture gradient from humid, rain forest zones through semiarid, steppe zones and a temperature gradient from tropical through temperate zones if human habitations existed (Fig. 1). Maximal annual temperature and total precipitation observed (Fig. 2A and C) approximate the upper limits of the ranges where the major terrestrial vegetation types (biomes) are distributed (annual mean temperature 30°C and total precipitation 4,500 mm; Begon et al. 1986). This broad climatic range is consistent with a wide range of annual mean temperature and total precipitation at the distribution sites worldwide (Benedict et al. 2007, Fischer et al. 2011).

The possibility that distribution records used in this study include temporary occurrences rather than permanent establishment cannot be excluded. However, reports from hot, dry sites strongly suggest that *Ae. albopictus* can inhabit areas with very low PE values. Of the four sites in Rajasthan State, western India, *Ae. albopictus* was recorded in 1969 in Ajmer (Kalra et al. 1976) and in 1970 and 2007 in Jaipur (Reuben and Panicker1971, Angel and Joshi 2008), but during 2001–2007 in Jodhpur and Kota (Joshi et al. 2006, Angel and Joshi 2008). In this area, indoor surveys of dengue vectors may detect only *Ae. aegypti* (Sharma et al. 1978, Verma et al.1991), whereas surveys focusing on tree holes in parks and gardens sometimes detected more *Ae. albopictus* than *Ae. aegypti*; the adults emerged from tree hole detritus throughout the year in Jodhpur (with the smallest PE, 17; Joshi et al. 2006, Angel and Joshi 2008). Persistence of *Ae. albopictus* at the hot, dry sites in western India is likely if humans create favorable habitats, although evidence from the literature is not conclusive on this issue. The species is also persistent in Toliara (with the second smallest PE, 19, western Madagascar) with eight dry months (Fontenille and Rodhain 1989), and Peshawar (with the third smallest PE, 21, northern Pakistan; Suleman et al. 1993), where precipitation was rather aseasonal with monthly PE 0–3 except for 5 in one month.

Persistence at the Indian highland sites, Mukteshwar and Shimla, requires confirmation because this area is characterized by high oceanity with mild summers as well as small WI_{10} (Table 2). As the thermal suitability for *Ae. albopictus* declines rapidly <20°C (Delatte et al. 2009, ECDC 2009), very mild summers (hottest monthly mean <20°C) may be less suitable for its reproduction than the shorter but hotter summers with equivalent WI_{10}. In western Himalaya, *Ae. albopictus* was reported as a common nuisance up to 1,500 m, and was collected at 1,700, 1,750, 1,800, and 1,900 m (Bhat 1975). It is necessary to clarify altitudinal persistence limits and associated climate conditions in subtropical and tropical zones.

Heterogeneity in the quality of climate data and a spatiotemporal discrepancy between climate observation sites and *Ae. albopictus* collection sites may further complicate efforts to define the marginal limits of *Ae. albopictus* climate tolerance. Nevertheless, even if a few sites have to be excluded, the broad climatic range we demonstrated remains valid.

Concentrated precipitation in warm months in Asia is brought by the Asian summer monsoon that extends from the Indian subcontinent through Japan and Micronesia (Wang and LinHo 2002). In temperate eastern Asia, PE excluding cold months still remained high (conditions at dryer sites in China were mentioned in results), and additional precipitation in winter further favors diapausing eggs by increased humidity (Sota and Mogi 1992b) and snow covers (Hanson and Craig 1995). Annual PE thus was a good indicator to indicate climate suitability for *Ae. albopictus* in the distribution range.

Climates in the Neighbor Regions Without *Ae. albopictus*. A fundamental problem in evaluating climate suitability outside the distribution range is that the distribution criteria may not accurately apply to sites under different types of climates. The problem is evident in previous *Ae. albopictus* niche modelling studies (Benedict et al. 2007, Medley et al. 2010, Fischer et al. 2011) which found that the native range models did not accurately predict the distribution in the invasion ranges, especially for Europe under the oceanic climate.

Our analyses reinforce earlier statements (Mattingly 1953, Hawley 1988) that the absence of *Ae. albopictus* from Eastern Africa and Australia is a mystery. The sites in these regions are relatively dry but definitely within the suitable range except for the two sites, Canberra and Bainsdale, in temperate Australia (Table 2; Fig. 3).

Suitable ranges for establishment in Australia differed among previous studies, depending on models used. Similar to our results, some studies concluded that the northern and eastern coasts were suitable (Sutherst 1993, Russell et al. 2005, an expert knowledge-based model by Fischer et al. 2011), whereas other studies regarded only the northern coast (Benedict et al. 2007) or the eastern coast as being suitable (a statistic based model of Fischer et al. 2011). Consistent with our results, Nicholson et al. (2014) regarded Sydney and Melbourne as being suitable for establishment based on the population growth potential of *Ae. albopictus* reared under temperatures mimicking those sites. However, we could not determine definitely whether the two cooler sites, Canberra and Bainsdale (Table 2; Fig. 3), are suitable or unsuitable, as the thermal conditions were comparable to the Indian highlands where *Ae. albopictus* persistence still needs confirmation (see above). Confirmation of establishment by studies on the population dynamics at sites under oceanic climate such as subtropical and tropical highlands of Asia and volcanic islands (e.g., Réunion, Delatte et al. 2008) or the Appalachian mountains of North America, could help to evaluate climate suitability in temperate Australia as well as part of Europe.

Russell et al. (2005) attributed the species' absence in Australia to diligent surveillance (frequent interceptions at international seaports). The northern coast of Australia is sparsely populated by humans, but this explanation is inapplicable to the eastern coast. Previous studies (Sutherst 1993, Benedict et al. 2007, Fischer et al. 2011) also indicated the suitability of Eastern Africa for *Ae. albopictus* establishment, but without discussion about reasons of the species' absence. In the relatively dry environments in Australia and Africa, environmental factors other than climate, such as human life styles, competitors, and predators, may play vital roles for *Ae. albopictus* persistence (Juliano and Lounibos 2005).

In contrast to results concerning Africa and Australia, our analyses demonstrated the presence of an aridity barrier preventing expansion into Western Asia. Previous studies (Sutherst 1993, Benedict et al. 2007, Fischer et al. 2011) also indicated that Western Asia is unsuitable for establishment of *Ae. albopictus*, but the conditions that prevented the establishment were not specified. Westernmost distribution sites in India and Pakistan (Fig. 4) approximate the western periphery where the summer monsoon brings rains (Wang and LinHo 2002). Further westward, annual precipitation is usually <400 mm (Table 3), and, moreover, concentrates in winter when, at high latitudes and altitudes, monthly means are <10°C. Under this discordance between temperature and precipitation, the annual PE criterion (≥ 16) in the summer monsoon range could mislead analyses because precipitation in cold winter makes the annual PE large and obscures the effects of severe aridity in summer when temperature is suitable for reproduction (Table 3). Therefore, we used PE $\geq$ 16 in warm months (>10°C) as a criterion, but further verification is needed. For example, three highland sites with precipitation >400 mm, which we regarded unsuitable because of warm month aridity (Table 3; Group 3), might be suitable if winter precipitation prepares larval habitats to be habitable through warm months.

Usefulness of Simple Climate Indices. An advantage of the analyses using WI_{10} and PE is that these simple indices can reveal the diversity of local climate attributes with respect to population dynamics of *Ae. albopictus* and suggest specific climatic variables that differ between sites and favor or inhibit the establishment. Even if the criteria derived from the native distribution is not applied directly to regions under different types of climates, the analyses we present establish a basis for hypotheses or predictions with explicit grounds (potentially testable) through careful examination of climate attributes and their relation to population dynamics of *Ae. albopictus*. Those indices can be calculated for any site with climate data. Analyses using simple indices can be a useful addition to the existing models and contribute to better understanding of the relation between climates and the distribution of *Ae. albopictus*.

Climatic Adaptation in *Ae. albopictus*. *Ae. albopictus* has been regarded as a species usually associated with heavy precipitation (Mattingly 1953). In drier environments, it is generally dominated by *Ae. aegypti* geographically (e.g., Fontenille and Rodhain 1989) and at microhabitat levels (Juliano et al. 2002). However, eggs of *Ae. albopictus* are more resistant to desiccation than those of forest species (Sota and Mogi 1992a). The adult of an Indonesian urban population is as resistant to desiccation as sympatric *Aedes aegypti* (L.) (Mogi et al. 1996). A Réunion population of *Ae. albopictus* developed to adults and took blood at constant temperature of 15–35°C, with an optimal temperature for development 29.7°C and the highest intrinsic rate of increase (r) at 30°C; eggs were not laid at 15°C but were laid at 35°C (Delatte et al. 2009). Population performance of temperate *Ae. albopictus* was lower at constant 35°C than 30°C, but not different from tropical *Ae. aegypti* (Farjana et al. 2012). Tolerance to broad temperature and humidity conditions as well as the broad climate range (Figs. 1 and 2) suggests that it originated in habitats subjected to a wide range of temperature, precipitation, and humidity conditions that could have provided it with high genetic and phenotypic plasticity.

The diversity of species of the *albopictus* subgroup is greatest in Indochina and India (Huang 1979), where prevailing natural vegetation is tropical seasonal (monsoon) forests with three to nine dry months (Blasco et al. 1996). The Asian monsoon system has persisted since Miocene with varying intensity (Clift et al. 2008, Wang et al. 2008). Studies on vegetation and faunas in tropical Asia during late Pleistocene suggest that the savannah environment persisted and was even more widespread than now during the glacial periods (Gathorne-Hardy et al. 2002, Hope et al. 2004, Louys and Meijaard 2010).

We hypothesize that *Ae. albopictus* originated in continental Asia, where natural vegetation was seasonal forests under the monsoon climate with distinct dry seasons and hot, wet summer, enabling rapid population growth. This scenario implies that mild oceanic climates would be not "mild" for the species. Genetic analyses of *Ae. albopictus* of eastern Asia detected no evidence of population isolation during the last glacial age (Porretta et al. 2012) despite rain forest fragmentation (Gathorne-Hardy et al. 2002). It must have adapted to human habitations during the recent several thousand years following the expansion of settlement agriculture over the Asian continent (Bird et al. 2004, Gupta et al. 2006).

For outdoor *Ae. albopictus*, genetic changes were essential to expand into the northern temperate region (acquisition of cold-hardy eggs and photoperiod-controlled diapause; Hawley et al. 1987). In contrast, aridity limits may be overcome if humans develop habitations rich with containers to keep water (accessible to the mosquito), discarded containers, trees, and other plants. Plants in yards, parks, orchards, and plantations provide both larval habitats (tree hole, fruit husk, leaf axil, and fallen leaf) and adult sugar sources (nectar and sap) as well as shades ameliorating microhabitat conditions. *Ae. albopictus* also may use indoor habitats (Dieng et al. 2010, Mukhtar et al. 2011). Its persistence in the semiarid, steppe zone without human habitations seems unlikely.

In view of the escalating human power to modify environments and the broad climate tolerance of *Ae. albopictus*, no human habitations may be free from risks of its invasion except for northern regions or highlands beyond its limits of coldness. Even the aridity barrier in Western Asia (Table 3; Fig. 4) could be weakened by development of human habitations favoring the species. In this sense, the Western Asian aridity barrier, as well as conditions of Eastern Africa and northern and eastern Australia, represents relative difficulty rather than impossibility of establishment.

For prediction and prevention of future expansion, it is essential 1) to determine establishment criteria under the oceanic climate, and 2) to understand the genetic variation in heat and desiccation resistance of *Ae. albopictus* and the way humans assist its persistence in hot, dry environments.

Supplementary Data

Supplementary data are available at *Journal of Medical Entomology* online.

Acknowledgments

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