

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

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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	<a href="http://doi.org/10.24517/00050494">http://doi.org/10.24517/00050494</a>

doi: 10.1093/jme/tjx156

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

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#### Footnotes to the first page

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

34

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

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

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

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

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

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

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## Materials and Methods

77

78 **Rationale for comparison.** In most mosquito taxa, species richness is highest in the tropics,  
79 with a few species extending or endemic to the temperate region, justifying the assumption  
80 that tropical populations or species are ancestral to temperate ones with winter diapause (Ross  
81 1964, Bradshaw and Lounibos 1977). This assumption is applicable to the subgenus  
82 *Stegomyia* where a few among  $\approx 130$  species extend their range or are endemic to the  
83 temperate region. Most *Stegomyia* species primarily breed in wild-plant containers such as  
84 tree holes, but a few depend on artificial containers in human habitats, a trait derived  
85 following the development of human settlements.

86 The *albopictus* subgroup (Huang 1972) includes 11 Asian species (Table 1). Of species other  
87 than *Ae. albopictus*, five have lost the ancestral tropical distribution. *Aedes flavopictus*  
88 Yamada covers the subtropics through the cool-temperate region up to 45°N (Tanaka et al.  
89 1979). The three morphological subspecies (*Ae. f. flavopictus* of the temperate region and two  
90 subtropical ones, each of the northern and southern Ryukyu Islands) are genetically well  
91 differentiated (Toma et al. 2002). Similarly, three geographical (temperate, northern and  
92 southern Ryukyus) subspecies in *Aedes japonicus* (Theobald) (Tanaka et al. 1979) are also  
93 genetically distinct (Cameron et al. 2010). This differentiation pattern is consistent with  
94 separation of the three geographical regions since the middle Pleistocene, ≈1 million years  
95 ago (Mya), at the latest (Ota 1998). The remaining four species, tentatively called as the  
96 *galloisi* complex (*Aedes galloisi* Yamada, *Aedes sibiricus* Danilov and Filippova, *Aedes*  
97 *galloisioides* Liu and Lu, and *Aedes neogalloisi* Chen and Chen) are distributed from  
98 highlands of western and central China to the southern sub-polar region up to 55°N (Danilov  
99 and Filippova 1978, Lei 1989, Dong et al. 2010). A phylogenetic study suggests *A. galloisi* to  
100 be a distinct lineage as ancient as the *scutellaris* group (Sota and Mogi 2006).

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

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

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

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

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

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

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

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

152 All of the wild species were recorded from lowlands through highlands (Table 2). Altitudinal  
153 ranges in particular regions are also wide; for *Ae. pseudalbopictus*, 100-2,400 m in Taiwan  
154 (Lien 1978), 320-1,790 m in Sichuan Province, China (Song et al. 1981, see Table S1), and  
155 50-1,250 m in eastern Java (Ramalingam 1974).

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



161 Taiwan. Of 116 stations, 20 (17%) and 45 (39%) were related to 2-4 species and 2-8 sites (all  
162 species inclusive), respectively. For convenience, weather station names and locations were  
163 used as a representative of the distribution sites. The nearest distribution site was within 10,  
164 30, 50, 70, 100, and 169 km for 42 (36%), 61 (53%), 82 (71%), 98 (85%), 110 (95%), and 116  
165 (100%) stations, respectively. The station data, including coordinates, altitudes, distance from  
166 each distribution site, and data sources, are also in Table S1.

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

178 Besides warmth and wetness, thermal continentality (the degree of seasonal temperature  
179 variation) influences dynamics of mosquito populations. Even if the annual mean temperature  
180 is the same (for example,  $15^{\circ}\text{C}$ ), seasonal variation can either be large (the hottest month  
181  $25^{\circ}\text{C}$ , the coldest month  $5^{\circ}\text{C}$ , the difference  $20^{\circ}\text{C}$ ) or small (corresponding values, 20, 10,  
182 and  $10^{\circ}\text{C}$ ). Thermal continentality was expressed by Conrad's continentality index (CCI);  
183  $CCI = 1.7R/\sin(A + 10) - 14$ , where  $R =$  difference between means of hottest and coldest  
184 months,  $A =$  latitude. CCI takes smaller values with increasing oceanity.

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

186 S2.

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

195

196

## Results

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

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

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

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

218 The thermally temperate sites (cumulative summer warmth  $WI_{10} < 120$ ) of the wild species  
219 were mainly tropical and subtropical highlands, and all the sites where  $WI_{10} < 80$  were  $>500$   
220 m (Fig. 1A, B). Of coolest ( $WI_{10} < 70$ ) and northernmost ( $>30^\circ N$ ) sites, three (No. 4, 5, 7) at  
221 the foot of the western Himalayas fit both categories (Table 6). These data indicate that (1)  
222 coolest sites (No. 1-12) were all highlands (1,100-2,500 m) and south of  $30^\circ N$  except the  
223 above-mentioned three (No. 4, 5, 7) at  $31-34^\circ N$ , (2) local warmth in the western Himalayas is  
224 also evident from the lower sites (No. 20, 21, 680-1,200 m) which were warmer than the  
225 lower Chinese sites (No. 13-19, 40-670 m) at equivalent latitudes ( $30-32^\circ N$ ), (3) at the coolest  
226 sites, annual and hottest-month temperatures were also lower than the northernmost sites (No.  
227 13-21), (4) the climate at highland sites ( $>1,500$  m) is oceanic ( $CCI < 30$ ), especially three  
228 sites out of the *Ae. albopictus* range (No. 1-3) and one additional Himalayan site (No. 10)  
229 were extremely oceanic ( $CCI \approx 12-18$ , with hottest months  $\approx 15-20^\circ C$ , coldest months  $\approx 6-8^\circ C$ ,  
230 differences  $\approx 8-12^\circ C$ ), and (5) in contrast, two northernmost lowland sites (No. 14, 17,  
231  $30-32^\circ N$ ,  $<100$  m) (two arrows in Fig. 1A) in eastern China were most continental ( $CCI \approx 50$ ,  
232 hottest months  $\approx 27-28^\circ C$ , coldest months  $\approx 2-4^\circ C$ , differences  $\approx 24-25^\circ C$ ).

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

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

239

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## Discussion

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

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

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

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

274 The Asian monsoon system has persisted during the Quaternary (Wang et al. 2005). Did *Ae.*  
275 *albopictus* originate before the last glaciation (Porretta et al. 2012), or in the postglacial age as  
276 a human inquiline like the domestic form of *Ae. aegypti* (Brown et al. 2014, Crawford et al.  
277 2017)? Pre-mating ethological isolation (choice of conspecifics) between *Ae. albopictus* and  
278 the wild species (*Ae. pseudalbopictus*, *Ae. seatoi*) and between the wild species (McLain and  
279 Rai 1986) supports the former. Similar levels of pre-mating isolation (high, but not perfect)  
280 resulted from geographical isolation since 2-10 Mya (based on estimates of island separation)  
281 among the *scutellaris* subgroup species (distributed from Indochina through western Pacific  
282 islands) (McLain et al. 1985), and 0.15-6 Mya (based on estimates from genetic divergence)  
283 between two *Drosophila* flies (Jennings and Etges 2010). These estimates do not indicate the  
284 minimum duration for establishment of pre-mating isolation but favor allopatric divergence  
285 among the *albopictus* subgroup species preceding to the postglacial sympatry.

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

291 Wild (ancestral) populations of *Ae. albopictus* coexist with the wild species in reserve forests  
292 on the Deccan Plateau (Thenmozhi et al. 2012) and along the coast (Rajavel and Natarajan  
293 2008) in India, and in pre-development forests in Sri Lanka (Amerasinghe and Munasingha  
294 1988b). Information from subtropical southern China is variable. It is said to be dominant at  
295 wild and cultivated bamboo forests in Yunnan Province (Dong et al. 2010), but Lu et al.  
296 (1997) regard it as a semi-wild species inferior to *Ae. pseudalbopictus* at forests far from  
297 houses. In Guizhou Province, it is absent from forests >2 km apart from houses (Chen 1987).  
298 In a nature reserve of Guizhou Province, *Ae. albopictus* was recorded together with the two  
299 wild species (Wang et al. 2012), but this reserve includes agro-ecosystems supporting >4,000  
300 residents. In the subtropical Ryukyu Islands, Japan, *Ae. albopictus* is absent from natural  
301 forests that are separated from developed sites (Miyagi and Toma 1980, Toma and Miyagi  
302 1981). Altogether, *Ae. albopictus* occurs more often in forested habitats with wild species in  
303 tropical rather than subtropical localities. Thus, available information reinforces the tropical  
304 origin of *Ae. albopictus*.

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

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

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

311 considering the compensation of winter mortality by summer reproduction. Mogi et al. (2012)  
312 also assumed that the northern limit depends on the balance between summer reproduction  
313 and winter mortality instead of simple abiotic thresholds (for example, coldest-month  
314 temperature). This approach is common in analyzing the relation between climate and insect  
315 distribution under a seasonal climate. For example,  $R_y$  (year-long replacement rate) of  
316 Bradshaw et al. (2004) and  $\lambda$  (annual population growth rate) of Crozier and Dwyer (2006)  
317 both imply the distribution limits may be affected by biotic as well as abiotic factors  
318 influencing summer reproduction or winter mortality. More generally, the classical niche  
319 concept distinguishes between a fundamental niche (a range delineated by physical conditions,  
320 including climate, and essential resources but excluding biotic interactions) and a realized  
321 niche (a narrower range under the presence of competitors and natural enemies) (Hutchinson  
322 1978, Begon et al. 1986). Therefore, even if climate remains unchanged, apparent climatic  
323 limits can either advance or retreat following habitat shifts or environmental changes that  
324 increase or decrease the availability of essential resources and the magnitude of species  
325 interactions, and thereby disturb an existing balance between reproduction and mortality.  
326 Indeed, insect populations around northern limits persist in particular habitats more suitable  
327 for population growth than the other habitats (Oliver et al. 2009), implying the changing  
328 northern limits following the acquisition or loss of favorable habitats.

329 Water-holding containers and blood-meal hosts are essential resources for *Ae. albopictus* and  
330 are abundant in human habitats. Although the impact of these resources has not been  
331 quantitatively compared between natural and human habitats, it could be very large,  
332 especially under historical conditions before the development of water services and  
333 mosquito-proof houses. This view is well illustrated by persistence of *Aedes aegypti* (L.) at a  
334 small port in central Kyushu during 1944-1952 under abundant concrete tanks for fire  
335 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



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

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

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

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

386 **Impacts under northern temperate climate.** The wild species occur widely at tropical and  
387 subtropical highlands, and some species appear adapted to the highland climate better than *Ae.*  
388 *albopictus*. In Taiwan, *Ae. pseudalbopictus* reaches higher (2,400 m) than *Ae. albopictus*  
389 (1,000 m) (Lien 1978), while lowland northern limits in China are 32 and 40°N, respectively.  
390 This discrepancy indicates that adaptation to cool, oceanic climate at southern highlands is not  
391 enough for the expansion deep into temperate lowlands under continental climate. This is  
392 consistent with (1) the difference of northern-temperate climate from oceanic  
393 southern-temperate and tropical-highland climate (Troll 1960, Darlington 1965), and (2) the  
394 hemispherical (northern vs. southern) difference in primary overwintering strategies of insects  
395 (Chown et al. 2004).

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

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

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

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

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

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

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

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

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

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

449

#### 450 **Acknowledgments**

451

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

453

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### Figure legend

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

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**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 ( $>30^\circ N$ ) 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 <sup>1</sup>					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>		+ <sup>2</sup>				Forest
<i>Ae. neogalloisi</i>			+ <sup>2</sup>			Forest
<i>Ae. galloisi</i>			+ <sup>2</sup>	+	+	Forest
<i>Ae. sibiricus</i>					+	Forest

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

<sup>2</sup>Highland; *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 <sup>1</sup>	Altitude (m) <sup>2</sup>	
		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) <sup>3</sup> , 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

<sup>1</sup>India and China indicate the continental part, respectively. \*, site unspecified within the region.

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

<sup>3</sup>Jiangsu\*, Anhui, Zhejiang, Fujian, Jiangxi, Hunan\*, Guizhou, Sichuan, Yunnan, Guangxi, Guangdong\*

Table 3. Thermal Index (WI<sub>10</sub>) and aridity-humidity index (PE) criteria for climate classification.

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

<sup>1</sup>See 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.

<sup>2</sup>Deserts may have ephemeral forbs and shrubs but lack continuous vegetation.

<sup>3</sup>Naming 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.

<sup>4</sup>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 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 <sup>1</sup>	WI <sub>10</sub>	AMT <sup>2</sup> (°C)	ATP <sup>3</sup> (mm)	No. Dry Month <sup>4</sup>	Species (No. sites) <sup>5</sup>
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)

<sup>1</sup>Aridity-humidity index.

<sup>2</sup>Annual mean temperature.

<sup>3</sup>Annual total precipitation.

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

<sup>5</sup>pse, *Ae. pseudalbopictus*; sub., *Ae. subalbopictus*; nov, *Ae. novalbopictus*; No. sites were shown when distribution sites  $\geq 2$ .

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

Region <sup>1</sup>	Station <sup>2</sup>	Latitude (°N)	Altitude (m)	PE <sup>3</sup>	WI <sub>10</sub> <sup>4</sup>	AMT <sup>5</sup> (°C)	ATP <sup>6</sup> (mm)	No. Dry Mo <sup>7</sup>	Species (No. sites) <sup>8</sup>
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

<sup>1</sup>C, central; S, southern; N, northern; SW, southwestern.

<sup>2</sup>Stations with asterisks are out of the *Ae. albopictus* range.

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

<sup>4</sup> “T” indicates tropical climate, while others are subtropical climate.

<sup>5</sup> Annual mean temperature.

<sup>6</sup> Annual total precipitation.

<sup>7</sup> In dry months, monthly PE=0 or 1.

<sup>8</sup> nov, *Ae. novalbopictus*; sub., *Ae. subalbopictus*; pse, *Ae. pseudalbopictus*; sea, *Ae. seatoi*; No. sites were shown when distribution sites  $\geq 2$ .

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 <sup>1</sup>	Region	Station <sup>2</sup>	Latitude (°N)	Altitude (m)	$WI_{10}$	AMT <sup>3</sup> (°C)	Hottest Mo (°C)	Coldest Mo (°C)	Range <sup>4</sup> (°C)	CCI <sup>5</sup>	Species (No. sites) <sup>6</sup>
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 <sup>1</sup>	Region	Station <sup>2</sup>	Latitude (°N)	Altitude (m)	WI <sub>10</sub>	AMT <sup>3</sup> (°C)	Hottest Mo (°C)	Coldest Mo (°C)	Range <sup>4</sup> (°C)	CCI <sup>5</sup>	Species <sup>6</sup>
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

<sup>1</sup>C, coolest distribution sites where WI<sub>10</sub> < 70; N, northernmost distribution sites >30°N.

<sup>2</sup> Stations with asterisks are out of the *Ae. albopictus* range.

<sup>3</sup>Annual mean temperature.

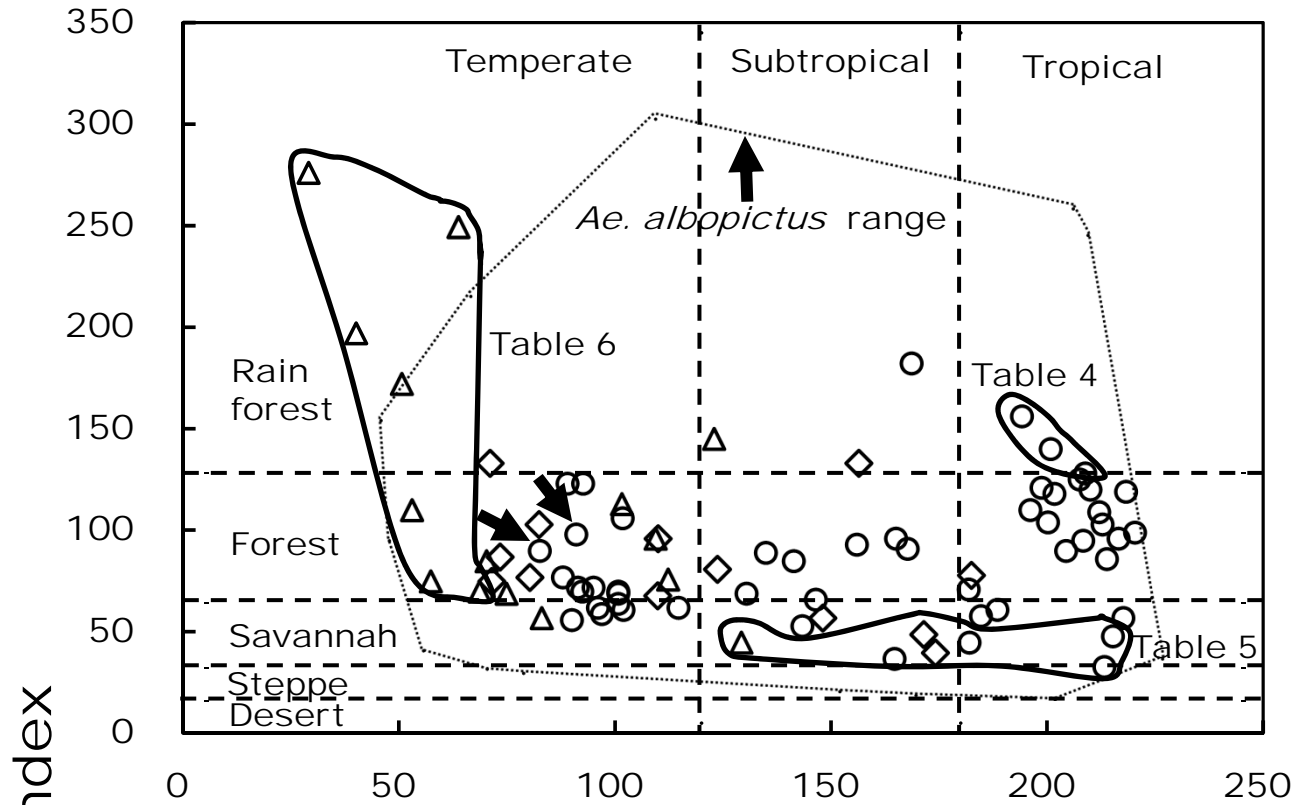
<sup>4</sup>Difference between hottest month mean and coldest month mean.

<sup>5</sup>Conrad's continentality index.

<sup>6</sup>pse, *Ae. pseudalbopictus*; sub., *Ae. subalbopictus*; pat, *Ae. patriciae*; nov, *Ae. novalbopictus*; No. sites were shown when distribution sites  $\geq 2$ .



(A) *Ae. pseudalbopictus*



(B) Other four species

