# 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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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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7                            **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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76                            **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 ≈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 subtopics 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

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differentiation (Huang 1972, Tanaka et al. 1979, Lu et al. 1997). The tropical populations are

fully inter-fertile with temperate populations that overwinter as diapause eggs (pharate larvae)

(O'Donnell and Armbruster 2009). These facts indicate that winter diapause in *Ae. albopictus*

evolved independently and later than the species discussed above. In the *albopictus* subgroup,

only *Ae. albopictus* is well adapted to artificial containers in human habitats.

The remaining five *albopictus* subgroup species, *Aedes novalbopictus* Barraud, *Aedes*

*patriciae* Mattingly, *Aedes pseudalbopictus* (Borel), *Aedes seatoi* Huang, and *Aedes*

*subalbopictus* Barraud, have maintained their ancestral tropical distribution (Huang 1972).

They breed primarily in tree holes and bamboo stumps and bite humans in forests (Harrison et

al. 1972, Amerasinghe and Munasingha 1988a, Rajavel and Natarajan 2008, Dong et al. 2010).

In Thailand, *Ae. seatoi* is said to be semi-domestic due to occurrence in bamboo stumps

around rural villages, but rarely breeds in jars near houses (Harrison et al. 1972). For

convenience, we call these five non-domesticated species collectively "the wild species".

Phylogenetic relations among *Ae. albopictus* and the wild species are unknown. However,

the *albopictus* subgroup is well defined based on adult morphology (Huang 1972). In genetic

analyses including other *Stegomyia* species, *Ae. albopictus* forms a clade with *Ae.*

*pseudalbopictus* and *Ae. subalbopictus* (Wang et al. 2012) and with *Ae. seatoi* (Pashley and

Rai 1983), indicating their evolutionary affinity. Ecologically, *Ae. albopictus* shares an

ancestral tropical distribution with the others but has unique derived traits (widespread

temperate distribution and human dependence). The comparison between *Ae. albopictus* and

the wild species could provide insights into the impact of domestication on climatic niches.

**Distribution data.** To characterize the whole distribution range of the wild species, we

assembled distribution data regardless of information on population density. Distribution

records span ≈90 years (since 1928 when *Ae. pseudalbopictus* was described), during which

administrative systems, place names, and English expressions have been changed extensively.

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 (≈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 (Rattanarithikul 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

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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 $t > 10$ºC. Thus, $WI_{10}$ is a simple

170    indicator of cumulative warmth above 10ºC. $WI_{10}$ 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 (°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°C ), seasonal variation can either be large (the hottest month

181    25°C , the coldest month 5°C , the difference 20°C ) or small (corresponding values, 20, 10,

182    and 10°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 ≤ 200 m) distribution sites in

191  eastern Asia reach the border with the cool-temperate region (≈40°N, $WI_{10} \approx 45$), and CCI

192  values in temperate China and Korea are 45-60 (highly continental, hottest months 25-28°C,

193  coldest months often < 0°C, the differences usually > 25°C) (Mogi et al. 2012 and its

194  Appendix).

195

196                                                   **Results**

197

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

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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°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°N except the

223    above-mentioned three (No. 4, 5, 7) at 31-34°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°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≈12-18, with hottest months≈15-20°C, coldest months≈6-8°C,

230    differences≈8-12°C), and (5) in contrast, two northernmost lowland sites (No. 14, 17,

231    30-32°N, <100 m) (two arrows in Fig. 1A) in eastern China were most continental (CCI≈50,

232    hottest months≈27-28°C, coldest months≈2-4°C, differences≈24-25°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

240 **Discussion**

241

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

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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, Ry (year-long replacement rate) of

316    Bradshaw et al. (2004) and λ (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).

14

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. albopictu*s 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 (Sota1993) and varies by

385 habitats in the adult (Mogi et al. 1996b), so genetic changes under semiarid climate are likely.

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

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

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

17

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 ≈18°C) (Makiya 1968)

422 and Yixing (31°N, ≈16-17°C) (Yang 1988). In subtropical Okinawa (26°N, ≈22°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, ≈24°C) population has

425 diapause-related genes (Chen et al. 2015), but photoperiodic diapause is absent in Yonakuni

426 and Ishigaki islands (24°N, ≈24°C) (Higa et al. 2007) as well as in Hainan Island (20°N,

427 ≈24°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**

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454                              **References Cited**

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

**Table legends**

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712　**Table 1.** Species of the *albopictus* subgroup of the *scutellaris* group of *Aedes* (*Stegomyia*) in

713　　Asia, arranged approximately from the ancestral tropical distribution to the derived

714　　northerly distribution.

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

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

717　　classification.

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

719　　128).

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

721　**Table 6.** Distribution sites where summer is coolest ($WI_{10} < 70$) and/or at highest latitudes

722　　(>30°N) arranged by the increasing order of $WI_1$

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

| Species | Distribution[1] | | | | | Habitat |
|---|---|---|---|---|---|---|
| | T | ST | SWT | NWT | CT | |
| *Ae. novalbopictus* | + | + | | | | Forest |
| *Ae. patriciae* | + | + | | | | Forest |
| *Ae. seatoi* | + | + | | | | Forest |
| *Ae. subalbopictus* | + | + | | | | Forest |
| *Ae. pseudalbopictus* | + | + | + | | | Forest |
| *Ae. albopictus* | + | + | + | + | | Human-made |
| *Ae. flavopictus* | | + | + | + | + | Forest |
| *Ae. galloisioides* | | +[2] | | | | Forest |
| *Ae. neogalloisi* | | | +[2] | | | Forest |
| *Ae. galloisi* | | | +[2] | + | + | Forest |
| *Ae. sibiricus* | | | | | + | Forest |

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

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

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

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

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

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

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

[1]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.

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

[3]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.

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

[1]Aridity-humidity index.

[2]Annual mean temperature.

[3]Annual total precipitation.

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

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

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

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

[3] Aridity-humidity index. "S" indicates semiarid, steppe climate, while others are sub-humid, savannah climate.

[4]"T" indicates tropical climate, while others are subtropical climate.

[5]Annual mean temperature.

[6]Annual total precipitation.

[7]In dry months, monthly PE=0 or 1.

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

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

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

| No. | Category[1] | Region | Station[2] | Latitude (°N) | Altitude (m) | $WI_{10}$ | AMT[3] (°C) | Hottest Mo (°C) | Coldest Mo (°C) | Range[4] (°C) | CCI[5] | Species[6] |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 14 | N | E. China | Huoshan | 31.40 | 88 | 82.8 | 15.2 | 27.4 | 2.4 | 25.0 | 50.3 | pse |
| 15 | N | W. China | Liangping | 30.68 | 455 | 88.1 | 16.6 | 26.8 | 5.7 | 21.1 | 41.0 | pse |
| 16 | N | W. China | Langzhong | 31.58 | 385 | 90.2 | 16.8 | 26.6 | 6.1 | 20.5 | 38.5 | pse |
| 17 | N | E. China | Hangzhou | 30.23 | 43 | 91.2 | 16.5 | 28.4 | 4.3 | 24.1 | 49.4 | pse |
| 18 | N | W. China | Dazhou | 31.20 | 344 | 92.6 | 17.0 | 27.5 | 6.1 | 21.4 | 41.2 | pse |
| 19 | N | W. China | Wanzhou | 30.81 | 189 | 100.9 | 18.0 | 28.3 | 7.0 | 21.3 | 41.4 | pse |
| 20 | N | W. Himalaya | Dharmsala | 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 |

[1]C, coolest distribution sites where $WI_{10} < 70$; N, northernmost distribution sites >30°N.

[2] Stations with asterisks are out of the *Ae. albopictus* range.
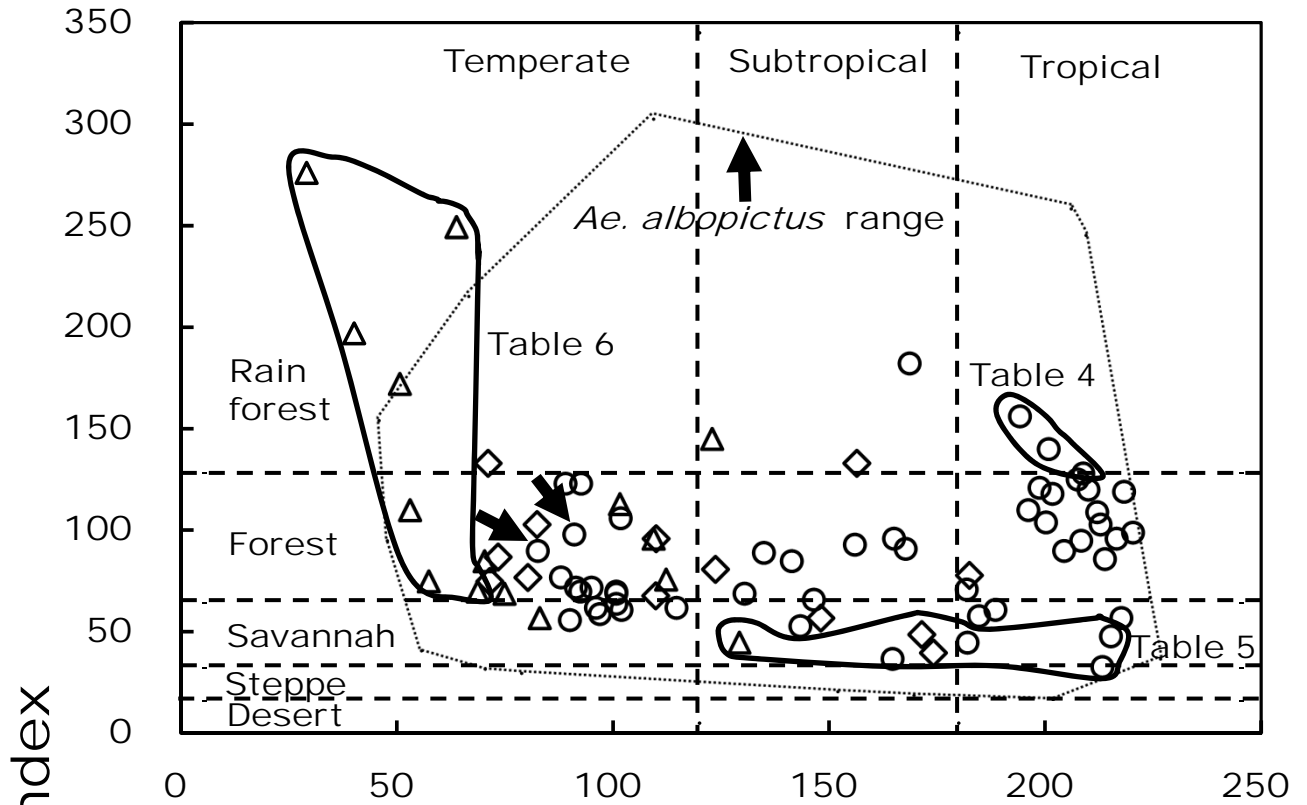
[3]Annual mean temperature.

[4]Difference between hottest month mean and coldest month mean.

[5]Conrad's continentality index.

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

**(A) *Ae. pseudalbopictus***

**(B) Other four species**

WI₁₀ index