Analyses of the Northern Distributional Limit of *Aedes albopictus* (Diptera: Culicidae) With a Simple Thermal Index

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ABSTRACT Worldwide invasion of *Aedes albopictus* (Skuse) has become a serious concern in vector control. In temperate regions, an important goal has been to predict northern range limits after new introductions or global climate change. We propose a simple thermal suitability index (TSI) that can be calculated from monthly mean temperatures and may predict the northern distributional limits of *Ae. albopictus*. Analyses of known distributions revealed that TSI yields a common criterion (TSI = 1) below which establishment is thermally prohibited throughout the northern hemisphere. However, temperature conditions around northern limits differ among regions, depending on thermal continentality (the degree of seasonal temperature variation). Thermal continentality is high on the Asian Continent, intermediate in North America and Japan, and low (i.e., oceanic) in Europe. On the Asian Continent, there may be maximal winter coldness above which establishment is prohibited irrespective of summer reproduction. In Europe, establishment is possible under summer warmth lower than in other regions but there may be minimal summer warmth below which establishment is difficult despite high winter survival during mild winters. Among the thermal indices that have been commonly used as establishment criteria, the annual mean temperature of 10°C proved to be a common criterion irrespective of thermal continentality, whereas coldest month means and warmth during the reproductive season (often expressed as accumulated degree-days above 11°C) are strongly influenced by thermal continentality. Although annual mean temperatures can be a practical criterion, TSI was more informative in evaluating thermal suitability for this species.

KEY WORDS Culicidae, *Aedes albopictus*, northern limit, temperature, continentality

Since the late 20th century, the worldwide invasion of *Aedes albopictus* (Skuse) by transoceanic traffic of used tires and ornamental plants such as lucky bamboo has been a serious and continued threat to public health (e.g., European Centre for Disease Prevention and Control [ECDC] 2009). Risks of further spread will continue or increase, because of the presence of potentially suitable regions, global climate change that may expand suitable ranges northward and southward, as well as increasing invasion opportunities.

The performance of mosquito populations in new environments is influenced by many factors such as temperature, humidity, precipitation (amounts and seasonal patterns), and availability of essential resources such as larval habitats, adult resting habitats, bloodmeal hosts, and sugar sources. These and other factors collectively determine the establishment risk. However, *Ae. albopictus* uses a variety of small containers (often primarily those generated and watered by humans) as larval habitats (Tanaka et al. 1979, Hawley 1988) and bites humans, farm animals, pets, and peridomestic animals (Savage et al. 1993, Richards et al. 2006, Sawabe et al. 2010). Therefore, fundamental resources for its establishment may be available in most rural and urban environments. Although summer dryness has been regarded as a barrier to its expansion into western North Americas (Nawrocki and Hawley 1987, Washburn and Hartmann 1992), the northern limits of *Ae. albopictus* have been discussed primarily in relation to temperature.

Previous studies attempting to explain and predict the northern limits of *Ae. albopictus* distribution may be grouped into three broad categories: the correlation approach, ecological niche modeling, and the population dynamics approach. Correlation approaches aim to detect thermal factors that correlate well with known northern limits to predict range limits in new environments. Nawrocki and Hawley (1987) regarded January mean temperature of 0 and −5°C as a limit for stable establishment and seasonal expansion in North America and Asia. The potential range in Europe was delineated by July mean temperature of 20°C as well as January means of 0 and −5°C (Mitchell 1995, Knudsen et al. 1996). In Japan, Kobayashi et al. (2002) found that the northern limit was correlated with an annual mean of 11°C, a January mean of −2°C,

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and 1,350 accumulated degree-days (DD) above 11°C per year (estimated to allow ≈3.5 generations). A January mean of 0°C, an annual mean of 11°C, and/or 1,350 DD above 11°C have been accepted in later studies (Eritja et al. 2005, Medlock et al. 2006, Takumi et al. 2009, Neteler et al. 2011, Roiz et al. 2011, Wu et al. 2011). However, the biological relevance of these criteria is not necessarily clear. Even −5°C is much warmer than the supercooling point (temperature at which tissues freeze and insects die out) of *Ae. albopictus* eggs (ca. −27°C, irrespective of geographical origins and cold acclimation; Hanson and Craig 1995a). In fact, diapausing eggs survived winter months with daily minimums frequently <−10°C (Hanson and Craig 1995b). A conservative threshold for larval development, 11°C (Hawley 1988), does not directly justify the annual mean 11°C or 1,350 DD above 11°C as northern limit criteria.

Ecological niche modeling identifies ecological niches from a wide variety of environmental parameters at *Ae. albopictus* positive localities. The models usually include several temperature and precipitation indices and other factors influencing establishment of the species, and express environmental suitability as several or more grades (Benedict et al. 2007, Medley 2010, Fischer et al. 2011). Despite potential usefulness, models based on native Asian distributions do not necessarily fit well to distributions in other regions where the species has become established, especially Europe (Benedict et al. 2007, Medley 2010, Fischer et al. 2011). Medley (2010) suggested niche shifts because of genetic changes in new environments as a cause of this lack of fit, but specific factors have not been identified. A model based on world occurrence better predicted both native and introduced distributions (Fischer et al. 2011), but an average niche may mask regional differences that could have practical importance. Additionally, inclusion of multiple parameters in niche modeling may make biological meaning less straightforward. Finally, grades indicating relative suitability do not directly indicate whether establishment is possible or not.

One issue that has not been well examined in the studies cited above is that temperature effects on *Ae. albopictus* populations in summer and winter can be compensated. Even high mortality in a cold winter may allow establishment if it is compensated by rapid population growth in summer. Similarly even low reproduction in a mild summer may allow establishment if a mild winter enables high survival. We refer to analyses combining population performances in reproductive and overwintering seasons as a population dynamics approach.

In a pioneering work, Hawley et al. (1989) discussed the northern limit of *Ae. albopictus* in North America from the viewpoint of whether summer reproduction can counterbalance winter mortality. An extension of this approach involves estimation of reproductive season lengths of *Ae. albopictus* in Europe on the basis of temperature and photoperiod effects on development, survival, and reproduction (Medlock et al. 2006, ECDC 2009, Takumi et al. 2009). In a model based on expert knowledge (ECDC 2009), establishment risks in Europe were graded by combining the suitability of summer temperature, January temperature, and annual precipitation, each described by a sigmoidal curve. Sutherst (1993) evaluated the worldwide distribution potential of *Ae. albopictus* with an Ecoclimatic Index (EI) (Sutherst and Maywald 1985). Improved EI maps for *Ae. albopictus* are shown for Australia (Russell et al. 2005) and China (Wu et al. 2011). EI is a composite index grading year-round suitability by combining favorableness of temperature, moisture, and day length for growth in each of 52 wk as well as yearly total cold stress (reduction rate) and heat stress. The population dynamics approach could reveal the biological underpinnings of successful establishment more directly than the other approaches, but require quantification of the relationships between *Ae. albopictus* performance and climatic factors, which may be technically challenging.

Despite various useful trials and significant progress in our knowledge, factors and processes that determine northern limits of *Ae. albopictus* are still not well understood. Simple indices that can be easily calculated for each locality and have clear biological meanings could supplement existing prediction maps and facilitate our understanding of the risk of establishment and/or further expansion of *Ae. albopictus* in areas of interest.

The current article has two aims. First, we propose a new thermal index and examine its usefulness in explaining northern limits of *Ae. albopictus.* This composite index is derived from consideration of the population dynamics of *Ae. albopictus* but an establishment criterion is derived from actual temperature and distribution data. Second, we compare this new index with thermal criteria previously used and show that thermal conditions around northern limits differ depending on differences in thermal continentality.

Below, we use "establishment" or "stable establishment" to indicate naturalization, a situation in which introduced populations persist in the wild by continuing reproduction (Walther et al. 2009). "Temporary establishment" indicates that introduced populations may reproduce during favorable seasons and even persist for a few years but eventually disappear naturally. Temporary establishment corresponds to Walther et al.'s (2009) casual stage of an invasion process. "Thermal continentality" or simply "continentality" indicates the degree of seasonal temperature variations, the best-known aspect of climatic continentality.

Materials and Methods

A New Index. We assume that a single year for *Ae. albopictus* in temperate regions consists of an active season and an inactive season. The two seasons are distinguished by whether temperature is above or below a critical temperature for development and reproduction. The active season starts with larval hatch from overwintering eggs and ends with oviposition of the last eggs to overwinter. It is further assumed that active season performance (development and reproduction) depends on thermal accumulation above a critical temperature (no adverse effect at high temperature), whereas populations decrease in inactive seasons because of mortality that depends on thermal accumulation below a critical temperature (no increased survival at lower temperature). Greater performance during the active season results in more females in summer and autumn and more eggs to overwinter, whereas higher performance during the inactive season results in more larvae hatching in spring.

These assumptions are partly supported by laboratory and field observations for *Ae. albopictus.* Adverse effects of high temperatures on development were evident at constant 35°C, but development and reproduction were facilitated with increasing temperature from 20 to 30°C at ≈80% relative humidity (RH) (Delatte et al. 2009, Farjana et al. 2011). Population declines in summer were not recognized in temperate Japan where daily means are around 25°C even though daily maxima are >30°C, and monthly mean humidity is >70% RH (Makiya 1973, 1974; Mori and Wada 1978). Adverse effects of high temperature combined with dryness were observed in the laboratory (Alto and Juliano 2001, Juliano et al. 2002) and suggested in the subtropics (Juliano et al. 2002). If such effects occur around the northern limits, our assumption of no adverse effects at high temperature could overestimate reproductive potentials, which is preferable to underestimation of potential risks. At low temperature (but above the supercooling point), mortality of diapausing *Ae. albopictus* eggs kept humid depends on both exposure duration and coldness in the field (Hawley et al. 1989, Hanson 1995).

We selected 10°C as a critical temperature for dividing a year into active and inactive seasons. In temperate regions, *Ae. albopictus* produces diapausing eggs when photoperiods are <13–14 h in autumn (Mori et al. 1981, Pumpini et al. 1992, Urbanski et al. 2012). In Nagasaki, Japan, diapausing eggs first appear in mid September (mean 24.3°C), and almost all eggs laid in October (19.0°C) enter diapause, but surviving females still bite and lay eggs in November (mean 13.7°C, mean minimum 10.1°C) (Mori and Wada 1978, Mori et al. 1981). Diapausing eggs begin to hatch in mid March when mean temperature exceeds 10°C (Mori et al. 1981). In Rome, Italy, ovitraps are positive until late December (temperature <10°C), and eggs begin to hatch when daily means reach 10°C in spring (Toma et al. 2003). Although 11°C has been accepted as a conservative threshold for larval development since Hawley (1988), the daily mean of 10°C could allow very slow development under fluctuating temperature. As critical temperatures for starting and ending active seasons in Europe, Medlock et al. (2006) and Takumi et al. (2009) used 10–11 and 9–10°C, respectively.

As indicators of population performance in active and inactive seasons, we modified Kira's (1976, 1991) Warmth Index (WI) and Coldness Index (CI) that were originally proposed to explain plant distributions in eastern Asia (the original 1945 and 1948 literature were unavailable). WI, an index of warmth in a growing season, is calculated as summation of monthly mean temperature (t°C) above 5°C (the threshold for plant growth); $\mathrm{WI} = \sum(t - 5)$ where summation is made for n month in which $t > 5$°C. CI, an index of winter coldness, is calculated as $\mathrm{CI} = -\sum(5 - t)$ where summation is made for $(12 - n)$ winter months in which $t < 5$°C; a minus sign is added to avoid confusion with WI. An advantage of these indices is simplicity of calculation as compared with summation of DD. We modified WI and CI in two respects. First, a critical temperature 10°C is adopted in place of 5°C. Second, a minus sign in CI was removed.

$$\mathrm{WI} = \sum(t - 10),$$

where summation is made for n month in which $t >$ 10°C

$$\mathrm{CI} = \sum(10 - t),$$

where summation is made for $(12 - n)$ month in which $t <$ 10°C

Although botanists have used WI and CI separately to analyze different aspects of plant distributions (e.g., Fang et al. 1996, Nakamura et al. 2007), we formulated a new index TSI (thermal suitability index for *Ae. albopictus*) as

$$\mathrm{TSI} = \mathrm{WI}/\mathrm{CI}.$$

TSI quantifies the year-round performance as the magnitudes of expected temperature-dependent reproductive success relative to temperature-dependent winter mortality. TSI is not calculable for subtropical and tropical lowlands where the coldest month mean is ≥10°C.

Distribution Data. *Ae. albopictus* distribution data were compiled from the literature. Each locality was assigned to be either positive or negative except for two localities in China (see below). Positive localities indicate the presence of established populations of *Ae. albopictus.* Negative localities include localities without *Ae. albopictus* records (establishment is either impossible or possible but no invasion or detection has occurred) and those where *Ae. albopictus* was once recorded but there is insufficient support for its establishment. Population persistence only in indoor environments (the Netherlands; ECDC 2009) was regarded as negative. As far as possible, information was collected for localities designated as cities or towns.

The main information sources of distribution data for Japan are Kurihara et al. (1997) and Kobayashi et al. (2002, 2008). A few recent records from northernmost localities near the confirmed establishment range were considered positive. Distribution information for northeast China is not consistent. The northern limit was regarded as southern Liaoning Province (Lu et al. 1997), whereas the species was reported from 10 localities all over Liaoning as well as Ning-an in Heilongjiang Province (Wang et al. 2006). The latter records are based on adults collected in the field and are somewhat problematic, because *Ae. albopictus* and *Aedes flavopictus* Yamada (with more northerly distribution) are morphologically similar (Tanaka et al. 1979, Lu et al. 1997) and identification by adult scale patterns is possible only for intact specimens. As for Liaoning Province, *Ae. albopictus* was found in Chaoyang but not in Shenyang and Tielin in 2006, and, despite previous records from some other localities, only Dalian was regarded as positive in this province (Wang et al. 2009). In 2008, the species was collected in Shenyang, where it was temporarily detected in 1960s and 1980s without stable establishment (Li et al. 2010). Wang et al. (2009) and Li et al. (2010) thought that winter coldness in Shenyang and Chaoyang prohibits stable establishment despite likely frequent invasion through the tire trade. Wu et al. (2011) included Shenyang, Chaoyang, and Dalian (read from their map) in the distribution range, but regarded the former two as the summer expansion range. The species has been reported frequently from Dalian (Zhang et al. 2003, Liang et al. 2006, Kong et al. 2009), where it has persisted for >30 yr (Wang et al. 2009). Taken together, we regarded only Dalian as a locality where stable establishment was confirmed, and Chaoyang and Shenyang were considered as temporary establishment localities where stable establishment was prevented climatically at least during the 20th century. Some cities listed as census sites in the provinces of Henan (Liu et al. 2010) and Jiangsu (Yang et al. 2008), both in the *Ae. albopictus* distribution range (Lu et al. 1997), were regarded as positive, although the results are not shown for each city. For eastern Asia, cities in extra-northern-limit areas (Hokkaido, Japan, Kobayashi et al. 2008; Jilin Province, China, Lu et al. 1997; Primorsky, Russia, Gutsevich et al. 1974) were included as negative localities.

In the United States, only localities east of the Mississippi River are included in the analysis. This area is primarily comprised of Eastern Temperate Forest (Ecological regions of North America Level I #8.0; http://www.epa.gov/wed/pages/ecoregions.htm). For some cities and towns, positive or negative distribution information was assembled from the literature. However, the most comprehensive distribution map is drawn by county (Moore 1999, and Map: Distribution of *Aedes albopictus* in the United States, by County, 2000; http://www.cdc.gov/ncidod/dvbid/arbor/albopic_97_sm.htm). An up-dated map for the northeast region is also drawn by county (Andreadis 2009). We included county-level positive or negative distribution information into the analysis with county seats. Although county seats of positive counties may not be confirmed establishment localities, they are developed environments and must have invasion opportunities, because in the United States, this species has spread along roads (Moore and Mitchell 1997).

The main source of distribution information for Europe is ECDC (2009). In addition to cities or towns with direct information, some cities with positive or negative information from larger administrative units (such as county) were included.

In North America and Europe, newly detected populations, especially northern and isolated ones, may be controlled immediately even though climate would allow establishment. However, localities without evidence for establishment were regarded as negative. Latitudes and altitudes of localities were represented by those of weather stations where temperature data were obtained.

Temperature Data. We used monthly and annual mean temperatures calculated from weather-station data. Means for 1971–2000 in Japan and the United States were obtained from the Japan Meteorological Agency (http://www.jma.go.jp) and the U.S. National Climatic Data Center (http://cdo.ncdc.noaa.gov/cgi-bin/climatenormals/climatenormals.pl), respectively. For the Asian Continent and Europe, data partly were obtained from the Japan Meteorological Agency (as above). These means for 1971–2000 or roughly equivalent years are mainly based on Global Historical Climatology Network (GHCN) data compiled by the U.S. National Climatic Data Center. For other Asian and European localities, means calculated mainly from GHCN data were obtained from Worldclimate (http://www.worldclimate.com); means for years within 1951–2000 (at least >10 yr) were used except for a few localities that included some years before 1951. When means from more than one weather station were available for a single locality, the warmer station was adopted to avoid underestimation of establishment risks. In climate statistics, each monthly mean and an annual mean may be calculated separately, so the mean of monthly means may differ from the annual mean if there are missing data. Measurements in Fahrenheit were converted to Celsius.

As our concern is primarily the northern limits of the species, we used localities of altitudes $\leq$200 m, TSI < 3 and with information on the presence or absence of *Ae. albopictus.* Temperature data were unavailable for many localities meeting these requirements, so final locality numbers were 41 for Japan, 34 for Asian Continent (Korea, China, and Russian Far East), 124 for North America (United States), and 33 for Europe.

Continentality. To evaluate thermal continentality (the degree of seasonal temperature variations) without predetermined criteria, we calculated a continentality index for each locality. Although the simplest index is the annual range of monthly mean temperature (Holmlund and Schneider 1997, Nakamura et al. 2006), we used Conrad's continentality index (CCI) because it describes well continentality levels of land localities ranging from the tropics through the subarctic (Hela 1953). CCI is calculated as

$$\mathrm{CCI} = 1.7R/\sin(A + 10) - 14$$

where R = annual range of temperature (difference between means of hottest and coldest months), A = latitude. CCI values approach 0 with increasing oceanity and 100 with increasing continentality.

Statistical Analysis. Statistical tests were performed by using SPSS Base10.0J (SPSS Inc., 1999).

Data Presentation. Conclusions about the relationship between temperature and distribution of *Ae. albopictus* may be misleading if positive or negative information is inaccurate and/or temperatures used do not accurately represent positive or negative localities. All localities, latitudes, altitudes, monthly and annual mean temperatures, as well as status of *Ae. albopictus* and its source literature, are compiled in the Supp. Appendix (online only) or available from the authors.

Results

TSI, *Ae. albopictus* Distribution, and Temperature. TSI values are ≥1 for all *Ae. albopictus* positive localities (Fig. 1). Shenyang and Chaoyang, where *Ae. albopictus* existed only temporarily, have TSI between 0.7–0.8. All other localities with TSI < 1 are negative. Throughout northern temperate lowlands (≤200 m), TSI < 1 can be an accurate criterion indicating that *Ae. albopictus* establishment is thermally prohibited.

In the Asian Continent and Japan, most localities with TSI > 1 are positive, indicating that, in the native range, *Ae. albopictus* is ubiquitous throughout urban and rural lowlands up to the northern limits. Some negative localities with 1.2 > TSI > 1 in Japan are located very close to the northern limit. In North America and Europe, many localities with TSI > 1, ranging up to values close to three, are negative, suggesting that some of thermally suitable localities have not been occupied yet. This difference between native and invasion ranges remains even though a few northernmost positive localities based on recent records in Japan prove to be only temporary occurrence (see Distribution Data).

In Asia and North America, positive localities are nearly continuously distributed over almost the full latitudinal ranges where TSI > 1 (south of 41–42° N). However, in Europe, a gap exists between the northernmost positive locality (Locarno, ≈46° N) and northernmost localities with TSI >1 (Antwerpen, London, Bruxelles, ≈51° N). In Europe, positive localities generally have larger WI (and thus larger TSI) than negative localities with similar CI (winter coldness) (Fig. 2), suggesting that localities with warmer summers are more likely to be colonized by *Ae. albopictus* when TSI < 3. The same tendency, although less evident, is seen in North America with increasing CI (Fig. 2).

Absence of *Ae. albopictus* could result from factors other than temperature (insufficient survey, absence of invasion opportunities, efficient control, or unfavorable conditions such as excess dryness). Therefore, thermal conditions required for establishment were analyzed for positive localities and two Chinese localities where thermal conditions probably prohibited stable establishment.

Although TSI of positive localities cover similar ranges (1.00–2.81, 1.04–2.94, 1.10–2.93, and 1.08–2.96 for Japan, the Asian Continent, North America, and Europe, respectively), actual thermal conditions differ among regions (Table 1). Annual ranges of monthly mean temperatures (differences between hottest and coldest months) are smallest in Europe and do not overlap with those from the Asian Continent and North America (Table 1). The largest annual range (22.3°C, Parma, Italy) in Europe overlaps with the smallest values (22–23°C) at seven Japanese localities (Shiogama, Kesennuma, Oofunato, Kamaishi, Miyako situated at the depths of narrow coastal bays, and Mito, Sendai ≈10 km from the sea). In North America, annual ranges are <24°C at four localities: Georgetown (23.1°C) and Dover (23.6), DE; in the Middle Atlantic Coastal Plain, Cape May (22.9), NJ; in the Atlantic Coast Pine Barrens and Portsmouth (23.8), OH; in the Western Alleghany Plateau (each

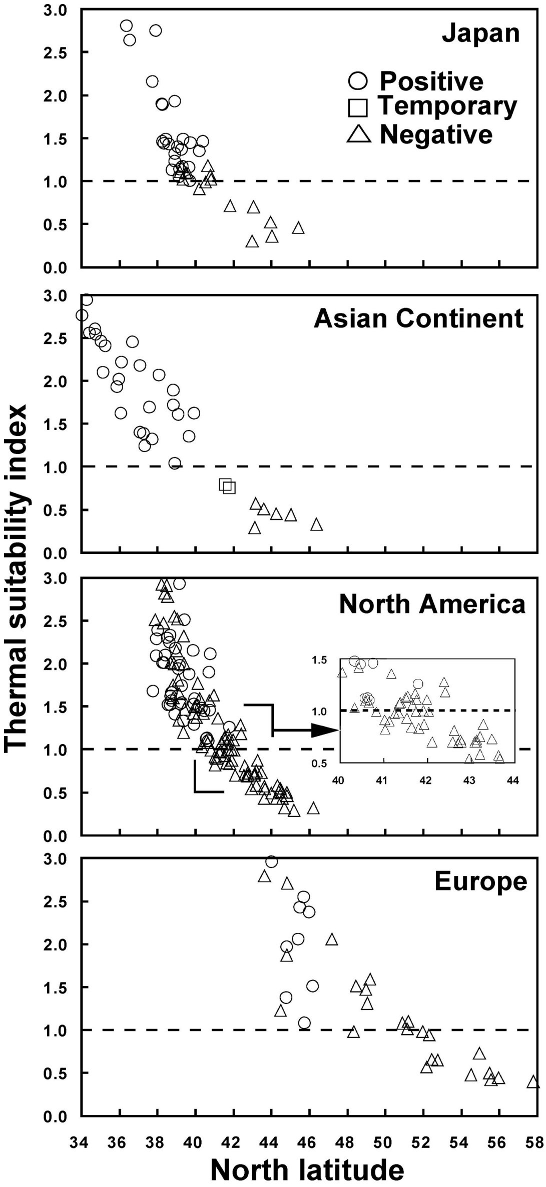

Fig. 1. Thermal suitability indices (TSI) across latitude for localities where *Ae. albopictus* is positive, temporary, or negative. Temporary establishment is represented by only Chaoyang and Shenyang, northeast China (see text). Broken line, TSI = 1.

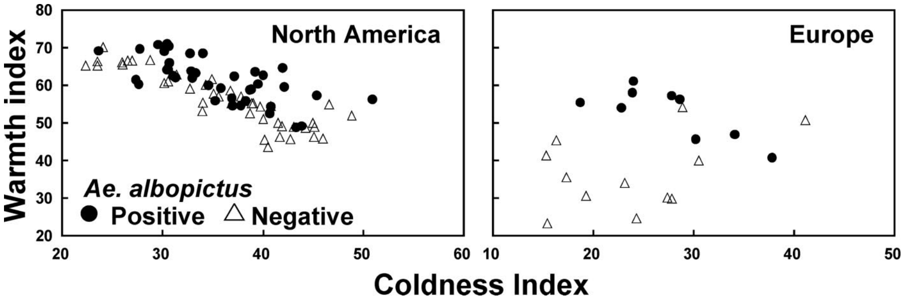

Fig. 2. Warmth Index (WI) and Coldness Index (CI) for localities with thermal suitability index (TSI) >1 in North America and Europe.

environment being Continental United States level III ecoregion #63, 84, and 70; http://www.epa.gov/wed/pages/ecoregions.htm). Ecoregion #70 is far from the sea but in the periphery of the Appalachians, a unique area under a climate similar to the Köppen–Geiger's European type climate in eastern North America (see Discussion). Conrad's continentality index indicates that the thermal condition on the Asian Continent is most continental (hot summer and cold winter), while Europe is most oceanic (both summer and winter are mild); those in North America and Japan tend to be intermediate. There are no overlaps in the continentality indices between Europe and other regions and between Japan and the Asian Continent.

The relation between WI and CI for positive localities with TSI of 1–3 was described by linear regressions (Fig. 3). WI and CI values yielding TSI = 1 estimated from the regressions are smaller in Japan than on the Asian Continent, and are intermediate in North America. This result indicates that both summer and winter temperatures around northern limits are milder in Japan than on the Asian Continent, and intermediate in North America (Table 1). Accumulated DD above 11°C and generation numbers at estimated northern limits are also smaller in Japan, larger in the Continental Asia, and intermediate in North America (Table 1). These values must be smallest in Europe, but were not estimated, because it is unknown whether the present distribution in Europe roughly indicates its maximal northward expansion (Fig. 1).

Relationship of Continentality to TSI and the Other Thermal Indicators. Figure 4 shows the relationship of Conrad's continentality indices to TSI, annual mean temperature, WI, and the coldest month (usually January) mean for positive localities and Chaoyang and Shenyang, temporary establishment localities. Annual and coldest month means have been used as indicators of northern limits in previous studies, while WI can be a substitute for accumulated DD in the active season, which also has been previously used as a northern limit indicator.

TSI is independent of thermal continentality (Fig. 4, TSI). The correlation between annual mean temperature (AMT) and thermal continentality is marginally significant because of inclusion of higher temperatures on the Asian Continent (Fig. 4, AMT), but, if we exclude eight Asian localities where AMT > 14°C, the relationship is not significant ($r^2 = 0.005$; $F = 0.47$; df = 1, 89; $P > 0.05$). Both TSI = 1 and AMT = 10°C can be robust indicators of *Ae. albopictus* northern range limits, below these climatic thresholds the establishment is thermally prohibited irrespective of thermal continentality.

WI and coldest month means of positive localities, however, are strongly influenced by thermal continentality. WI increases with increasing continentality

Table 1. Regional differences in temp conditions for *Ae. albopictus* positive localities with $3 < \mathrm{TSI} \geq 1$

Region	n	Annual range of temp (°C)[a]	Continentality index[b]	No. months (>10°C) at the northernmost locality[c]	Estimated northern limit (TSI = 1)[d]		
					WI = CI[e]	Degree-days above 11°C[f]	No. generations per year[g]
Asian Continent	26	28.4a (25.9–31.0)	52.3a (47.3–57.5)	7 (April–Oct.)	52 (48–55)	1,373 (1,251–1,464)	3.8 (3.4–4.1)
North America	39	25.6b (22.9–29.2)	43.3b (37.6–50.2)	7 (April–Oct.)	46 (43–48)	1,190 (1,098–1,251)	3.3 (3.0–3.4)
Japan	25	23.7c (22.0–26.2)	39.6c (35.1–44.7)	6 (May–Oct.)	43 (41–45)	1,129 (1,068–1,190)	3.1 (2.9–3.3)
Europe	9	20.9d (18.8–22.3)	29.1d (25.5–32.4)	nc	nc	nc	nc

[a] Difference between means of hottest and coldest months; mean and range in parentheses. ANOVA $F = 88.51$, df = 3, 95, $P < 0.001$; Means with different letters are significantly different from others ($P < 0.05$) by Scheffe's test.

[b] Mean and range in parentheses. ANOVA $F = 190.86$, df = 3, 95, $P < 0.001$; Means with different letters are significantly different from others ($P < 0.05$) by Scheffe's test.

[c] Among localities included in the analysis. Hachimori, Japan; Beijing, Asian Continent; Chicago, North America. nc, not calculated.

[d] Ranges in parentheses indicate lower and upper estimates based on 95% CL of regression coefficients. Rounded to integers.

[e] Rounded to integers.

[f] (WI at estimated northern limit - No. months (>10°C) at the northernmost locality) × 30.5. 11°C = Thermal threshold for development (Kobayashi et al. 2002). 30.5 = Mean no. of days per month. Rounded to integers.

[g] Degree-days/365. 365 = Degree-days above 11°C required for one generation (Kobayashi et al. 2002).

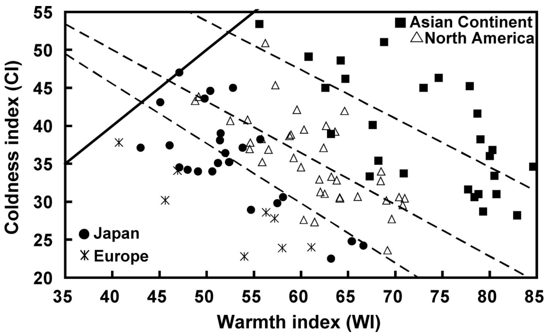

Fig. 3. The relationship between Warmth Index (WI) and Coldness Index (CI) for localities where *Ae. albopictus* is positive. Linear regressions of CI on WI (broken lines) are $CI = -0.64\ WI + 85.8$ (95% CL of regression coefficient = ±0.29; $F = 21.2$; df = 1, 24; $P < 0.001$) for the Asian Continent, $CI = -0.68\ WI + 77.2$ (CL of regression coefficient = ±0.24, $F = 32.8$; df = 1, 37; $P < 0.001$) for North America, and $CI = -0.79\ WI + 77.0$ (CL of regression coefficient = ±0.32; $F = 26.4$; df = 1, 23; $P = < 0.001$) for Japan. Solid line, WI = CI.

(Fig. 4, WI) in accordance with regional differences in WI at estimated northern limits (Table 1). In contrast, coldest month means decrease with increasing continentality (Fig. 4, CMT). Coldest month means as an establishment criterion apparently differ among regions (i.e., ca. −2°C in Japan and ca. −5°C in the Asian Continent and North America). The criterion in Europe is not yet validated because of fewer data, but may be higher than in Japan.

Conrad's continentality indices of Chaoyang and Shenyang, both temporary establishment localities, are larger than all the positive localities. TSI, and annual and coldest-month temperature means of these localities also lie out of the range of positive localities examined, whereas WI values are equivalent to those at a few positive localities on the Asian Continent as well as many in Japan, North America, and Europe. Hottest month means of Chaoyang and Shenyang come close to 25°C. These facts suggest the presence of maximal winter coldness above which establishment is impossible irrespective of summer warmth levels.

Discussion

TSI and Thermal Conditions Around Northern Distribution Limits. TSI is a robust method for predicting the northern distribution limit of *Ae. albopictus* across multiple continents (Fig. 1) that exhibit distinct climatic conditions (Table 1; Fig. 4). Population performances of *Ae. albopictus* differ by differences in thermal continentality. Under a continental climate, the population can recover rapidly from high mortality during severe winters, whereas, under an oceanic climate, slower population growth can offset lower mortality during mild winters. Population performances in summer and winter can therefore be compensated, and neither summer nor winter condition alone can be a reliable indicator to evaluate establishment risks (Fig. 4). The strength of TSI is that it accounts for population performances during both

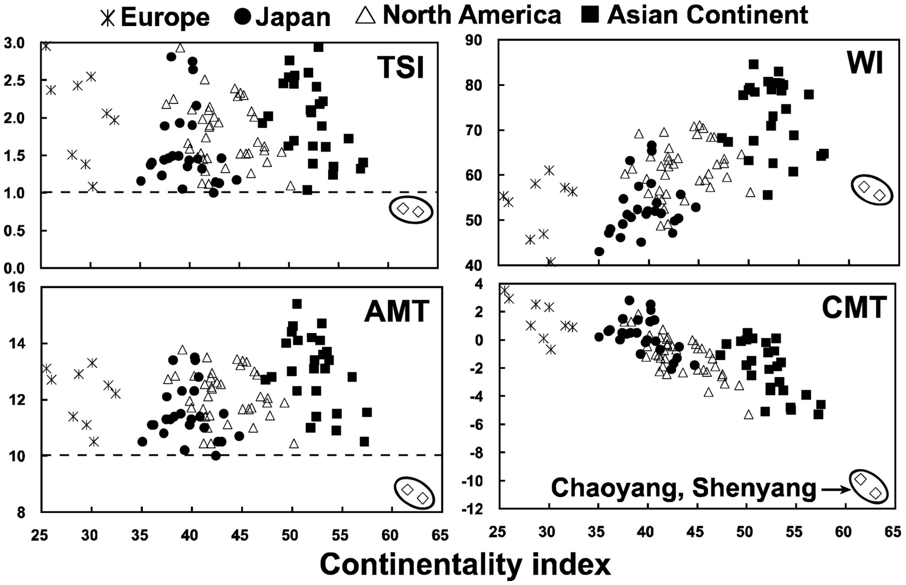

Fig. 4. Thermal suitability index (TSI), annual mean temperature (AMT) (°C), Warmth Index (WI), and coldest month mean temperature (CMT) (°C) plotted on Conrad's continentality indices (CCI) for localities where *Ae. albopictus* is positive and Chaoyang and Shenyang where establishment is temporary. Broken line, TSI = 1 for TSI and annual mean = 10°C for AMT. Correlation coefficients between each indicator and CCI (excluding Chaoyang and Shenyang) are $r^2 = 0.001$, $F = 0.056$, $P > 0.05$ for TSI, 0.056, 5.79, $P < 0.05$ for AMT, 0.46, 81.7, $P < 0.001$ for WI, and 0.55, 116.2, $P < 0.001$ for CMT (df = 1, 97 for all).

winter and summer with its elements WI and CI, and suggests why establishment is possible or impossible with regard to population dynamics of *Ae. albopictus.*

The specific thermal conditions around northern limits of *Ae. albopictus* differ by differences in thermal continentality, which on average is highest in the Asian Continent and lowest (i.e., highest oceanity) in Europe, with intermediate values in North America and Japan (Table 1). The conditions can also vary significantly in finer spatial scales. The conditions of some coastal localities in Japan overlap with those in Europe (Table 1; Fig. 3), because of higher oceanity than inland localities. Complex mountainous terrains produce complex climatic zonation. In northeast Italy, for example, a study area of 6,200 km^2 (equivalent to a 79 × 79 km square) is, in general, under temperate-oceanic climate, but locally under four sub-climates (sub-Mediterranean, sub-continental, continental, and alpine) (Roiz et al. 2011).

When data from more than one station were available for a single city, we selected a warmer station to avoid underestimating establishment risks. For example, data at four stations were available for Chicago, the northernmost positive locality in North America. TSI were 1.26 (annual mean 11.0°C, alt. 181 m), 1.13 (10.6°C, 189 m), 0.89 (9.5°C, 201 m), and 0.84 (9.3°C, 192 m), respectively, of which the first value (1.26) was used. This variation suggests that not all sites in the city of Chicago are thermally suitable for stable establishment. Around northern limits, temperature variations at the scale of urban heat islands can have significant effects on introduced populations of *Ae. albopictus.* A model based on the current distribution of the species in Europe predicted the suitability of Paris surrounded by unsuitable areas (ECDC 2009).

Our analyses support prior speculation that, despite repeated introductions, winter coldness has prohibited stable establishment of *Ae. albopictus* in Chaoyang and Shenyang, northeast China (Wang et al. 2009, Li et al. 2010, Wu et al. 2011). There, January mean minima approach −18°C, so daily minima may approach or fall below −27°C, the supercooling point where diapausing eggs of *Ae. albopictus* inevitably die out (Hanson and Craig 1995a). In Chaoyang, all eggs kept in humid soil in outdoor containers died before spring (Wang et al. 2009).

In Chaoyang and Shenyang, *Ae. albopictus* was most abundant at or limited to tire accumulation sites where used tires are often brought from infested localities (Wang et al. 2009, Li et al. 2010). It may be possible that cohorts introduced in spring increases rapidly during summer, and a small proportion of diapausing eggs in more benign micro habitats survive winters milder than the average even though the population finally becomes extinct. If new cohorts are introduced before extinction of preceding cohorts, the population may appear persistent. Around northern limits, continuous discovery may not necessarily be an evidence of stable establishment.

The importance of summer warmth as a factor delineating northern limits of *Ae. albopictus* also has been discussed previously (Mitchell 1995, Kobayashi et al. 2002, ECDC 2009), but actual warmth levels required for establishment vary by continentality (Table 1; Fig. 4). Accumulated DD above 11°C and generation numbers at the estimated northern limit in Japan (Table 1) were smaller than Kobayashi et al.'s (2002) estimates (1,350 DD and 3.5 generations). This discrepancy can be attributed to two causes: 1) the three northernmost localities (Shinjo, Morioka, and Miyako) regarded as negative in Kobayashi et al. (2002) have later proved to be positive, and 2) estimates based on linear regressions can be smaller than values at known positive localities.

Northern Limits in Europe. Thermal conditions at the northern limits in Europe were not estimated, because the current distribution may not have yet reached the potential northern limit (ECDC 2009). Tentative values calculated from nine positive localities (Fig. 3) are WI = CI = 38 (95% CL 32–41), leading to 946 (763–1,037) accumulated DD and 2.6 (2.1–2.8) generations. However, the estimates become smaller if establishment potential is confirmed at higher latitudes (46–51° N) with TSI > 1 (Fig. 1). For example, Caen, Brest, and Nantes (47–50° N), in northwest France, all with TSI > 1.5, were regarded as negative, but *Ae. albopictus* was found in a few localities in northwest France for 2–3 continuous years (ECDC 2009).

Alternatively, those localities may be thermally unsuitable for *Ae. albopictus* persistence. At these three sites, annual means (10.7–11.5°C), coldest-month means (5.0–6.2°C), and CI (15.4–19.3), as well as TSI, are within levels of positive localities in Europe and the other regions (Figs. 3 and 4), but WI (23.3–35.5), accumulated DD (529–869), and expected generations (1.5–2.4), all indicators of summer warmth, are below those of all the positive localities (Fig. 4; Table 1). Hottest-month mean temperatures (15.9–18.5°C) exceed 15°C, which ECDC (2009) regarded as a critical summer temperature below which suitability is zero, but population growth must be very slow because of prolonged development at low temperature (Delatte et al. 2009).

In Asian and American lowlands, WI < 40 is associated with larger CI (>45, and much larger under continental climate), and will never allow establishment (TSI < 1), while CI < 20 is always associated with enough warmth (WI > 60), thermally suitable for establishment (TSI > 3). A combination of mild summer (WI < 40, accumulated DD <900, generations <2.5) and mild winter (CI < 20, coldest-month means >5°C) is a condition that *Ae. albopictus* has not experienced in Asia and America. On updated Köppen–Geiger climate maps (Kotteki et al. 2006, Peel et al. 2007), Europe, including the United Kingdom but excluding Mediterranean coasts and the Iberian Peninsula, falls within a climate category of Cfb (temperate climate characterized by warm summer and absence of dry season). This climate type, often called oceanic or maritime, is absent in temperate eastern Asia and eastern North America (except for the Appalachians) characterized by hot summer (rainfall patterns are variable). Therefore, it may be difficult to support thermal suitability in Europe north of the Alps based on the distribution and population dynamics of *Ae. albopictus* in Asia and America.

After the first confirmed establishment in Texas in 1986, northward expansion of *Ae. albopictus* in North America was rapid, approaching the present northern limit within several years (Moore 1999). Northward expansion in Europe has been slower; the species was abundant in several cities in Albania in 1970s (Adhami and Reiter 1998), and first confirmed in northern Italy in 1990 (Dalla Pozza and Majori 1992), but establishment in the north of the Alps has not been confirmed despite repeated detection of introduced populations (ECDC 2009). This suggests that northward expansion is more difficult than prior predictions due at least partly to insufficient summer warmth despite warm winters (Fig. 2). In contrast to the Asian Continent, determination of minimal WI, accumulated DD or generation numbers required for establishment is essential for delineating the potential range under highly oceanic climate in Europe.

Climatic adaptation traits of the European population (supposed origins are China and the United States; ECDC 2009) need to be investigated further to examine their fitness for reproduction under the oceanic climate. In North America, conditions for diapause induction of *Ae. albopictus* have adapted to latitudinal and altitudinal climatic gradients since its invasion (Focks et al. 1994, Lounibos et al. 2003, Urbanski et al. 2012). Adaptive change in seasonality is also suggested for the *Ae. albopictus* population in Rome, Italy (ECDC 2009). In temperate Japan, diapausing eggs first appear in early autumn when the temperature is warm enough to allow one more generation under average conditions if eggs hatch shortly after oviposition (Mori et al. 1981; see A New Index in Materials and Methods). This early seasonal onset of diapause can assure completion of reproduction before exposure to low temperature. However, under highly oceanic climates where both summer and winter are mild, maximal exploitation of warm periods for reproduction could be a more effective strategy. As suggested by ECDC (2009), over longer time scales, genetic changes by either evolution of the present population or invasion of new populations can be an important risk factor for Europe.

Advantages and Limitations of the New Index. Both TSI < 1 and AMT < 10°C can be a criterion indicating that northern establishment of *Ae. albopictus* is thermally prohibited throughout the northern hemisphere. TSI>1 or AMT > 10°C as an indicator for thermal suitability appears valid for Asia and North America, but has yet to be confirmed for Europe as discussed above.

However, even though two localities have equivalent TSI values or annual means, the degree of seasonal temperature variations may differ between the localities. The advantage of TSI over AMT is, as stated above, that WI and CI, elements of TSI, are simple indicators of the effects of those variations on population performance.

For calculation of TSI, a critical temperature that distinguishes reproductive and overwintering seasons has to be determined. We selected 10°C based on literature information, and it worked ideally. However, this value can be optional. For example, adoption of 11°C as a criterion would result in a critical TSI value for establishment smaller than unity but other conclusions would remain unchanged. A critical temperature could also be selected by iteration as a temperature that brings a critical TSI value close to unity. Diapausing eggs may be laid over a period covering wide temperature ranges (see A New Index in Materials and Methods). Use of critical temperatures different in spring and autumn is an option to make TSI biologically more realistic.

Effectiveness of TSI in delineating altitudinal distribution limits of *Ae. albopictus* in thermally seasonal highlands where diapausing eggs pass cold months (<10°C) remains to be confirmed. The situation for the southern limits appears basically the same as in Europe, as southern cool regions such as southeast Australia, Tasmania, New Zealand, and southern South America are under oceanic climates, represented largely or partly by the Köppen–Geiger's Cfb type (Kotteki et al. 2006, Peel et al. 2007).

Mean temperatures for long periods are appropriate to evaluate risks of stable establishment. However, annual fluctuations in temperature may be large enough to influence establishment risks around northern limits, especially through variation in overwintering survival (Hawley et al. 1989, Hanson 1995, Hanson and Craig 1995a, Andreadis 2009). Analyses of yearly variations and historical trends in TSI, WI, and CI around northern limits could lead to better understanding of possible effects of global climate change on the distribution of *Ae. albopictus.*

The distribution of *Ae. albopictus*, especially in newly infested regions, is always changing, and global temperature is rising at an increasing rate (Intergovernmental Panel on Climate Change [IPCC] 2007). For the United States, for example, the main information source for *Ae. albopictus* distribution (Moore 1999) is not the latest, and mean temperatures for 1970–2000 include ≈15 yr before establishment of *Ae. albopictus.* Updated information on population establishment and climate should be periodically examined to verify our results.

In conclusion, our analyses of the northern distribution limits of *Ae. albopictus* with a simple thermal index revealed that 1) establishment risks of *Ae. albopictus* may be determined by relative performance during the reproductive and overwintering seasons, and 2) thermal conditions required for establishment are strongly influenced by thermal continentality that varies on various geographical scales. For precise prediction of future distributions after new invasion or global climate change, population dynamics and, in the longer-term, possibility of genetic changes under different climate types should be considered.

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