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Possible Effects of Future Climate Changes on the Maximum Number of Generations of *Anopheles* in Monsoon Asia

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1. Introduction

The predicted increase in global temperatures is expected to affect ecosystem, human health and society. In particular, a longer growing period due to climate warming is expected to enhance the growth and reproduction of some kinds of organisms (Kiritani, 2006; Ohta & Kimura, 2007). Northern and altitudinal shifts in vector species that cause infectious diseases have been observed worldwide (Barker & Lindsay, 2000; Hales et al., 2002). Conversely, the endemicity of vector-borne diseases such as malaria has decreased during the past century (Gething et al., 2010). The reason for this decrease is the economic development and disease control during this period (Hay et al., 2009; Gething et al., 2010). However, the recession of malaria during the last century did not correspond to a reduction in the ranges of vector species. Because of the complex relationship between malaria and climate (Martin & Lefebvre, 1995), the potential distribution of vectors and climate conditions of their habitats without human interference need to be elucidated.

Malaria is the chief disease caused by vectors breeding on shallow surface waters. Because survival and reproduction rates of mosquitoes are mainly determined by the temperature and humidity of their habitats, climate factors determine whether a location is suitable for the transmission of a wide range of infectious diseases. Projected changes in temperatures and the hydrological cycle will cause changes in the geographical distributions and population dynamics of vectors, thus altering the patterns of infectious disease transmission (Martin & Lefebvre, 1995; Martens et al., 1999). In particular, one of the most interesting aspects is how climate change could affect the geographical distributions and incidence patterns of the diseases caused by mosquitoes.

However, most investigators assessing the impacts of climate change on the incidence and geographical range of malaria assume that mosquito distribution would not change under future climate conditions (Martens et al., 1999; van Lieshout et al., 2004). These investigators assessed the risk of malaria transmission based on the geographical distribution of particular mosquito species by country or administrative unit (World Health Organization, 1989; Jetten & Takken, 1994). However, mosquitoes are not always uniformly distributed within a country, and their range typically crosses national borders (Kashiwada & Ohta, 2010). Martin & Lefebvre (1995) developed the Malaria Potential Occurrence Zone model,

which was applied with outputs derived from 5 General Circulation Models (GCMs) to provide first-order estimations of the changes in potential malaria transmission suitable for vectors; they revealed an increased incidence of seasonal malaria at the expense of perennial malaria. Rogers & Randolph (2000) assessed the current and future global distributions of malaria by using parasite dynamics with a GCM output and the estimated changes in human population living in malaria-transmission zones.

Most entomological studies are unable to incorporate a detailed distribution of the vector mosquito species, even though it is the basis for the risk assessment of malaria transmission. Monsoon Asia has a few observation sites of *Anopheles* mosquitoes (Kashiwada & Ohta, 2010). Thus, mechanistic model estimations of *Anopheles* distribution are necessary to enhance the existing data regarding their distribution. In addition, although vector distribution in Africa has been extensively studied, research on *Anopheles* in Asia, consisting of more than the half the entire human population, is sparse. Bhattacharya et al. (2006) studied the impacts of climate on *Anopheles* and malaria in India. Their study is the meaningful one of very few researches intended for Asian regions.

Therefore, we studied the effects of future climatic changes on the maximum number of generations per year of *Anopheles* mosquitoes in Monsoon Asia by using our model (Kashiwada & Ohta, 2010) and climate data in the absence of human interference. First, we studied the characteristics of changes in the energy and water balance of mosquito habitats owing to future climate changes. Second, we estimated the changes in the seasonal and geographical distribution patterns of *Anopheles* mosquitoes and discussed the changes in the potential distribution of malaria risk in Monsoon Asia under future climatic conditions.

2. Recent models for estimating vector distribution

Various types of approaches are used for estimating a range of meteorological variables for the vector species, depending on the purpose such as establishing an early warning system for malaria risk and making a high-resolution global map of the disease. Most studies use meteorological data, which are essential for estimating the vector distribution and malaria risk. However, meteorological records are usually obtained from urban areas, and coverage can be relatively sparse or inappropriate in less-developed countries (Martens & Thomas, 2005).

2.1 Integrated process-based epidemic model

An integrated and process-based model for estimating the “transmission or epidemic potential” index of a malaria-mosquito population (Craig et al., 1999; Martens et al., 1999; van Lieshout et al., 2004) improves the previous approaches by incorporating female mosquito density (a calculation of the basic reproduction rate), associated favorable climate conditions, and human population densities. This index approach is very useful for determining the risk of malaria transmission in a community where no mosquito observations have been conducted. However, climate conditions suitable for adult female mosquitoes are not always optimal for the immature stages of mosquitoes. Bayoh & Lindsay (2003) concluded that the optimal temperature range for *Anopheles* development narrows as the mosquito develops. Furthermore, the immature stages of mosquitoes live in water environments such as puddles, pools, or streams (Hoshen & Morse, 2005). Thus, the water temperature range suitable for the growth and development of the mosquitoes should be considered (Hopp & Foley, 2001; Kashiwada & Ohta, 2010).

Although some issues relate to the life history of mosquitoes, these epidemiological methods are useful and valuable for rapidly assessing malaria risk. Recently, Billingsley et al. (2005) successfully integrated these entomological techniques and compared malaria risk in different ecological and epidemiological settings. Conner & Mantilla (2008) attempted to develop and test integrated early warning systems that aim to provide early warnings regarding changes in epidemic risk in southern Africa based on seasonal climate forecasts. However, Ebi (2009) suggested that increased climate variability render early warning systems based on these variables more unreliable.

2.2 High-resolution map model

Hay et al. (2009) focused largely on malaria parasites and created a map of malaria endemicity within previously defined stable spatial limits of *Plasmodium falciparum* transmission by using a model-based geostatistical procedure and human population data. On the other hand, Martin & Lefebvre (1995) developed the Malaria Potential Occurrence Zone model with climate data that estimates malaria risk on the basis of the minimum and maximum temperatures and humidity required for the vector species. In addition, some species of mosquitoes in Africa have been mapped using simple climate data (Lindsay & Martens, 1998; Lindsay et al., 1998; Hay et al., 2002). Recent studies mapping vector species attempted to explain the geographic distribution of *Anopheles* and *Aedes* mosquitoes by analyzing climate variables for the mosquito observation sites by using niche-based distribution models (Foley et al., 2008, Medley, 2010) or a fuzzy logic model (Craig et al., 1999; Ebi et al., 2005). These studies have generated high-resolution maps of the vectors over large areas by using climate data; these maps are good indicators of the present distributions of the vectors. However, these maps do not represent the temporal occurrence of the vectors, because the calculation time intervals in these studies were typically at least 1 month. Mosquito development and the life cycle during the immature life stages occur at time scales ranging from several days to a few weeks (Hopp & Foley, 2001; Depinay et al., 2004).

2.3 Biological model

The most popular biological model expresses malaria parasites dynamics by using climate factors such as temperature (Martens et al., 1999; Rogers & Randolph, 2000). Other ecophysiological and entomological approaches have been employed to explain the temporal occurrence of vectors by describing their life histories. These models calculate development according to air temperature at each developmental stage of the insect, based on the assumption that the growth of an insect depends on the temperature of its habitat (Hopp & Foley, 2001; Ikemoto, 2003; 2005; 2008; Depinay et al., 2004; Pascual et al., 2006). Temperature affects the survival of the parasite only during the life cycle of *Anopheles* mosquitoes. According to experimental data, the optimal air temperature is between 22°C and 30°C; temperatures exceeding this value affect the activity of *Anopheles* mosquitoes. Although such ecophysiological models can generally explain the temporal population dynamics of pest insects at a specific site, they are unable to estimate the geographical distribution of the *Anopheles* vector (Depinay et al., 2004; Ikemoto, 2005). Therefore, the quantities of the available water and temperatures of the available aquatic habitats, which vary rapidly, must be incorporated into the model, because immature mosquitoes develop in natural or artificial water bodies as mentioned above. However, the volumes and temperatures of water in the small puddles in which immature mosquitoes live have not been measured over a broad area.

2.4 Habitat-oriented model

Besides simple climatic variables such as air temperature and precipitation, the activities of the mosquitoes depend on the variables of their native habitats such as water and soil conditions. Lindsay et al. (1998) showed that the activities of *Anopheles gambiae* and *Anopheles arabiensis* depend on the humidity index (the ratio of precipitation to potential evaporation during the optimum 5 months). The Malaria Potential Occurrence Zone model (Martin & Lefebvre, 1995) is a numerical model based on physics and biology and estimates whether environmental conditions are favorable for both the malaria parasite and its vectors. A characteristic of this model is that it uses a parameter for minimum atmospheric moisture, which is defined as the ratio of precipitation to potential evaporation obtained from simple meteorological data. The water conditions in the abovementioned studies are monthly or annual mean values. Hopp & Foley (2001) expressed the time variation of the surface water balance and soil moisture content by using a simple bucket model. In addition, air temperature instead of water temperature has been used in the model; this variable has been used to obtain the distribution of *Aedes* mosquitoes (Hopp & Foley, 2001). To determine the distributions of mosquitoes, the simple bucket model of Hopp & Foley is a very effective tool for developing accurate data for the daily water budget at the soil surface. This water balance model has been developed mainly in the fields of boundary-layer meteorology and agricultural meteorology.

3. Model description

The abovementioned review study revealed that many types of model construction require different data to estimate the distributions of mosquitoes. In this study, we selected the *Anopheles* mosquito, because some species live particularly in Monsoon Asia. Although various *Anopheles* species are located at a given site, we used the physiological data of some species available from references to consider their broad-scale distribution. The life history of *Anopheles* mosquitoes is described as a function of climate variables on the basis of an ecophysiological approach coupled with models of the energy balance of surface water and soil.

We constructed a model consisting of 3 parts: the primary part of the model calculates the growth of the mosquito (section 3.1), and the 2 subprocesses of the model determine the moisture conditions of the mosquito habitat (section 3.2) and calculate water temperature (section 3.3). The calculation time interval for all 3 parts of the model is 1 day. Methods using these models provide simultaneous spatial and temporal distributions of *Anopheles* mosquitoes at a fine resolution.

3.1 Mosquito growth model

The daily development of *Anopheles* mosquitoes was calculated using the temperature-dependent growth rate when the immature mosquitoes had an available water body to live in. This developmental value was summed each day until the mature-adult stage when the *Anopheles* mosquitoes are capable of laying eggs (Fig. 1a). The soil moisture content at root depth was determined before developing the growth model of the mosquito, as described in the next section. The threshold of soil moisture content was set at 70% of the value of the holding capacity (Dunne & Willmott, 1996) to exclude the emergence of mosquitoes during the dry season from the validation process. When the soil moisture content exceeded the threshold, the developmental rate of the mosquitoes was determined by the temperatures of

the habitat. Water temperature was used to calculate the development of the egg, larval, and pupal stages; air temperature was used to calculate the development of the adult mosquito (Fig. 1b). The development at a given time (in this study, this value was assumed as 1 day) can be described as follows:

$$\Delta d_k = \frac{1}{D_{temp}} \times \Delta t_k \quad (1)$$

where Δd_k is the development at k th day, D_{temp} is the duration for the completion of each developmental stage (day) at a given constant temperature ($^{\circ}\text{C}$), and Δt_k is the time unit of development. The inverse of the D_{temp} for each stage ranges from 0 to 1, with 0 representing no development and the amount of development increasing until the value approaches 1 (Lardeux et al., 2008). Values for D_{temp} were obtained from the results of laboratory studies and field observations of some *Anopheles* species (Mogi & Okazawa, 1996; Bayoh & Lindsay, 2003; Hu et al., 2003; Depinay et al., 2004; Lardeux et al., 2008). The relationships between the temperature threshold and mosquito development at each developmental stage were determined by the results obtained from these studies (Kashiwada & Ohta, 2010). With reference to these relationships, the growth begins when the temperature exceeds 15°C (Fig. 1a). The value of Δd_k was summed on a day-to-day basis to determine the amount of development. Cumulative Δd_k was determined separately in each developmental stage ("stage" expressed in Fig. 1a)—egg, larva, pupa, and adult—as their developmental rates are calculated differently. Each stage of development is completed when the accumulated development is 1. The developmental stage then proceeds with the next one. The value of Δd_k for each developmental stage was summed continuously as follows to determine the duration of mosquito development in the life history of the mosquito:

$$C_{total} = \sum_{k=l}^m \Delta d_{egg,k} + \sum_{k=m+1}^n \Delta d_{larva,k} + \sum_{k=n+1}^o \Delta d_{pupa,k} + \sum_{k=o+1}^p \Delta d_{adult,k} \quad (2)$$

where C_{total} is the cumulative development; l , $m+1$, $n+1$, and $o+1$, denote the start day of each developmental stage; m , n , o , and p denote the end day of each developmental stage; and $\Delta d_{egg,k}$, $\Delta d_{larva,k}$, $\Delta d_{pupa,k}$, and $\Delta d_{adult,k}$, are the development of eggs, larvae, pupae, and adults at the k th day. The value of each Δd_k ranges from 0 to 1; hence, C_{total} ranges from 0 to 4 (Fig. 1c). Values between 0 and 1 were attributed to embryonic development. Larval and pupal development was assigned values between 1 and 2, and between 2 and 3, respectively. Values exceeding 3 were assigned after the emergence of adults. Values exceeding 4 were attributed when adult mosquitoes oviposited eggs. The alternation of generations was counted over a 1-year period (G_q : q th generation), and the maximum number was recorded as the maximum number of generations (G_{max}) to estimate the frequency of occurrence (Kiritani, 2006; Kashiwada & Ohta, 2010).

3.2 Water balance model for moisture conditions of the mosquito habitat

The growth and development of immature mosquitoes can occur in small water bodies such as puddles or artificial water containers. To consider the potential distribution of *Anopheles* mosquitoes, the availability of a "natural" water surface was assumed in this study. There was no consideration of human activities such as irrigation or sewerage systems. Under natural conditions, the mosquito habitat would be small pools in marshes or wetlands with

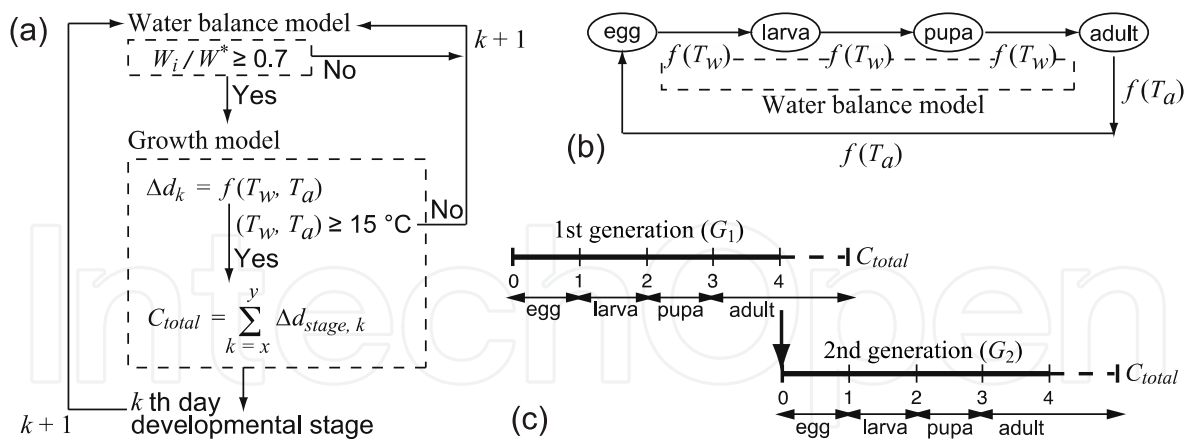


Fig. 1. Model procedures. (a) Determination of moisture conditions and mosquito growth; (b) Relationship between life history and temperatures; (c) Calculation of mosquito growth.

some plant cover. Therefore, in the present study, *Anopheles* mosquitoes were assumed to develop in a small water body with soil, which is an area of several tens of square meters. The soil moisture content in the mosquito habitat must be estimated to exclude areas that are too arid for an immature mosquito to survive. Subsequently, soil moisture content at the depth of plant roots was calculated using the water budget approach proposed by Hopp & Foley (2001) and Tao et al. (2003). The soil moisture content was calculated on the i th day (W_i) by using the following equation:

$$W_i = \min (W_{i-1} + P_i + M_i - AE_i \quad \text{or} \quad W^*) \quad (3)$$

where W_{i-1} is the soil moisture content at the end of the previous ($i - 1$) day, P_i is the daily precipitation (mm), M_i is the daily snow melt on the i th day, AE_i is the actual evapotranspiration on the i th day, and W^* is the holding capacity of soil moisture, which reflects the types of soil texture as well as organic content and plant root depth in soil, according to Dunne & Willmott (1996). When the W_i value obtained from these calculations was larger than W^* , W_i was equal to W^* . A similar procedure by Tao et al. (2003) was adopted to define the value of AE_i as a ratio of the available moisture content to the potential evapotranspiration calculated using the FAO Penman–Monteith method (Allen et al., 1998). Calculation of the potential evapotranspiration requires data for net radiation, air temperature, air humidity, and wind speed. Net radiation was calculated using an energy balance equation as described in the next section (Ohta et al., 1993a; 1995; Ohta & Kimura, 2007), with basic climate factors and geographical data such as albedo and altitude. The values of air temperature and humidity were directly used in the model. In the present study, wind speed was assumed to be constant at 2 m s^{-1} , according to Allen et al. (1998), because the wind speed in modeled plant populations is uncertain.

3.3 Estimation of the temperature of water bodies inhabited by mosquitoes

Although the temperatures of the water bodies in which *Anopheles* mosquitoes live directly affect immature mosquito development, water temperature has unfortunately not been measured with fine resolution either spatially or temporally, in contrast to what has been performed for air temperature and precipitation. Many researchers (e.g., Hopp & Foley, 2001) often substituted air temperature for water temperature. However, the daily average

water temperature in temperate regions is 2–4°C lower than the daily average air temperature during the period of insufficient net radiation in the winter (Ohta et al., 1993a; Ohta & Kimura, 2007). Conversely, the daily average water temperature is 1–2°C higher than the daily average air temperature in the spring (Ohta et al., 1993a; Ohta & Kimura, 2007). Because these seasonal changes in the differences between air and water temperatures are complex, it cannot be assumed that air temperature is equivalent to water temperature. If these daily differences in temperatures are summed during the growing season of the mosquitoes, the calculation error will gradually increase.

The contribution of the energy fluxes in the soil, stored per unit water column, to the energy balance of shallow waters can be omitted if the energy balance is estimated daily or for a prolonged period. Because the energy stored in plant biomass is very small compared to the other components of the energy balance equation, the energy balance of shallow waters without the percolation and flux of irrigation (Ohta et al., 1993a; 1995; Ohta & Kimura, 2007) can be simply expressed using the following equation:

$$R_n = 15h(e_{sat} - e_a) + h(T_w - T_a) \quad (4)$$

where R_n is the net radiation at the water surface ($W\ m^{-2}$), h is the transfer coefficient for sensible heat, e_{sat} is the saturation vapor pressure at the water temperature (kPa), e_a is the water vapor pressure in air (kPa), T_w is the water temperature at a depth of 0.05–0.10 m (K), and T_a is the air temperature (K). It is assumed that the value of h without the plants is nearly constant at $8.36 \times 10^{-5}\ W\ m^{-2}\ K^{-1}$. In the presence of a relatively large difference between T_w and T_a , the net radiation affecting T_w can be given by

$$R_n = R_{na} - h_R(T_w - T_a) \quad (5)$$

where R_{na} is the net radiation ($W\ m^{-2}$) to be calculated assuming that T_a equals T_w , $h_R (= 4\sigma T_a^3)$ is the radiative heat transfer coefficient ($W\ m^{-2}$), and σ is the Stefan-Boltzmann constant ($W\ m^{-2}\ K^{-4}$). From equations (4) and (5), the daily mean of T_w can be obtained numerically by using the daily means of the basic climate observation values as described by Ohta et al. (1993a; 1995) and Ohta & Kimura (2007).

This modeled shallow water condition is nearly the same as the ideal habitat for the immature stages of *Anopheles* mosquitoes considered in the present study. Therefore, T_w was estimated using the simple energy balance model as well as with the methods developed by Ohta et al. (1993a; 1995) and Ohta & Kimura (2007). Calculation of T_w requires basic climate observation values, including air temperature, solar radiation, cloud cover, and vapor pressure.

3.4 Validation of the model

Our model as described above was validated using many observations in the study area obtained from published data (Ono, 1992; Dev, 1996; Konradsen et al., 1998; Lee et al., 2002; Chen et al., 2002; Overgaard et al., 2002; Toma et al., 2002; Singh et al., 2004; Yeom et al., 2005; Chen et al., 2006; Rueda et al., 2006). The main results of the model validation are summarized below.

If the value of the cumulative development (C_{total}) calculated from the k th day was greater than 3, we defined the k th day as the day of mosquito emergence. This calculation was then conducted in all cases where the developmental start day was 1st–365th day of the year. As the mosquito could have emerged across different years, the calculation period included 2

years. The first date of mosquito emergence was defined as the mosquito appearance date, and the end date of mosquito emergence was defined as the mosquito disappearance date (Kashiwada & Ohta, 2010). The predicted emergence or disappearance dates obtained from the model were concordant with the observation data. Although the root mean square errors between the observed and modeled values for these dates were approximately 25 days, the values were acceptable for simulating the potential mosquito distribution, because the mosquito occurrence observations were repeated over several weeks to a few months, as described previously (Dev, 1996; Konradsen et al., 1998; Overgaard et al., 2002).

During comparison of the more detailed observation data at representative sites, which ranged from temperate to subtropical zones (Ono, 1992; Konradsen et al., 1998; Lee et al., 2002; Toma et al., 2002), the model was able to estimate seasonal patterns of occurrence of mosquitoes with reasonable accuracy (Kashiwada & Ohta, 2010). In addition, the geographical distributions of the northern limit of the mosquitoes in Monsoon Asia obtained from this model were corroborated by the observed distributions in summer (Kashiwada & Ohta, 2010).

4. Data used for calculation

4.1 Current climate data

Data for the Asian monsoon region (70–150° E, 10° S–50° N) were used in the model. All meteorological data had a spatial resolution of 0.5° longitude × 0.5° latitude. The Climatic Research Unit – Global Climate Dataset, available through the IPCC Data Distribution Center (New et al., 1999) was used for the model calculations. Monthly data for air temperature, precipitation, shortwave radiation, vapor pressure, and cloud cover were included in the dataset for 1961–1990 climate normals. If daily data were not available for the model, monthly values were converted to daily data by using linear interpolations or cubic spline, ensuring consistency of the daily values with monthly average or total values. Elevation data derived from GTOPO30 (U.S. Geological Survey) were used to calculate vapor pressure and longwave radiation in the present study, as well as correction methods described in Ohta et al. (1993b). Elevation data in GTOPO30 are regular at a spatial resolution of 30 arcseconds (approximately 1 km); we averaged and converted them to a spatial resolution of 30 arcminutes. The monthly surface albedo (0–1) in each 0.5° longitude × 0.5° latitude resolution (Ohta et al., 1993a) was used. When the air temperature was less than 0°C, the value of surface albedo was set to 0.7.

4.2 Future climate data

The future climate variables used in this study were obtained from the climate projections of the Coupled General Circulation Model (CGCM3.1) by the Canadian Centre for Climate Modelling & Analysis, which contributed to the IPCC 4th Assessment Report (Flato et al., 2000). The climate variables of the CGCM3.1/T63 involved daily mean air temperature, daily total precipitation, and daily accumulated shortwave radiation on a spatial resolution of 2.81° longitude × 2.81° latitude. These values are outputs from the IPCC 720 ppm stabilization experiment (A1B scenario) using the CGCM3.1 for the years 2001–2100 initialized from a simulation experiment starting from the end of the 20th century. In the present study, the spatial resolution of the output data from CGCM3.1/T63 was converted into a spatial resolution of 0.5° longitude × 0.5° latitude by using the interpolation method.

5. Energy and water balances of the habitat of mosquitoes

5.1 Net radiation at the water surface

Soil moisture content and water temperature were determined by the net radiation obtained from equations (4) and (5). In addition, because net radiation is the only energy source on which all life depends, it is essential to draw the geographical distribution of net radiation to estimate the life history of mosquitoes. Fig. 2 compares the seasonal changes in the geographical distribution of net radiation between the current and future climates.

In the current climate, the amount of monthly mean net radiation in warm- and cool-temperate and subarctic climate zones changes seasonally, reflecting the difference in the characteristics of geographical location and the effects of the Asian monsoon. In subtropical and tropical climate areas at latitudes below 20°N, hardly any seasonal changes in net radiation occur throughout the year. In summer, the amount of net radiation at latitudes above 20°N as well as in subtropical and tropical climate areas increases rapidly.

The amount of net radiation in areas with alpine, ice, and desert climates is negative, except in summer; this implies the emission of thermal radiation from underlying surfaces into the atmosphere. In the future climate conditions, areas with negative net radiation in autumn, winter, and spring will decrease gradually. A noteworthy difference between the current and future climates in Eastern China is the increase in the amount of net radiation from June to October during which the average amplitude of the increase is approximately 30 W m⁻². This is mainly because the amount of shortwave radiation during the same period obtained from the CCGM3.1 increases independently of increases in air temperature.

5.2 Moisture conditions of the mosquito habitat

Fig. 3 represents the seasonal changes in geographical distribution of soil moisture conditions for the mosquito habitat under the present and future climates. This value is expressed as the ratio of W_i / W^* . The calculation was conducted daily; the value of the 15th day of each month is indicated on the map. These maps indicate that many of the areas of the Asian monsoon region generally have humid conditions. The values of W_i / W^* in humid regions (e.g., the whole areas in subarctic, temperate, and subtropical or tropical zones), in alpine regions (e.g., the Himalayas), and in the arid belt (i.e., The Gobi, Takla Makan, and Great Indian Desert, and the Mongol Plateau) do not change seasonally, and water conditions in these areas are constant throughout the year (Fig. 3a). In contrast, the values of W_i / W^* in some areas, including in the entire area of the Indian Peninsula and excluding the west coast and Indochina (i.e., Myanmar, Thailand, Laos, Cambodia, and Vietnam), change seasonally (Fig. 3a). Especially, from December to April, the soil moisture contents in these areas are remarkably limited, reflecting the dry season with small precipitation.

These characteristics of soil moisture content in the mosquito habitat under the current climate conditions would not change under the future climate conditions (Fig. 3a and 3b). Thus, the increases in evapotranspiration from the soil surface due to the increases in air temperature, shortwave radiation, and net radiation in the future climate condition do not affect the soil moisture content in the mosquito habitat.

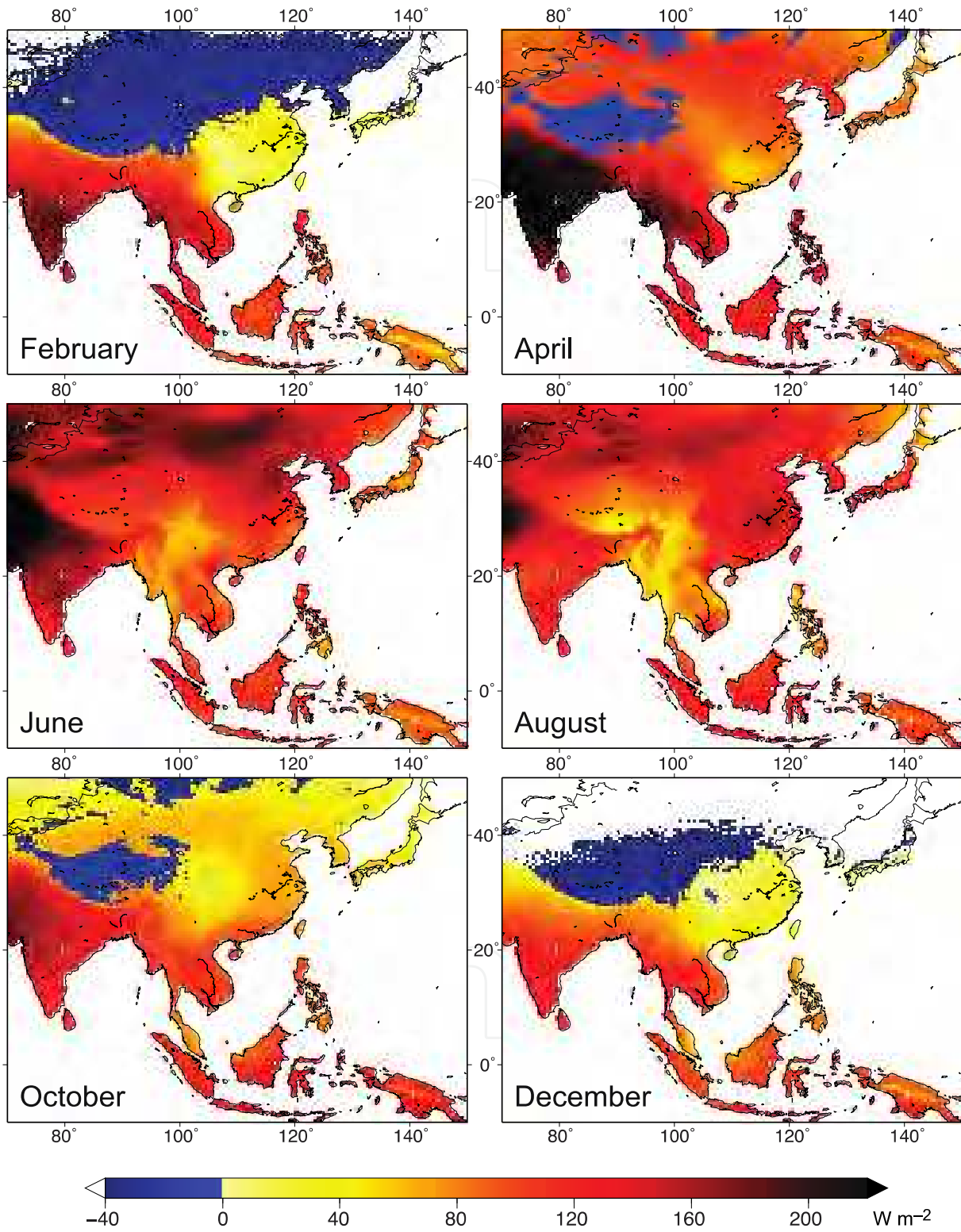


Fig. 2a. Seasonal patterns of geographic distribution of monthly net radiation at water surfaces under current climate (W m^{-2}).

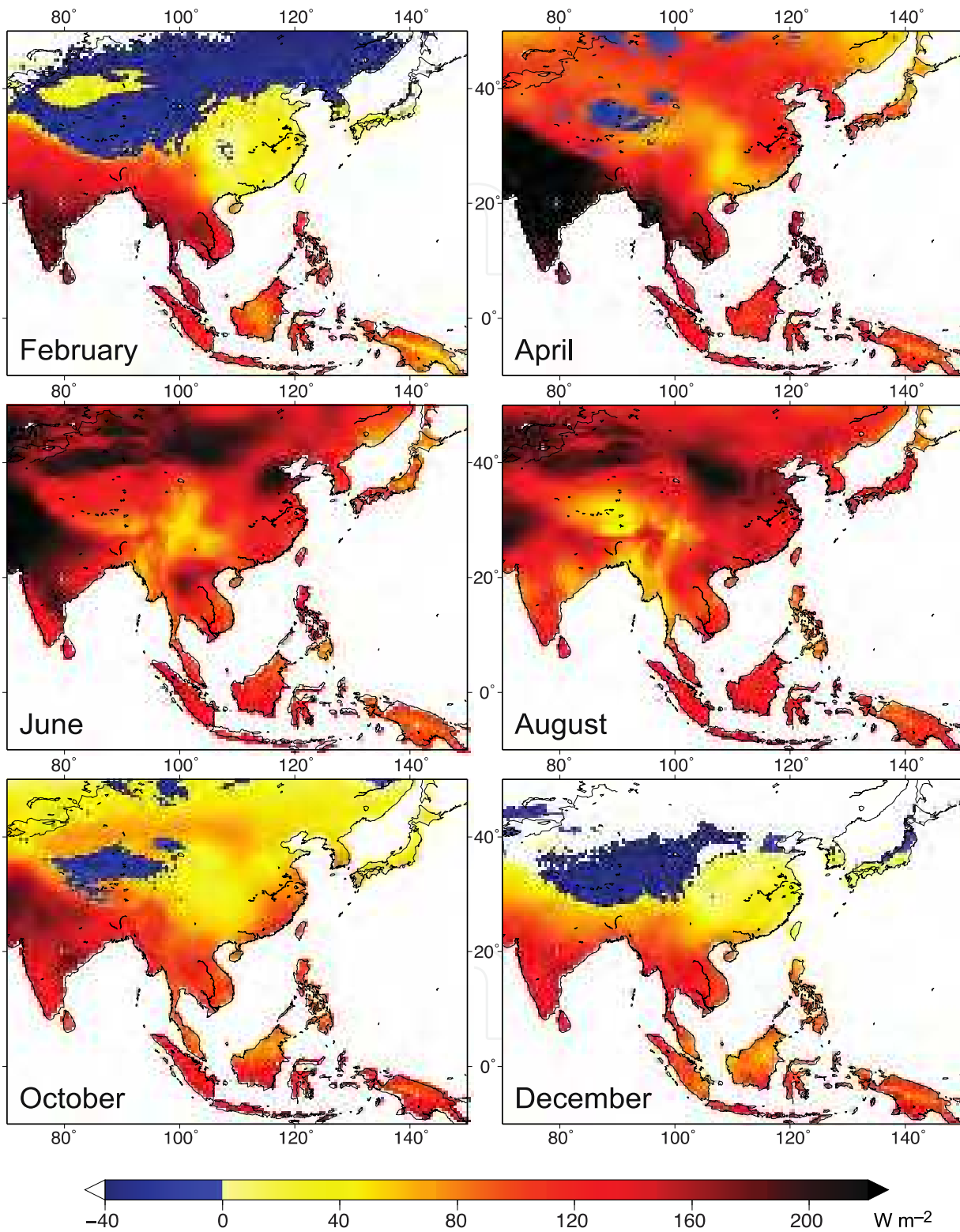


Fig. 2b. Seasonal patterns of geographic distribution of monthly net radiation at water surfaces under future climate ($W m^{-2}$).

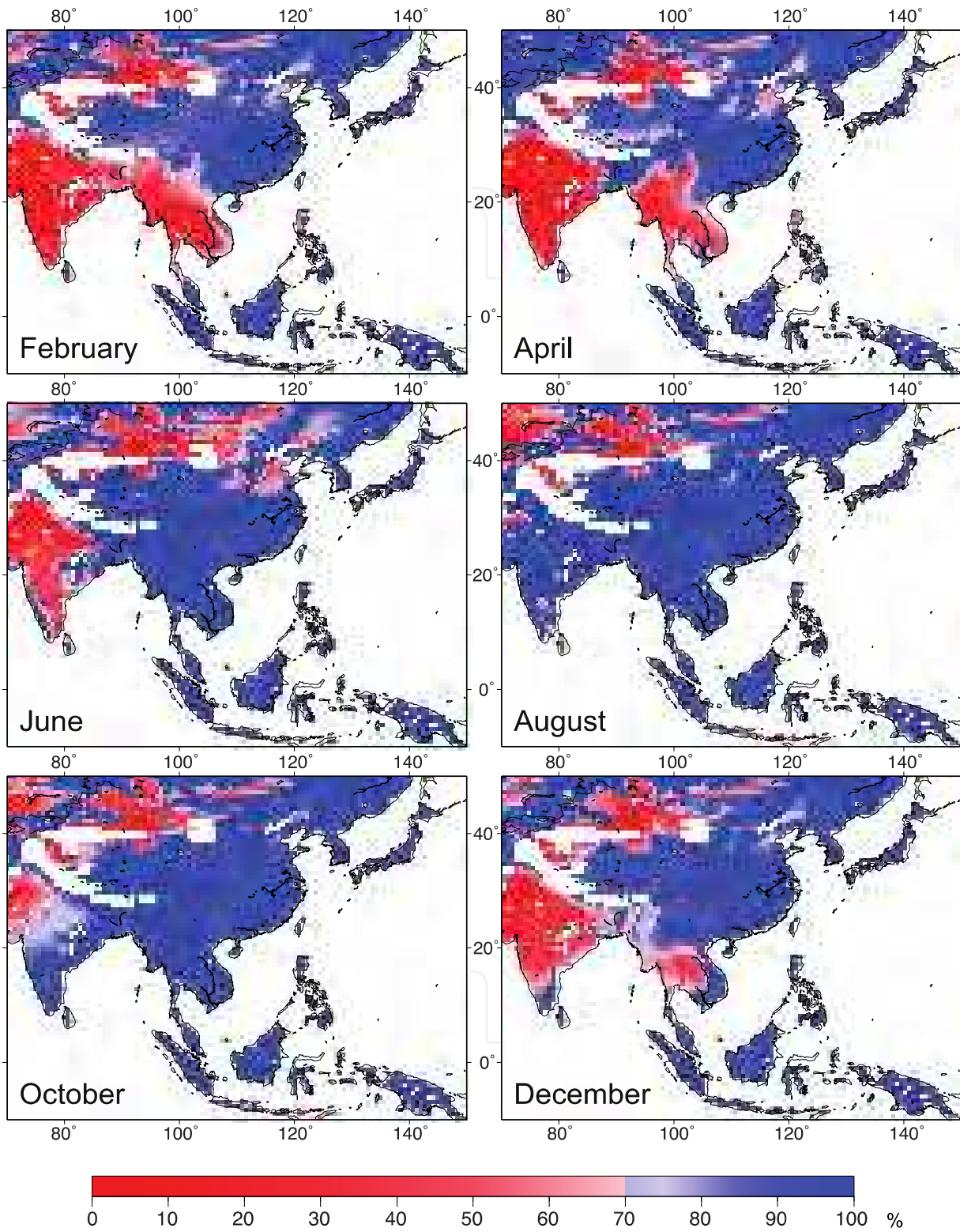


Fig. 3a. Seasonal patterns of geographic distribution of the monthly mean soil moisture under current climate (%).

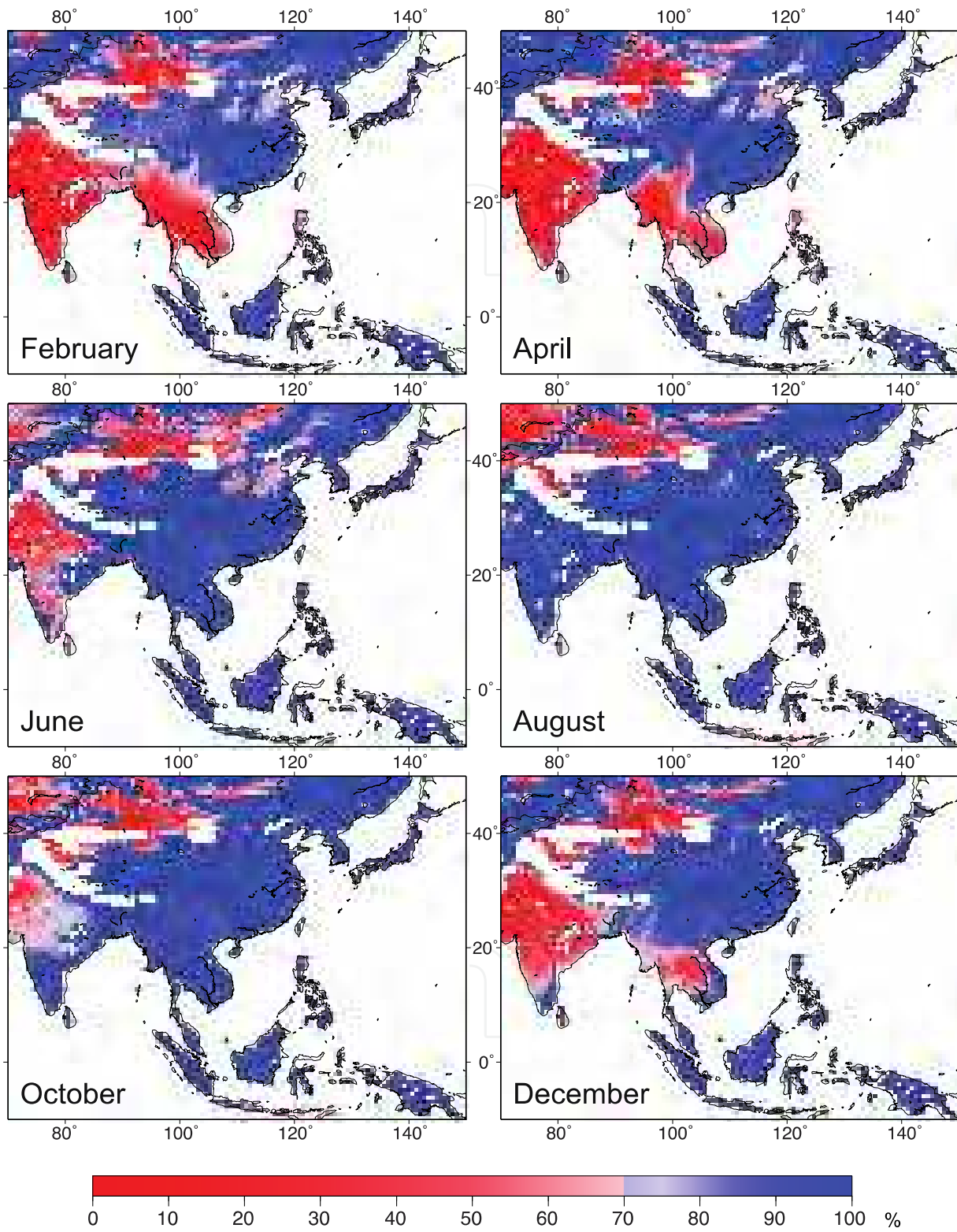


Fig. 3b. Seasonal patterns of geographic distribution of the monthly mean soil moisture under future climate (%).

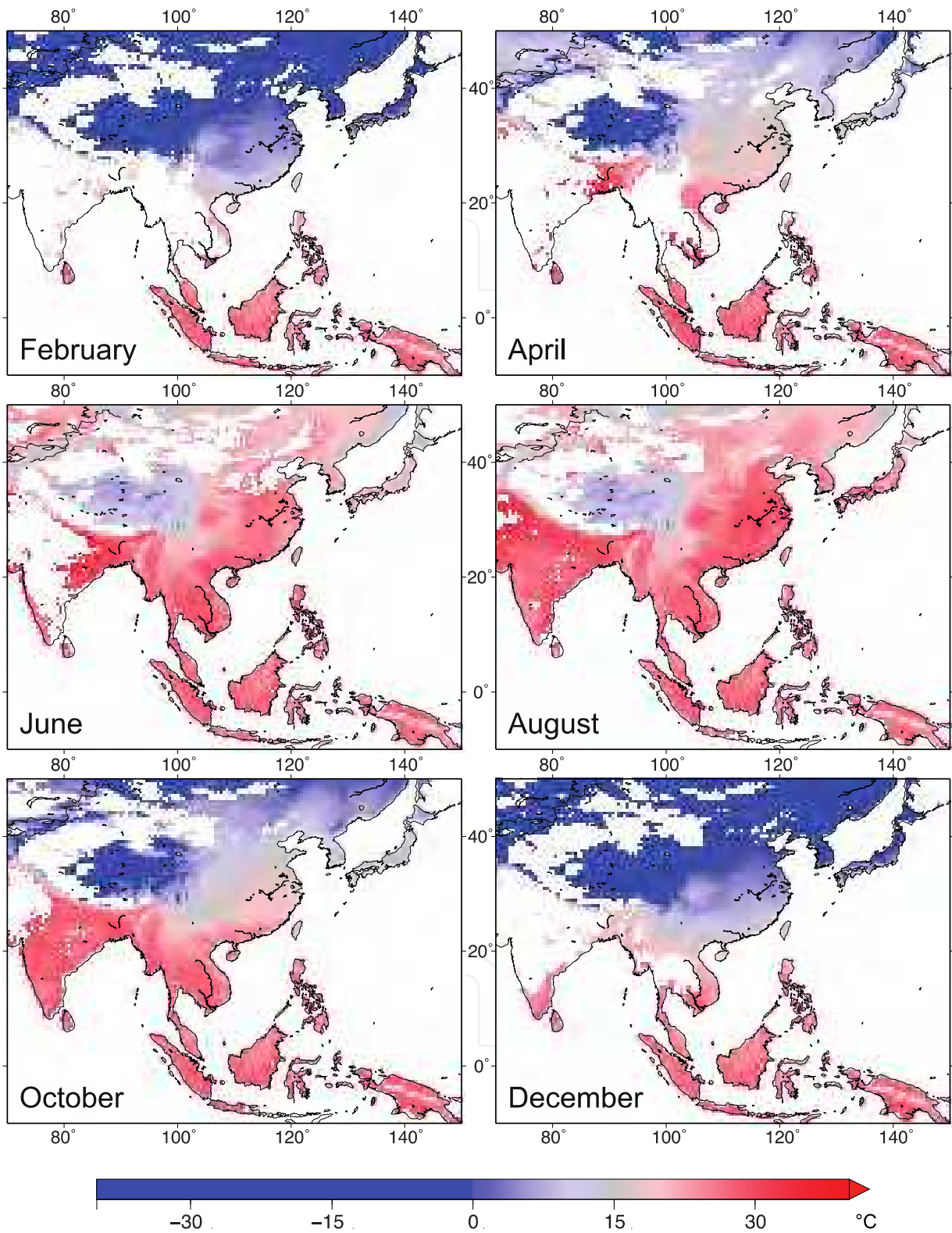


Fig. 4a. Seasonal patterns of geographic distribution of the daily mean water temperature under current climate ($^{\circ}\text{C}$). The white areas denote the scarcity of surface water of soil unsuitable for mosquitoes.

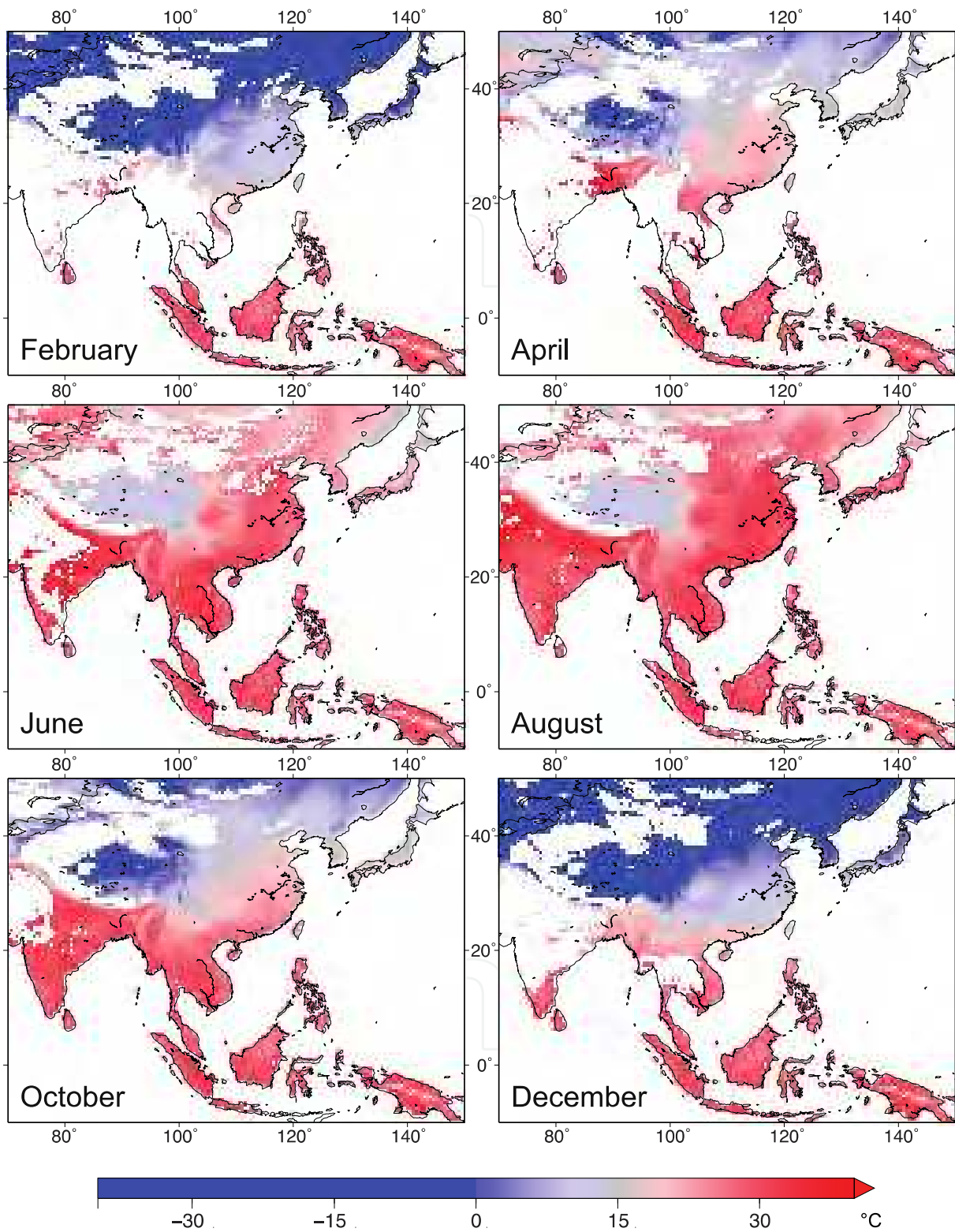


Fig. 4b. Seasonal patterns of geographic distribution of the daily mean water temperature under future climate (°C). The white areas denote the scarcity of surface water of soil unsuitable for mosquitoes.

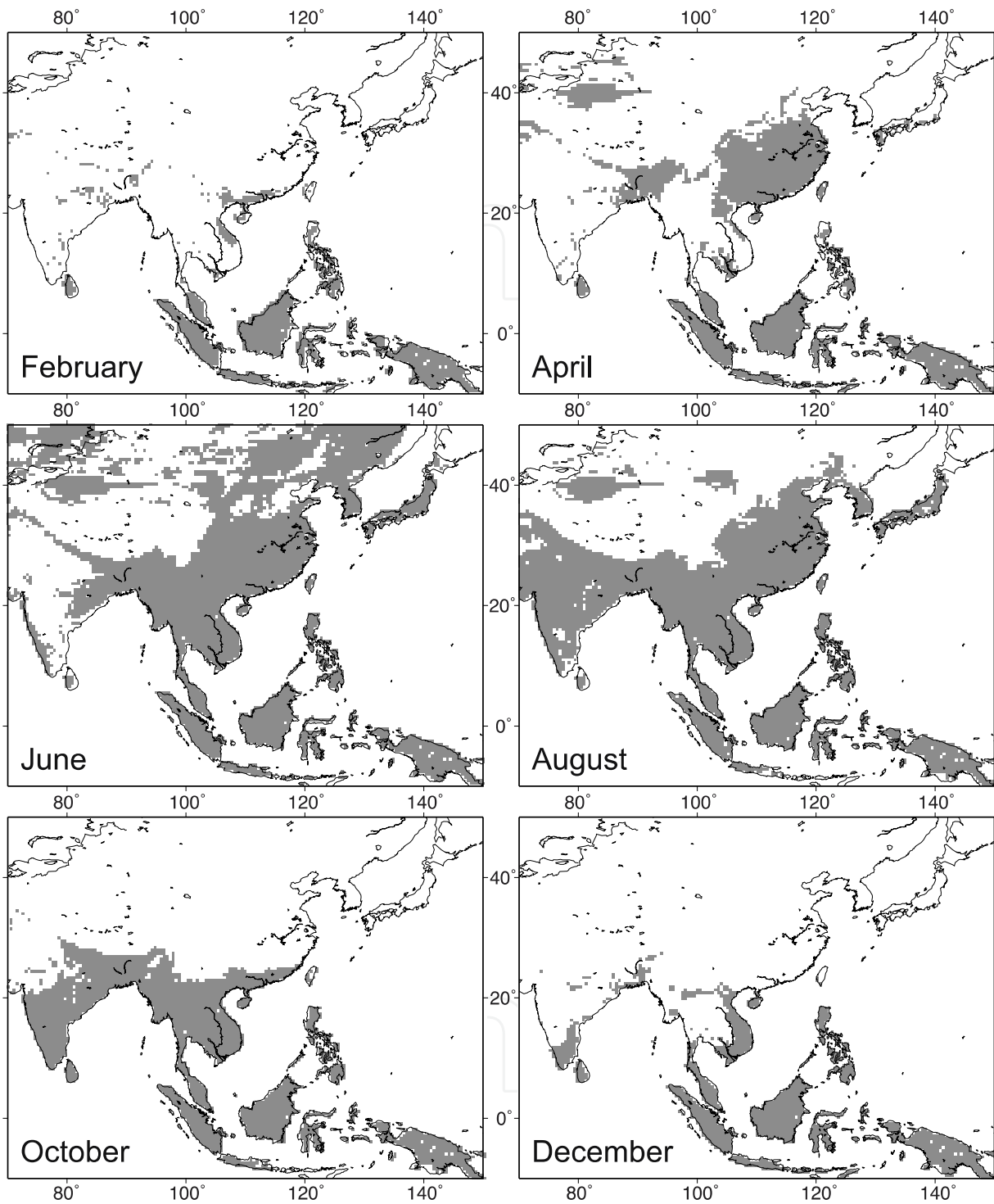


Fig. 5a. Geographic distribution of bimonthly adult mosquito occurrence under current climate. Gray shading denotes the area in which the maximum development reached the adult stage (when the cumulative developmental stage (C_{total}) exceeded 4).

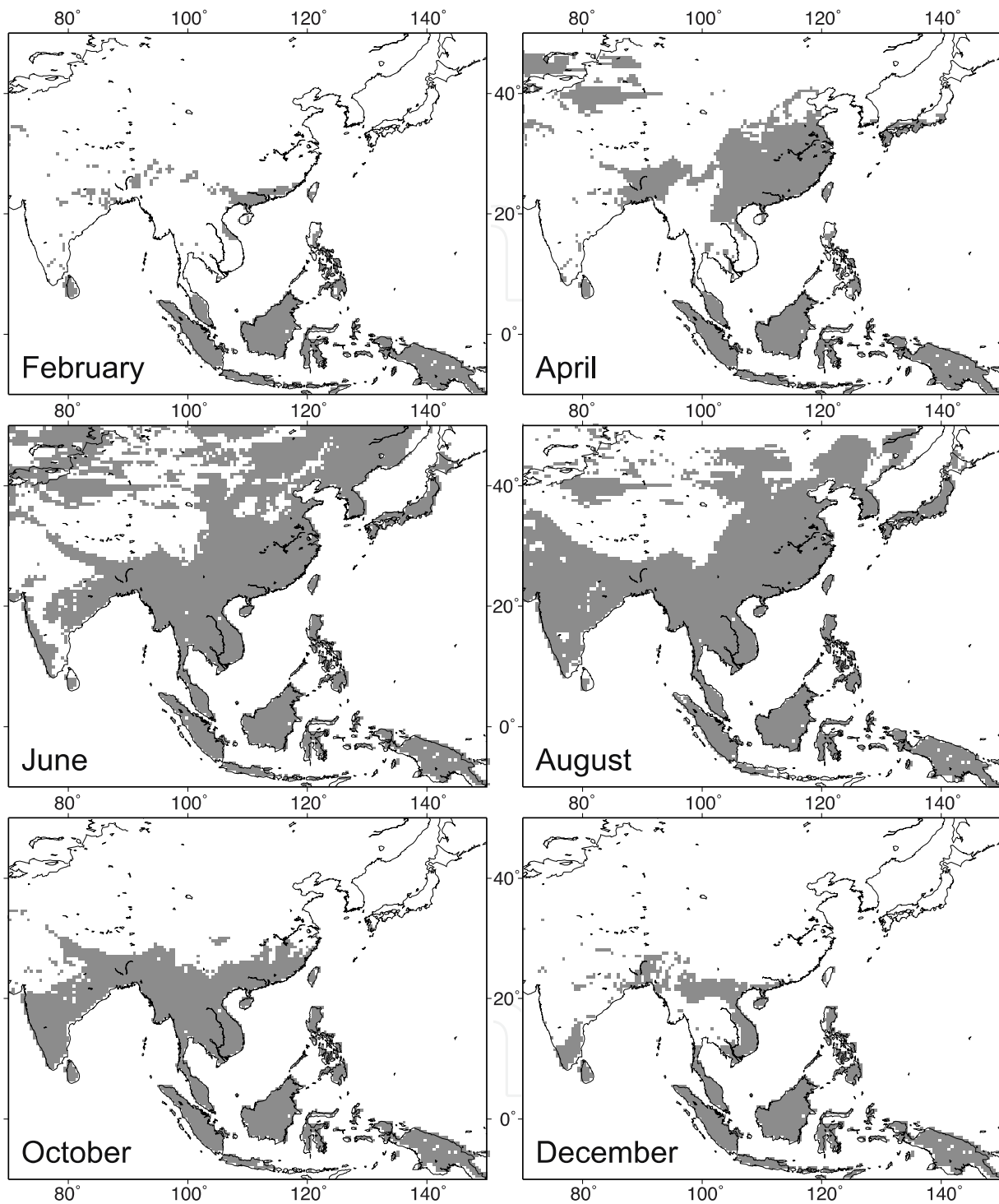


Fig. 5b. Geographic distribution of bimonthly adult mosquito occurrence under future climate. Gray shading denotes the area in which the maximum development reached the adult stage (when the cumulative developmental stage (C_{total}) exceeded 4).

5.3 Temperature of the water bodies inhabited by mosquitoes

Fig. 4 shows the changes in the temperature of the water in which immature mosquitoes live in the future climate conditions. The smallest difference between the water temperatures in tropical and subarctic regions is found in mid-summer; the difference gradually becomes larger, peaking in winter (Fig. 4). The seasonal patterns of the geographical distribution of water temperatures in Monsoon Asia show a trend similar to those of air temperatures. The temperatures of ponded shallow water increase by approximately 1.0–2.5°C in the future climate (Fig. 4), synchronizing the changes in air temperatures obtained from the CGCM3.1. However, the magnitudes of increase in water temperature in the future climate are approximately 0.5–1.0°C smaller than the magnitudes of increase in air temperature. This is because the temperature rise is suppressed by the energy characteristics of water.

The white areas in Fig. 4 denote the scarcity of surface water of soil unsuitable for mosquitoes. As described in section 3.1, because mosquito development begins when water temperatures exceed 15°C, the blue areas in Fig. 4 denote the shortage of thermal resources for mosquitoes, and the red areas in Fig. 4 represent the growing period of mosquitoes in terms of water temperatures. On comparing Fig. 4a and 4b, it is apparent that the red areas in southeastern China along the Tropic of Cancer extend in April and December. Furthermore, the red areas in eastern China, especially those including densely populated cities, extend in October. The water temperatures in the southern and eastern parts of China in the future climate increase by approximately 3°C compared with those in the current climate. When considering future mosquito growth, it is important to consider that this value in China is greater than that in temperate regions, the eastern part of Indochina (approximately 2°C), and inland India (approximately 1.5°C).

6. Spatiotemporal distribution of *Anopheles* mosquitoes

6.1 Shift of seasonal changes in geographical distribution

To clarify seasonal variations in the geographical distribution of adult mosquito abundance, the developmental stage of the mosquitoes was determined using the model described in section 3. Fig. 5 shows the abundance of mosquitoes when the cumulative developmental stage (C_{total}) reached 4. The most notable observation in Fig. 5a is that mosquito emergence in the present climate is limited seasonally in most areas of Monsoon Asia, including subarctic regions, cool- and warm-temperate regions, and the Indian and Indochina Peninsula. However, in large areas of tropical regions in Southeast Asia, including Sumatra, Kalimantan, Sulawesi, New Guinea, and the Philippines, the adult emergence of *Anopheles* occurs year round. Adult mosquitoes in semi-arid tropical countries such as Thailand and Myanmar appeared only from June to October. In inland India, mosquitoes only appeared from August to October. The appearance of adult mosquitoes in temperate regions such as Japan, Korea, and northeastern China was limited to summer.

In the future climate (Fig. 5b), although there is little change in adult emergence in temperate regions in spring, the northern distribution limit of adult mosquitoes in mid-summer could shift approximately 200–300 km north. In autumn, the northern distribution limit of adult emergence in subtropical regions such as southern China could shift approximately 100 km north. In addition, *Anopheles* could still potentially appear even in winter. This suggests that the areas where mosquitoes are able to appear year round could expand in the subtropical regions of southern China. On the other hand, the emerging pattern of *Anopheles* in tropical regions, excluding the southwestern coastal areas of the

Indian Peninsula, in the future climate are unchanged, compared to that in the current climate.

6.2 Changes in the average developmental length and geographical distribution of the maximum number of generations of *Anopheles* mosquitoes

The duration of mosquito development from egg hatching to adult was counted from the day when the egg stage began to the day of oviposition activity. This duration, which is required for the development of the adult mosquito, was defined as the developmental length in the present study. The average developmental length ($D_{average}$, day) during a year was calculated as follows:

$$D_{average} = \left(\sum_{q=1}^{G_{max}} D_q \right) \times \left(\frac{1}{G_{max}} \right) \quad (6)$$

where D_q is the developmental length (day) of the q th generation from egg hatching to adult emergence, q is the number of generations, and G_{max} is the maximum number of generations as described in section 3.1. $D_{average}$ indicates the necessary duration of development from an egg to the adult mosquito. Model estimations of $D_{average}$ in the current climate obtained using equation (6) range from approximately 2 weeks to more than 1 month (Fig. 6). The $D_{average}$ value in the regions with the shortages of water and thermal resources is higher than that in the regions suitable for the growth of mosquitoes. When the $D_{average}$ in the current climate is less than 20 days, the $D_{average}$ in the future climate is approximately 2 days shorter than that in the current climate; when the $D_{average}$ in the current climate is more than 20 days, the $D_{average}$ in the future climate is approximately 3 days shorter than that in the current climate (Fig. 6).

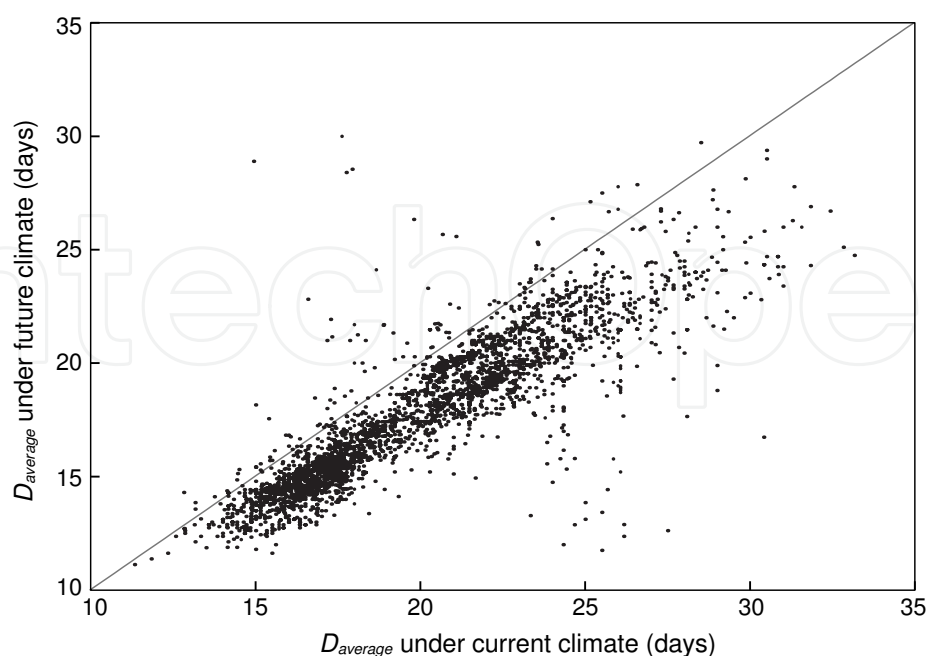


Fig. 6. The average duration of mosquito development (day) under current and future climates.

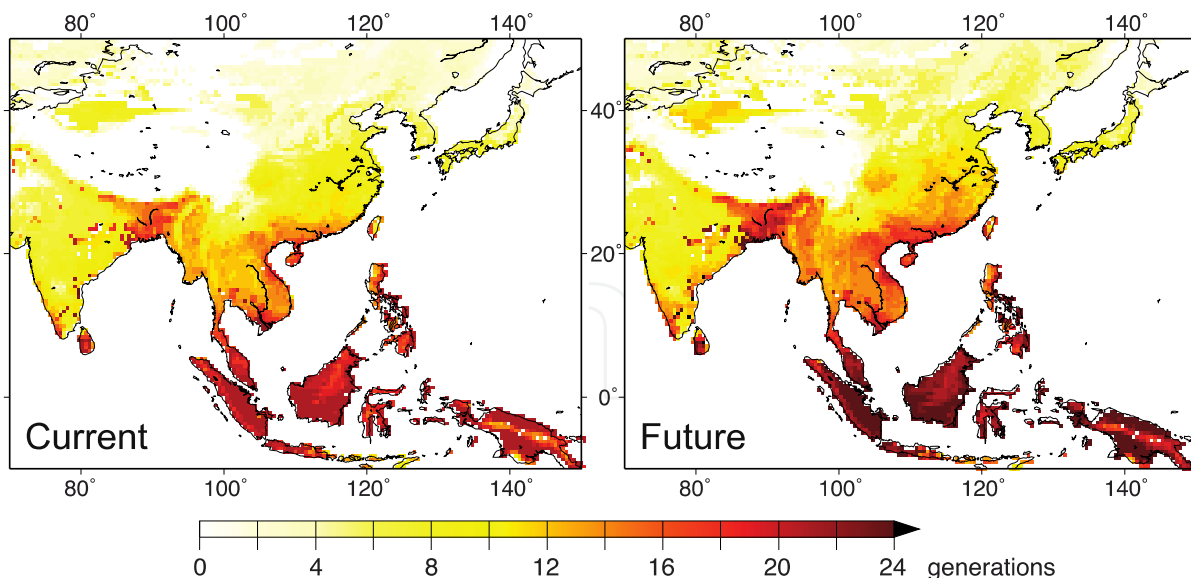


Fig. 7. Geographic distribution of the maximum number of generations under current and future climates.

These smaller $D_{average}$ values in the future climate increase the maximum number of successive generations (G_{max}) in most areas and increase the frequency of mosquito occurrence (Fig. 7). Fig. 7 indicates that G_{max} depends on the availability of moisture (Fig. 3) and on water temperature (Fig. 4). The values of G_{max} in temperate regions and inland India were approximately 6 to 8 generations in the current climate. The G_{max} in the eastern part of Indochina and southern China were approximately 14 to 16 generations. The G_{max} values in tropical regions were more than 20 generations.

In the future climate conditions, the G_{max} in tropical regions and southern and southeastern China would increase by approximately 3 generations under warmer climate conditions. The G_{max} in temperate regions would increase by approximately 2 generations, and the G_{max} in inland India would increase by approximately 1–2 generations, although the growing period of the mosquitoes is still limited to the period from August to October. However, the increase in the G_{max} in eastern Indochina would be slightly less than 1 generation in the future climate conditions. In addition, the G_{max} in southern Thailand would decrease by 1 generation.

7. Discussion and conclusions

The present model, driven by simple meteorological data, was able to predict the effects of future climate change on the temporal variations and the potential distribution of the *Anopheles* mosquito that possibly transmits malaria in Monsoon Asia. Four main conclusions can be drawn from the results.

First, although the G_{max} values in the future climate would not increase in regions where water resources are a limiting factor for the growth of mosquitoes, the future G_{max} values would generally increase by approximately 2–3 generations (Fig. 7). This is because the future climate projected by the CGCM3.1 would improve the current thermal environment in regions with shortage of thermal resources (Fig. 2), especially increased water temperature suitable for the growth of mosquitoes (Fig. 4). However, the water resources in

semi-arid regions would remain unchanged in the future climate (Fig. 3). Consequently, the G_{max} values in the future climate increase by the function of smaller $D_{average}$ values (Fig. 6) owing to the increase in water temperature (Fig. 4). Accordingly, the southern part of China will experience the most remarkable changes in vector distribution in future climate conditions. The northern limit of the current distribution of tropical *Plasmodium falciparum* malaria in Monsoon Asia could shift approximately 100 km north, especially in autumn (Fig. 5). Another region with distinct changes in vector distributions in future climate conditions is the eastern part of China, which currently has a low density of the current vector species. The northern limit of the current distribution of temperate *Plasmodium vivax* malaria in Monsoon Asia could shift approximately 200–300 km north, especially in spring (Fig. 5). The survival of the mosquitoes in the southwestern coastal regions of India in early summer would be likely in the future climate conditions (Fig. 5), reflecting improved soil moisture conditions (Fig. 3).

Second, the shifts in the seasonal patterns of the geographical distributions of vectors projected in this study are concordant with those of the malaria potential obtained from other studies (Martens et al., 1999; Rogers & Randolph, 2000; van Lieshout et al., 2004; Bhattacharya et al., 2006). The integrated model with socioeconomic processes predicts the expansion of tropical malaria in southern China (Rogers & Randolph, 2000; van Lieshout et al., 2004). According to Martens et al. (1999), the temperate regions where malaria can occur would extend in the future climate in eastern China; this prediction is concordant with our results. In addition, the future geographical distributions of vectors in the southwestern coastal regions of India mentioned above conform to the projected endemic regions obtained from the simulation with a regional climate model (Bhattacharya et al., 2006). Interestingly, the northern limit of the geographical distribution of the vectors estimated in the present study is less than that estimated by Martin & Lefebvre (1995) who studied the annual potential. Also, it must be noted that the geographical distributions obtained from these studies indicate the epidemic potential of malaria (Hay et al., 2009; Gething et al., 2010) and not that of the vector. Although long-term trends for malaria transmission were not significantly associated with a recent climate warming (Gething et al., 2010), it was found from this study that the potential ranges of vector species could change due to future climatic conditions.

Third, the present model that described the developmental processes of a representative *Anopheles* mosquito is unable to adequately or precisely indicate the temporal patterns of the mosquito emergence, especially in tropical regions. Using the original concept of “intrinsic optimum temperature for development” and a thermodynamics model, Ikemoto (2005) concluded that the growth of *Anopheles* mosquitoes is suppressed and stressed by temperatures exceeding 30°C. According to our projections, the future G_{max} values in the all the tropical regions would increase by 2 generations. However, considering that high temperatures injure mosquitoes (Depinay et al., 2004; Ikemoto, 2005; 2008), it is possible that these increases in G_{max} in tropical regions will not occur. The possibility of a subsequent generation is only one of the factors for determining the magnitude of a population. This might lead to overestimations in tropical regions. Therefore, a population dynamics model that can simulate the growth of many individual mosquitoes stochastically should be applied to predict the future distribution of mosquitoes. The model based on population dynamics provides useful data regarding the magnitudes of a mosquito population in future climate conditions as well as the maximum number of generations for the risk assessment of malaria. Pascual et al. (2006) suggests that the observed temperature changes would be

significantly amplified by the mosquito population dynamics with a difference in the biological response at least 1 order of magnitude larger than that in the environmental variable.

Finally, the probability of our results regarding changes in G_{max} may increase or decrease the range of the mosquitoes owing to different climate models or future scenarios for greenhouse gas emissions. To elucidate the probability of the projection range, mosquito abundance must be simulated using our model with a variety of future emission scenarios and climate models.

8. Acknowledgements

We wish to thank Prof. Yasushi Morikawa, Prof. Hiroshi Koizumi, and Prof. Shoji Nishimura (Waseda University) for their useful comments on this study. We are also grateful to Miss Momoyo Kashiwada for her technical and devoted support on handling the climate data and collecting the related articles. This study was funded in part by the Ministry of Education, Science and Culture of Japan, Grant-in-Aid for Scientific Research (C-21510022) and a Waseda University Grant for Special Research Projects (2008B-244; 2010A-088).

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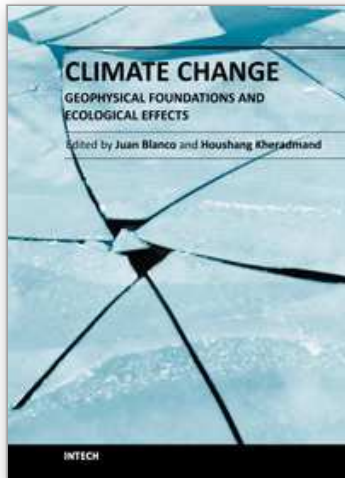
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Climate Change - Geophysical Foundations and Ecological Effects

Edited by Dr Juan Blanco

ISBN 978-953-307-419-1

Hard cover, 520 pages

Publisher InTech

Published online 12, September, 2011

Published in print edition September, 2011

This book offers an interdisciplinary view of the biophysical issues related to climate change. Climate change is a phenomenon by which the long-term averages of weather events (i.e. temperature, precipitation, wind speed, etc.) that define the climate of a region are not constant but change over time. There have been a series of past periods of climatic change, registered in historical or paleoecological records. In the first section of this book, a series of state-of-the-art research projects explore the biophysical causes for climate change and the techniques currently being used and developed for its detection in several regions of the world. The second section of the book explores the effects that have been reported already on the flora and fauna in different ecosystems around the globe. Among them, the ecosystems and landscapes in arctic and alpine regions are expected to be among the most affected by the change in climate, as they will suffer the more intense changes. The final section of this book explores in detail those issues.

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