

**PERSISTENCE OF MOSQUITO VECTOR AND DENGUE:
IMPACT OF SEASONAL AND DIURNAL
TEMPERATURE VARIATIONS**

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ABSTRACT. Dengue, a mosquito-borne disease, poses a tremendous burden to human health with about 390 million annual dengue infections worldwide. The environmental temperature plays a major role in the mosquito life-cycle as well as the mosquito-human-mosquito dengue transmission cycle. While previous studies have provided useful insights into the understanding of dengue diseases, there is little emphasis put on the role of environmental temperature variation, especially diurnal variation, in the mosquito vector and dengue dynamics. In this study, we develop a mathematical model to investigate the impact of seasonal and diurnal temperature variations on the persistence of mosquito vector and dengue. Importantly, using a threshold dynamical system approach to our model, we formulate the mosquito reproduction number and the infection invasion threshold, which completely determine the global threshold dynamics of mosquito population and dengue transmission, respectively. Our model predicts that both seasonal and diurnal variations of the environmental temperature can be determinant factors for the persistence of mosquito vector and dengue. In general, our numerical estimates of the mosquito reproduction number and the infection invasion threshold show that places with higher diurnal or seasonal temperature variations have a tendency to suffer less from the burden of mosquito population and dengue epidemics. Our results provide novel insights into the theoretical understanding of the role of diurnal temperature, which can be beneficial for the control of mosquito vector and dengue spread.

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1. Introduction. With the worldwide situation of 2.5 billion people living in areas with risk of dengue, about 390 million annual new dengue infections, and 500,000 annual hospitalization [4, 5, 41], dengue fever poses serious global health concerns. Moreover, dengue fever is rapidly spreading in the world [4, 35, 41] affecting more than a hundred countries, and actual cause for its rapid spread is still in debate. Because of uncertainty in its transmission mechanism and absence of licensed vaccines or specific therapeutics, studies on the transmission dynamics of dengue are becoming increasingly important. Mathematical modeling can reveal some important insights into dengue transmission dynamics.

Increase in dengue cases, particularly in tropical and subtropical regions, might be due to multiple factors, including inefficient control of its vector (the *Aedes aegypti* mosquito), expansion of the vector, human population growth, urbanization, and climate change [3, 11, 23, 27, 34]. Among various causes, the majority of the cases are linked to climatic factors and human and vector mobility [4, 3, 23, 25]. Specifically, it is known that the environmental temperature can highly affect the dengue transmission [4, 35, 24], and as a consequence there remains substantial threat that continuous increase of global temperature can exacerbate the geographical expansion of the endemic range of dengue [3, 24, 10, 14, 15, 42]. Therefore, it is critical to understand how the environmental temperature can impact the transmission dynamics of dengue epidemics.

Dengue viruses are transmitted to humans through bites of infected *Aedes* mosquitos and uninfected mosquitos can become infected when they bite infected humans. These inter-species transmission rates as well as incubation periods following transmission have been found to depend on the environmental temperature [9, 17]. More importantly, a change in the environmental temperature can also alter many mosquito entomological parameters [45, 43], such as oviposition rate, maturation rate, and mortality rate, eventually impacting the dengue transmission dynamics. Limiting mosquito population is a commonly practiced method of dengue control as effective vaccines or therapeutics are yet to be developed [4, 45, 31]. Therefore, it is important to include such temperature-influenced entomological and transmission parameters properly into the transmission dynamics models in order to provide useful information for developing prevention and control measures.

As far as the vector-borne diseases are concerned, the temporal variation of the environmental temperature constitutes an important feature impacting disease dynamics [37, 40, 46]. It is a common practice to consider constant temperatures or intraannual seasonally varying temperatures to study the effects of environmental temperature on the insect populations and pathogen transmission [17, 22, 28]. However, in case of dengue virus transmission, only seasonal variation of the environmental temperature can not fully explain the disease epidemics; the diurnal (daily) temperature variation also plays an important role in the dengue transmission dynamics [17]. For example, a temporal change of dengue epidemics in Thailand is not associated with seasonal variation of the temperature, rather it is associated with variation of diurnal temperature fluctuation [17, 8, 20, 29, 30]. Moreover, in nature, mosquitoes and their pathogens undergo temperature conditions that fluctuate throughout the day, on top of experiencing seasonal conditions. Hence, in addition to seasonal variation, diurnal temperature variation needs to be

considered in order to accurately evaluate the effects of environmental temperature on dengue epidemics.

While the previous studies have explored temporal dynamics [17, 18, 21, 26, 44] and spatial spread [35, 23, 24, 15, 7, 36] of dengue, those existing models lack the temperature profiles with coupled diurnal and seasonal variations. How such two different periodic natures embedded in the environmental temperature can impact on disease outcomes and prevention effectiveness still remains unknown. In this study, we develop a model to describe the transmission dynamics of dengue under the environmental temperature with seasonal as well as diurnal variations. Non-linear effects of the environmental temperature in our non-autonomous model are incorporated through entomological and dengue dynamics parameters, which are derived based on laboratory experimental data. We focus on the theoretical and numerical aspects of the non-autonomous model analysis to study how seasonal and diurnal variations of the environmental temperature impact the mosquito reproduction number and the infection invasion threshold, consequently affecting the persistence of mosquito vector and dengue.

2. Mathematical model. We consider mutually exclusive compartments related to aquatic (A), susceptible (M_s), exposed (M_e), and infected (M_i) groups of the female mosquitos as well as susceptible (H_s), exposed (H_e), infected (H_i) and recovered (H_r) groups of humans. We denote the total female mosquito population and the total human population by $N_M(t)$ and $N_H(t)$, respectively. Interactions captured in our model are shown in a schematic diagram (Fig. 2.1) and the governing equations are given by the following system:

$$\begin{cases} \frac{dA}{dt} = k\delta(t) \left(1 - \frac{A}{C}\right) N_M - (\theta(t) + \mu_a(t))A, \\ \frac{dM_s}{dt} = \theta(t)A - \frac{b\beta_m(t)M_sH_i}{N_H} - \mu_m(t)M_s, \\ \frac{dM_e}{dt} = \frac{b\beta_m(t)M_sH_i}{N_H} - (\gamma_m(t) + \mu_m(t))M_e, \\ \frac{dM_i}{dt} = \gamma_m(t)M_e - \mu_m(t)M_i, \\ \frac{dH_s}{dt} = \Lambda_h - \mu_h H_s - \frac{b\beta_h(t)H_sM_i}{N_H}, \\ \frac{dH_e}{dt} = \frac{b\beta_h(t)H_sM_i}{N_H} - (\gamma_h + \mu_h)H_e, \\ \frac{dH_i}{dt} = \gamma_h H_e - (\alpha_h + \mu_h)H_i, \\ \frac{dH_r}{dt} = \alpha_h H_i - \mu_h H_r, \\ A(0) \geq 0, M_s(0) \geq 0, M_e(0) \geq 0, M_i(0) \geq 0, \\ H_s(0) \geq 0, H_e(0) \geq 0, H_i(0) \geq 0, H_r(0) \geq 0. \end{cases} \quad (2.1)$$

In this model, matured mosquitos ($N_M = M_s + M_e + M_i$) lay eggs with the per capita oviposition rate $\delta(t)$, among which a fraction k (a combination of the fraction of eggs hatching to larvae and the fraction of female mosquitoes hatched from all eggs) grow to the aquatic phase (larvae and pupae). Similar to the concept used in the standard logistic equation, a parameter C is introduced to represent the carrying capacity of the mosquito aquatic population, giving the net rate of change of the aquatic mosquito population as $k\delta(t)(1 - \frac{A}{C})N_M$ per unit time. The aquatic mosquitos develop into adult female mosquitoes at a maturation rate $\theta(t)$ and die at a mortality rate $\mu_a(t)$. We assume that female mosquitos newly emerged from the aquatic phase are all susceptible, which die with a natural mortality rate

$\mu_m(t)$. Here, Λ_h and μ_h represent recruitment rate and natural mortality rate of susceptible humans.

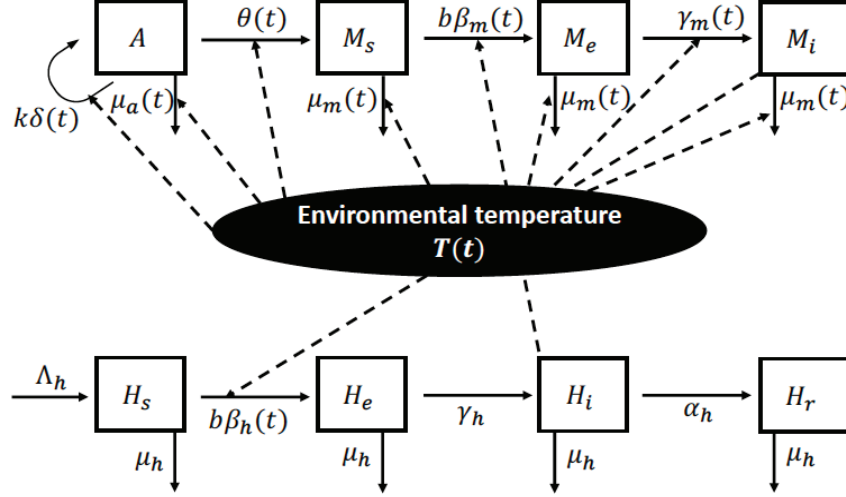


FIGURE 2.1. A schematic diagram of the dengue transmission model. A, M_s, M_e, M_i : aquatic, susceptible, exposed, and infected mosquitoes. H_s, H_e, H_i, H_r : susceptible, exposed, infected, and recovered humans. Solid arrows represent birth, maturation, infection, transfer, death, while dashed arrows indicate the effects of time dependent periodic environmental temperature, $T(t)$.

Dengue virus transmission occurs from infected humans to susceptible mosquitoes and from infected mosquitoes to susceptible humans through mosquito bites. Transmission related parameters b , $\beta_m(t)$, and $\beta_h(t)$ represent the per capita biting rate of mosquitoes, the transmission probability from human to mosquito, and the transmission probability from mosquito to human, respectively. An average extrinsic period of mosquitoes (i.e., an average duration of mosquitoes in exposed class) and an average intrinsic period of humans (i.e., an average duration of humans in exposed class) are denoted by $1/\gamma_m(t)$ and $1/\gamma_h$, respectively. Infected humans get recovered from dengue at a rate α_h , and once recovered, these recovered humans do not lose immunity as mentioned in Bhatt et al. [4]. As described in [4, 31], dengue virus is generally non-pathogenic. Therefore, our model does not include deaths due to disease.

Based on experimental evidences [9, 17, 44], our model incorporates the effects of environmental temperature via entomological and dengue dynamics parameters. In particular, parameters $\delta(t)$, $\mu_a(t)$, $\theta(t)$, $\mu_m(t)$, $\gamma_m(t)$, $\beta_m(t)$, and $\beta_h(t)$ of our model are influenced by the diurnally and seasonally varying environmental temperature. In the absence of detailed diurnal and seasonal temperature profile, i.e., homogeneous environment, our system (2.1) is similar to the dengue model proposed previously in Pinho et al. [26].

2.1. Entomological parameters. We denote the temperature profile by $T(t)$ that captures both diurnal and seasonal variation of the environmental temperature. We used the experimental data [43, 44], which measure how a change in temperature changes the oviposition rate, aquatic phase mortality rate, rate of emergence of female mosquito from aquatic phase, and female mosquito mortality rate. As in our previous study [36], we fitted the data to appropriate functional curves (Fig. 2.2), which give the following relationships:

$$\delta(t) = \begin{cases} \epsilon_\delta, & T(t) < a_\delta, \\ \epsilon_\delta + \frac{\delta_m [T(t) - a_\delta]^{N_\delta}}{\delta_h^{N_\delta} + [T(t) - a_\delta]^{N_\delta}}, & T(t) \geq a_\delta, \end{cases} \quad (2.2)$$

$$\mu_a(t) = a_{0\mu_a} + a_{1\mu_a} T(t) + a_{2\mu_a} T(t)^2 + a_{3\mu_a} T(t)^3 + a_{4\mu_a} T(t)^4, \quad (2.3)$$

$$\theta(t) = \begin{cases} \epsilon_\theta, & T(t) < a_{1\theta}, \\ \epsilon_\theta + a_{0\theta} T(t) (T(t) - a_{1\theta}) \sqrt{a_{2\theta} - T(t)}, & a_{1\theta} \leq T(t) \leq a_{2\theta}, \\ \epsilon_\theta, & T(t) > a_{2\theta}, \end{cases} \quad (2.4)$$

$$\mu_m(t) = a_{0\mu_m} + a_{1\mu_m} T(t) + a_{2\mu_m} T(t)^2. \quad (2.5)$$

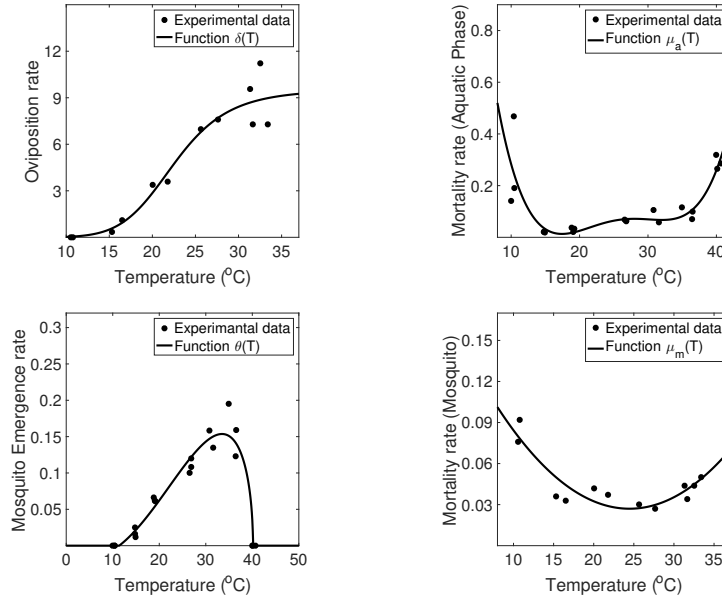


FIGURE 2.2. Best-fit curves provided by the experimental data [44] for $\delta(T)$ (oviposition rate), $\mu_a(T)$ (aquatic phase mortality rate), $\theta(T)$ (mosquito emergence rate from aquatic phase), and $\mu_m(T)$ (mosquito mortality rate).

2.2. Dengue dynamics parameters. We follow the similar techniques implemented in our previous study [36] to reasonably estimate the functional form of dengue dynamics parameters depending on the environmental temperature. Briefly, based on an enzyme kinetic model [9, 17], the incubation time period of dengue, i.e.

the average duration for which mosquitos stay in exposed class before they become infectious, is given by

$$\gamma_m(t) = \frac{1}{a_{0\gamma_m}} e^{a_{1\gamma_m} T(t)}. \quad (2.6)$$

Lambrechts et al. [17] have provided reasonable estimates of dengue transmission probability from humans to mosquitos as well as from mosquitos to humans. Following the trend identified by Lambrechts et al. [17], we use the E-max model (Fig. 2.3) to describe the temperature-dependent formula of the transmission probability from humans to mosquitos as follows [36]:

$$\beta_m(t) = \begin{cases} \epsilon_{\beta m}, & T(t) < a_{\beta m}, \\ \epsilon_{\beta m} + \frac{[T(t) - a_{\beta m}]^{N_{\beta m}}}{\beta_{m,h}^{N_{\beta m}} + [T(t) - a_{\beta m}]^{N_{\beta m}}}, & T(t) \geq a_{\beta m}. \end{cases} \quad (2.7)$$

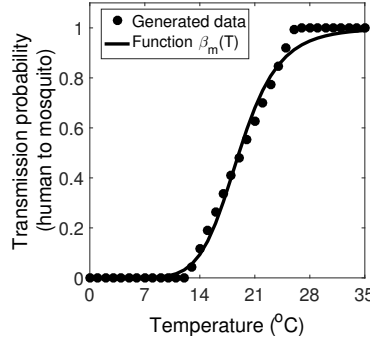


FIGURE 2.3. Best-fit curve provided by the data generated from the previous estimates [17] for the transmission probability from human to mosquito, $\beta_m(T)$.

Similarly, as done in Lambrechts et al. [17], we approximate the temperature-dependent transmission probability from mosquitos to humans to the proportion of midgut-infected mosquitoes transmitting virus, and obtain the following expression:

$$\beta_h(t) = \begin{cases} \epsilon_{\beta h}, & T(t) < a_{1\beta h}, \\ \epsilon_{\beta h} + a_{0\beta h} T(t) (T(t) - a_{1\beta h}) \sqrt{a_{2\beta h} - T(t)}, & a_{1\beta h} \leq T(t) \leq a_{2\beta h}, \\ \epsilon_{\beta h}, & T(t) > a_{2\beta h}. \end{cases} \quad (2.8)$$

2.3. Temperature profile. As done in previous studies [37], seasonal variation of the environmental temperature can be described well by the following sinusoidal function of seasonal period τ_m :

$$T_m(t) = T_0 + \epsilon_m \sin\left(\frac{2\pi}{\tau_m} t + \phi_m\right),$$

where T_0 represents the annual mean temperature, ϵ_m denotes the amplitude of the seasonal temperature, and ϕ_m represents the phase shift in the seasonal temperature. To the seasonal mean temperature, $T_m(t)$, we now impose the diurnal

temperature fluctuation $\Psi_d(t)$ using another sinusoidal function of period τ_d :

$$\Psi_d(t) = \epsilon_d \sin\left(\frac{2\pi}{\tau_d}t + \phi_d\right),$$

where ϵ_d and ϕ_d denote the amplitude and the phase shift in the diurnal temperature variation. As a result, net time varying temperature profile introduced into the model is:

$$T(t) = T_m(t) + \Psi_d(t).$$

Note that $T_m(t)$ is τ_m -periodic and $\Psi_d(t)$ is τ_d -periodic. Then choosing τ as the least common multiple of τ_m and τ_d , the temperature function $T(t) = T_m(t) + \Psi_d(t)$ becomes τ -periodic. Thus, $\delta(t)$, $\mu_a(t)$, $\theta(t)$, $\mu_m(t)$, $\gamma_m(t)$, $\beta_m(t)$, and $\beta_h(t)$ of our model all become τ -periodic, implying that our system is also τ -periodic. A typical example of the temperature profiles of $T_m(t)$, $\Psi_d(t)$, and $T(t)$ are shown in Fig. 2.4.

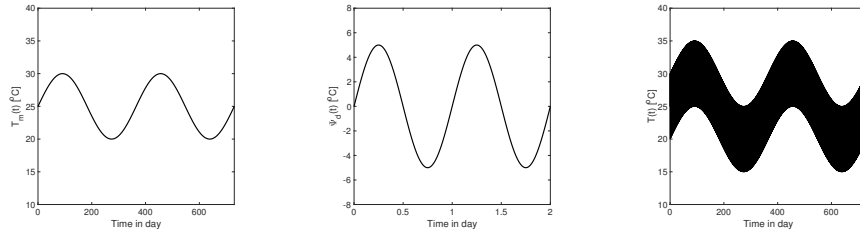


FIGURE 2.4. Temperature profile of $T_m(t)$ [Left], $\Psi_d(t)$ [Middle], and $T(t)$ [Right]. Parameters used are $T_0 = 25^\circ C$, $\epsilon_m = 5^\circ C$, $\tau_m = 365$ day, $\phi_m = 0$, $\epsilon_d = 5^\circ C$, $\tau_d = 1$ day, and $\phi_d = 0$.

The model parameters are given in Table 2.1.

3. Mathematical analysis. From [32, Theorem 5.2.1], we can show that for any

$$(A^0, M_s^0, M_e^0, M_i^0, H_s^0, H_e^0, H_i^0, H_r^0) \in \mathbb{R}_+^8,$$

the system (2.1) has a unique local nonnegative solution

$$(A(t), M_s(t), M_e(t), M_i(t), H_s(t), H_e(t), H_i(t), H_r(t)) \in \mathbb{R}_+^8.$$

Since

$$N_H(t) = H_s(t) + H_e(t) + H_i(t) + H_r(t), \quad (3.1)$$

(2.1) implies

$$\frac{dN_H(t)}{dt} = \Lambda_h - \mu_h N_H(t). \quad (3.2)$$

By the same arguments as in Zhao [47, Section 5.2], we have the following result:

Lemma 3.1. *System (3.2) admits a unique positive constant $H^* := \frac{\Lambda_h}{\mu_h}$ such that every solution $N_H(t)$ of (3.2) with $N_H(0) \geq 0$ satisfies*

$$\lim_{t \rightarrow \infty} N_H(t) = H^*. \quad (3.3)$$

TABLE 2.1. Model parameters

Parameter	Description	Value	Reference
k	Fraction of female larvae from eggs	0.5 (0-1)	[18, 26]
b	Per capita biting rate	0.1	[6, 26]
μ_h	Natural death rate of humans	$4.22 \times 10^{-5} \text{ d}^{-1}$	Calculated, [16]
$1/\gamma_h$	Intrinsic period	10 days	[6, 16, 18, 26]
α_h	Human recovery rate	0.1 d^{-1}	[18, 26]
δ_m	In $\delta(t)$	9.531	Data fitting
δ_h	In $\delta(t)$	22.55	Data fitting
N_δ	In $\delta(t)$	7.084	Data fitting
a_δ	In $\delta(t)$	0	Data fitting
ϵ_δ	In $\delta(t)$	10^{-6}	Data fitting
$a_{0\mu_a}$	In $\mu_a(t)$	2.914	Data fitting
$a_{1\mu_a}$	In $\mu_a(t)$	-0.4986	Data fitting
$a_{2\mu_a}$	In $\mu_a(t)$	0.03099	Data fitting
$a_{3\mu_a}$	In $\mu_a(t)$	-0.0008236	Data fitting
$a_{4\mu_a}$	In $\mu_a(t)$	7.975×10^{-6}	Data fitting
$a_{0\theta}$	In $\theta(t)$	8.044×10^{-5}	Data fitting
$a_{1\theta}$	In $\theta(t)$	11.386	Data fitting
$a_{2\theta}$	In $\theta(t)$	40.1461	Data fitting
ϵ_θ	In $\theta(t)$	10^{-6}	Data fitting
$a_{0\mu_m}$	In $\mu_m(t)$	0.1901	Data fitting
$a_{1\mu_m}$	In $\mu_m(t)$	-0.0134	Data fitting
$a_{2\mu_m}$	In $\mu_m(t)$	2.739×10^{-4}	Data fitting
$a_{0\gamma_m}$	In $\gamma_m(t)$	$5 \times 10^{4/3}$	Data fitting
$a_{1\gamma_m}$	In $\gamma_m(t)$	0.0768	Data fitting
β_{mh}	In $\beta_m(t)$	18.9871	Data fitting
N_{β_m}	In $\beta_m(t)$	7	Data fitting
ϵ_{β_m}	In $\beta_m(t)$	10^{-6}	Data fitting
a_{β_m}	In $\beta_m(t)$	0	Data fitting
$a_{0\beta_h}$	In $\beta_h(t)$	1.044×10^{-3}	Data fitting
$a_{1\beta_h}$	In $\beta_h(t)$	12.286	Data fitting
$a_{2\beta_h}$	In $\beta_h(t)$	32.461	Data fitting
ϵ_{β_h}	In $\beta_h(t)$	10^{-6}	Data fitting

Since

$$N_M(t) = M_s(t) + M_e(t) + M_i(t), \quad (3.4)$$

we are able to demonstrate the following mass conservation for aquatic phase $A(t)$ and the total population of female mosquitos $N_M(t)$ in (2.1). By computations, we obtain that $(A(t), N_M(t))$ satisfies the following coupled differential equations

$$\begin{cases} \frac{dA}{dt} = k\delta(t) \left(1 - \frac{A}{C}\right) N_M - (\theta(t) + \mu_a(t))A, \\ \frac{dN_M}{dt} = \theta(t)A - \mu_m(t)N_M, \\ A(0) = A^0, \quad N_M(0) = N_M^0. \end{cases} \quad (3.5)$$

It is easy to verify that $(0, 0)$ is a trivial solution of the system (3.5).

3.1. Mosquito reproduction number. Following the approaches provided by Bacaër and Guernaoui [2] and Wang and Zhao [40] for analysis of models with

seasonality, we derive the mosquito reproduction number, $\mathcal{R}^M$, for our periodic compartmental system (3.5). Linearizing the system (3.5) at $(0,0)$, we get the following linear system

$$\begin{cases} \frac{dA}{dt} = k\delta(t)N_M - (\theta(t) + \mu_a(t))A, \\ \frac{dN_M}{dt} = \theta(t)A - \mu_m(t)N_M, \\ A(0) = A^0, N_M(0) = N_M^0. \end{cases} \quad (3.6)$$

In view of system (3.6), we assume

$$\mathbf{F}^M(t) = \begin{pmatrix} 0 & k\delta(t) \\ 0 & 0 \end{pmatrix}, \quad (3.7)$$

and

$$\mathbf{V}^M(t) = \begin{pmatrix} \theta(t) + \mu_a(t) & 0 \\ -\theta(t) & \mu_m(t) \end{pmatrix}. \quad (3.8)$$

Suppose $\Psi_{\mathbf{V}^M(\cdot)}(t)$ is the monodromy matrix of the linear τ -periodic differential system $\frac{dv(t)}{dt} = \mathbf{V}^M(t)v$, and $r(\Psi_{\mathbf{V}^M(\cdot)}(\tau))$ is the spectral radius of $\Psi_{\mathbf{V}^M(\cdot)}(\tau)$. Assume $Z(t, s), t \geq s$, is the evolution operator of the linear τ -periodic system

$$\frac{dz(t)}{dt} = -\mathbf{V}^M(t)z, \quad (3.9)$$

that is, for each $s \in \mathbb{R}$, the 2×2 matrix $Z(t, s)$ satisfies

$$\frac{d}{dt}Z(t, s) = -\mathbf{V}^M(t)Z(t, s), \forall t \geq s, Z(s, s) = I,$$

where I is the 2×2 matrix. Thus, the fundamental solution matrix $\Psi_{-\mathbf{V}^M(\cdot)}(t)$ of (3.9) is equal to $Z(t, 0), t \geq 0$.

We assume that $\varphi(s)$, τ -periodic in s , is the initial distribution of adult mosquito population. Then $\mathbf{F}^M(s)\varphi(s)$ is the rate of new aquatic mosquitos produced by the adult mosquitos who were introduced at time s . Given $t \geq s$, then $Z(t, s)\mathbf{F}^M(s)\varphi(s)$ gives the distribution of those adult mosquitos who were newly produced in aquatic phase at time s and remain in the adult compartments at time t . It follows that

$$\psi^M(t) := \int_{-\infty}^t Z(t, s)\mathbf{F}^M(s)\varphi(s)ds = \int_0^\infty Z(t, t-a)\mathbf{F}^M(t-a)\varphi(t-a)da$$

is the distribution of accumulative new adult mosquitos at time t produced by all those adult mosquitos $\varphi(s)$ introduced at time previous to t .

Let C_τ^M be the ordered Banach space of all τ -periodic functions from $\mathbb{R}$ to $\mathbb{R}^2$, which is equipped with the maximum norm $\|\cdot\|$ and the positive cone $C_{\tau,+}^M := \{\varphi \in C_\tau^M : \varphi(t) \geq 0, \forall t \in \mathbb{R}\}$. Then we define a linear operator $L^M : C_\tau^M \rightarrow C_\tau^M$ by

$$(L^M\varphi)(t) = \int_0^\infty Z(t, t-a)\mathbf{F}^M(t-a)\varphi(t-a)da, \forall t \in \mathbb{R}, \varphi \in C_\tau^M. \quad (3.10)$$

Then L^M represents the next mosquito-generation operator [40], and we define the mosquito reproduction number as $\mathcal{R}^M := r(L^M)$, the spectral radius of L^M .

Here, if $\mathcal{W}^M(t, s, \lambda^M), t \geq s, s \in \mathbb{R}$ is the monodromy matrix of the linear τ -periodic system on $\mathbb{R}^2$

$$\frac{dw}{dt} = \left(-\mathbf{V}^M(t) + \frac{\mathbf{F}^M(t)}{\lambda^M} \right) w, \quad t \in \mathbb{R}, \quad (3.11)$$

with parameter $\lambda^M \in (0, \infty)$, then by Theorem 2.1 of [40], we have the following results.

Lemma 3.2. *The following statements hold*

- (i) *If $r(\mathcal{W}^M(\tau, 0, \lambda^M)) = 1$ has a positive solution λ_0^M , then λ_0^M is an eigenvalue of operator L^M , and hence, $\mathcal{R}^M > 0$.*
- (ii) *If $\mathcal{R}^M > 0$, then $\lambda^M = \mathcal{R}^M$ is the unique solution of $r(\mathcal{W}^M(\tau, 0, \lambda^M)) = 1$.*
- (iii) *$\mathcal{R}^M = 0$ if and only if $r(\mathcal{W}^M(\tau, 0, \lambda^M)) < 1$ for all $\lambda^M > 0$.*

$\mathcal{R}^M$ for homogeneous (constant temperature) case. We now briefly mention the homogeneous case, in which the environmental temperature remains constant over time. In this case, $\delta(t) \equiv \delta$, $\theta(t) \equiv \theta$, $\mu_a(t) \equiv \mu_a$, and $\mu_m(t) \equiv \mu_m$ are all positive constants. Then $\mathbf{F}^M(t) \equiv \mathbf{F}^M$ and $\mathbf{V}^M(t) \equiv \mathbf{V}^M$ become constant matrices. Substituting constant matrices $\mathbf{F}^M$ and $\mathbf{V}^M$, we obtain (see also [40, 38])

$$\mathbf{F}^M (\mathbf{V}^M)^{-1} = \begin{pmatrix} \frac{k\delta\theta}{\mu_m(\theta + \mu_a)} & \frac{k\delta}{\mu_m} \\ 0 & 0 \end{pmatrix}.$$

Then $\mathcal{R}^M$ can be expressed as the following explicit form

$$\mathcal{R}^M = r(\mathbf{F}^M (\mathbf{V}^M)^{-1}) = \frac{k\delta\theta}{\mu_m(\theta + \mu_a)}.$$

We have the results related to mosquito population extinction as stated in the following Lemma.

Lemma 3.3. [40, Theorem 2.2] *The following statements hold.*

- (i) $\mathcal{R}^M = 1$ if and only if $r(\Psi_{\mathbf{F}^M(\cdot) - \mathbf{V}^M(\cdot)}(\tau)) = 1$;
- (ii) $\mathcal{R}^M > 1$ if and only if $r(\Psi_{\mathbf{F}^M(\cdot) - \mathbf{V}^M(\cdot)}(\tau)) > 1$;
- (iii) $\mathcal{R}^M < 1$ if and only if $r(\Psi_{\mathbf{F}^M(\cdot) - \mathbf{V}^M(\cdot)}(\tau)) < 1$.

Thus, the mosquito-free equilibrium $(0, 0)$ is locally asymptotically stable for system (3.5) if $\mathcal{R}^M < 1$, and unstable if $\mathcal{R}^M > 1$.

Moreover, we have the following results related to the global dynamics of (3.5):

Lemma 3.4. Let $\Delta := \{(A, M) \in \mathbb{R}_+^2 : 0 \leq A \leq C\}$. Then the following statements hold.

- (i) *If $\mathcal{R}^M < 1$, then the trivial solution $(0, 0)$ is globally attractive in Δ for (3.5);*
- (ii) *If $\mathcal{R}^M > 1$, then the system (3.5) admits a unique positive τ -periodic solution $(A^*(t), M^*(t))$ which is globally attractive in $\Delta \setminus \{(0, 0)\}$, that is, for any $(A(0), N_M(0)) \in \Delta \setminus \{(0, 0)\}$, we have*

$$\lim_{t \rightarrow \infty} [(A(t), N_M(t)) - (A^*(t), M^*(t))] = 0, \quad (3.12)$$

$$\text{where } A^*(t) = C \left\{ 1 - \frac{\mu_m(t)[\theta(t) + \mu_a(t)]}{k\delta(t)\theta(t)} \right\}, \text{ and } M^*(t) = \frac{\theta(t)}{\mu_m(t)} A^*(t).$$

Proof. From [32, Theorem 5.2.1], we observe that Δ is positively invariant for system (3.5). We first prove the following claim.

Claim.

$$A(t) < C, \quad \forall t > 0. \quad (3.13)$$

Proof of the claim. Assume, by contradiction, that (3.13) is not true. Then there exists a $t_0 > 0$ such that $A(t_0) = C$. It follows from the first equation in system (3.5) that

$$0 = \left. \frac{dA}{dt} \right|_{t=t_0} = k\delta(t_0) \left(1 - \frac{A(t_0)}{C} \right) N_M(t_0) - [\theta(t_0) + \mu_a(t_0)]A(t_0),$$

which implies that $\theta(t_0) + \mu_a(t_0) = 0$. This contradiction shows that (3.13) holds.

From (3.13), it is easy to see that system (3.5) is strongly monotone in Δ (see, e.g., [32]). On the other hand, we assume that

$$\begin{cases} g_1(A, N_M) = k\delta(t) \left(1 - \frac{A}{C} \right) N_M - (\theta(t) + \mu_a(t))A, \\ g_2(A, N_M) = \theta(t)A - \mu_m(t)N_M. \end{cases}$$

Then for all $A > 0$, $N_M > 0$, $0 < \vartheta < 1$, we have

$$g_1(\vartheta A, \vartheta N_M) > \vartheta g_1(A, N_M), \quad g_2(\vartheta A, \vartheta N_M) = \vartheta g_2(A, N_M),$$

that is, system (3.5) is strictly subhomogeneous in Δ (see, e.g., [47]). Then we can use Lemma 3.3, [47, Theorem 2.3.4], and the similar arguments as in [39, Lemma 2.5] to complete the rest of the proof. $\square$

Let

$$\mathbb{X} := \{(A, M_s, M_e, M_i, H_s, H_e, H_i, H_r) \in \mathbb{R}_+^8 : 0 \leq A \leq C\}.$$

Then we can prove the following Lemma.

Lemma 3.5. $\mathbb{X}$ is positively invariant for system (2.1) and the system (2.1) has a unique and bounded solution with the initial value in $\mathbb{X}$. Further, the system (2.1) admits a connected global attractor G on $\mathbb{X}$ in the sense that G attracts all positive orbits in $\mathbb{X}$.

Proof. From [32, Theorem 5.2.1], we can observe that $\mathbb{X}$ is positively invariant for system (2.1). By (3.4), (3.5), Lemma 3.1, and Lemma 3.4, it follows that solutions of the system (2.1) are uniformly and ultimately bounded. Also, by [12, Theorem 3.4.8], it follows that the system (2.1) admits a connected global attractor G on $\mathbb{X}$. $\square$

3.2. Infection invasion threshold. In order to find the disease-free periodic state of (2.1), we set $M_e = M_i = H_e = H_i = H_r = 0$. Then $H_s(t)$ and (A, M_s) satisfy (3.2) and (3.6), respectively. By Lemma 3.4 and Lemma 3.1, we see that

$$E_0 = (A, M_s, M_e, M_i, H_s, H_e, H_i, H_r) = (0, 0, 0, 0, H^*, 0, 0, 0)$$

always exists, and

$$E_1(t) = (A, M_s, M_e, M_i, H_s, H_e, H_i, H_r) = (A^*(t), M^*(t), 0, 0, H^*, 0, 0, 0)$$

exists if $\mathcal{R}^M > 1$.

Theorem 3.1. Assume that $(A(t), M_s(t), M_e(t), M_i(t), H_s(t), H_e(t), H_i(t), H_r(t))$ is a solution of the system (2.1) with initial value $(A^0, M_s^0, M_e^0, M_i^0, H_s^0, H_e^0, H_i^0, H_r^0) \in \mathbb{X}$. If $\mathcal{R}^M < 1$, then

$$\lim_{t \rightarrow \infty} (A(t), M_s(t), M_e(t), M_i(t), H_s(t), H_e(t), H_i(t), H_r(t)) = E_0.$$

Proof. If $\mathcal{R}^M < 1$, then by (3.4), (3.5) and Lemma 3.4 (i), we see that

$$\lim_{t \rightarrow \infty} A(t) = \lim_{t \rightarrow \infty} M_s(t) = \lim_{t \rightarrow \infty} M_e(t) = \lim_{t \rightarrow \infty} M_i(t) = 0.$$

This implies that H_e is asymptotic to

$$\frac{dH_e}{dt} = -(\gamma_h + \mu_h)H_e,$$

which gives $\lim_{t \rightarrow \infty} H_e(t) = 0$. Similarly, H_i is asymptotic to $\frac{dH_i}{dt} = -(\alpha_h + \mu_h)H_i$, and hence, $\lim_{t \rightarrow \infty} H_i(t) = 0$. Finally, H_r is asymptotic to $\frac{dH_r}{dt} = -\mu_h H_r$, and hence, $\lim_{t \rightarrow \infty} H_r(t) = 0$. Given these asymptotic behaviors for H_e , H_i , and H_r , we see that H_s is asymptotic to system (3.2). Then by the theory of asymptotical semiflows (see, e.g., [48] or [47, section 3.2]) and Lemma 3.1, it follows that $\lim_{t \rightarrow \infty} H_s(t) = H^*$. This completes the proof. $\square$

Linearizing system (2.1) at the disease-free periodic state $E_1(t)$, we get the following system for the (M_e, M_i, H_e, H_i) components:

$$\begin{cases} \frac{dM_e}{dt} = -[\gamma_m(t) + \mu_m(t)]M_e + \frac{b\beta_m(t)M^*(t)}{H^*}H_i, \\ \frac{dM_i}{dt} = \gamma_m(t)M_e - \mu_m(t)M_i, \\ \frac{dH_e}{dt} = b\beta_h(t)M_i - (\gamma_h + \mu_h)H_e, \\ \frac{dH_i}{dt} = \gamma_h H_e - (\alpha_h + \mu_h)H_i, \\ M_e(0) \geq 0, M_i(0) \geq 0, H_e(0) \geq 0, H_i(0) \geq 0. \end{cases} \quad (3.14)$$

We next introduce infection invasion threshold $\mathcal{R}^0$ for our periodic compartmental epidemic model (2.1) by using the general theory in [40]. From (3.14), we define

$$\mathbb{F}(t) = \begin{pmatrix} 0 & 0 & 0 & \frac{b\beta_m(t)M^*(t)}{H^*} \\ 0 & 0 & 0 & 0 \\ 0 & b\beta_h(t) & 0 & 0 \\ 0 & 0 & 0 & 0 \end{pmatrix},$$

and

$$\mathbb{V}(t) = \begin{pmatrix} \gamma_m(t) + \mu_m(t) & 0 & 0 & 0 \\ -\gamma_m(t) & \mu_m(t) & 0 & 0 \\ 0 & 0 & \gamma_h + \mu_h & 0 \\ 0 & 0 & -\gamma_h & \alpha_h + \mu_h \end{pmatrix}.$$

Suppose $\Phi_{\mathbb{V}(\cdot)}(t)$ is the monodromy matrix of the linear τ -periodic differential system $\frac{dz(t)}{dt} = \mathbb{V}(t)z$, and $r(\Phi_{\mathbb{V}(\cdot)}(\tau))$ is the spectral radius of $\Phi_{\mathbb{V}(\cdot)}(\tau)$. Assume $Y(t, s)$, $t \geq s$, is the evolution operator of the linear τ -periodic system

$$\frac{dy(t)}{dt} = -\mathbb{V}(t)y, \quad (3.15)$$

that is, for each $s \in \mathbb{R}$, the 4×4 matrix $Y(t, s)$ satisfies

$$\frac{d}{dt}Y(t, s) = -\mathbb{V}(t)Y(t, s), \quad \forall t \geq s, \quad Y(s, s) = I,$$

where I is the 4×4 matrix. Thus, the fundamental solution matrix $\Phi_{-\mathbb{V}(\cdot)}(t)$ of (3.15) is equal to $Y(t, 0)$, $t \geq 0$.

We assume that $\phi(s)$, τ -periodic in s , is the initial distribution of infectious individuals. Then $\mathbb{F}(s)\phi(s)$ is the rate of new infections produced by the infected

individuals who were introduced at time s . Given $t \geq s$, then $Y(t, s)\mathbb{F}(s)\phi(s)$ gives the distribution of those infected individuals who were newly infected at time s and remain in the infected compartments at time t . It follows that

$$\psi(t) := \int_{-\infty}^t Y(t, s)\mathbb{F}(s)\phi(s)ds = \int_0^\infty Y(t, t-a)\mathbb{F}(t-a)\phi(t-a)da$$

is the distribution of accumulative new infections at time t produced by all those infected individuals $\phi(s)$ introduced at time previous to t .

Let C_τ be the ordered Banach space of all τ -periodic functions from $\mathbb{R}$ to $\mathbb{R}^4$, which is equipped with the maximum norm $\|\cdot\|$ and the positive cone $C_\tau^+ := \{\phi \in C_\tau : \phi(t) \geq 0, \forall t \in \mathbb{R}\}$. Then we define a linear operator $L : C_\tau \rightarrow C_\tau$ by

$$(L\phi)(t) = \int_0^\infty Y(t, t-a)\mathbb{F}(t-a)\phi(t-a)da, \quad \forall t \in \mathbb{R}, \phi \in C_\tau. \quad (3.16)$$

Then L represents the next infection operator [40], and we define infection invasion threshold as $\mathcal{R}^0 := r(L)$, the spectral radius of L .

Here, if $\mathcal{W}(t, s, \lambda^0)$, $t \geq s$, $s \in \mathbb{R}$ is the monodromy matrix of the linear τ -periodic system on $\mathbb{R}^4$

$$\frac{dw}{dt} = \left(-\mathbb{V}(t) + \frac{\mathbb{F}(t)}{\lambda^0} \right) w, \quad t \in \mathbb{R}, \quad (3.17)$$

with parameter $\lambda^0 \in (0, \infty)$, then by Theorem 2.1 of [40], we have the following results.

Lemma 3.6. *The following statements hold*

- (i) *If $r(\mathcal{W}(\tau, 0, \lambda^0)) = 1$ has a positive solution λ_0^0 , then λ_0^0 is an eigenvalue of operator L , and hence, $\mathcal{R}^0 > 0$.*
- (ii) *If $\mathcal{R}^0 > 0$, then $\lambda^0 = \mathcal{R}^0$ is the unique solution of $r(\mathcal{W}(\tau, 0, \lambda^0)) = 1$.*
- (iii) *$\mathcal{R}^0 = 0$ if and only if $r(\mathcal{W}(\tau, 0, \lambda^0)) < 1$ for all $\lambda^0 > 0$.*

$\mathcal{R}^0$ for homogeneous (constant temperature) case. We now briefly mention that $\mathcal{R}^0$ formulated above can also recover the basic reproduction number, $\bar{\mathcal{R}}_0$, that we derived previously for the dynamics when the environmental temperature remains constant over time [36]. In the homogeneous (constant temperature) case, i.e. $T(t) = T$, all of $\delta(t) = \delta, \mu_a(t) = \mu_a, \theta(t) = \theta, \mu_m(t) = \mu_m, \gamma_m(t) = \gamma_m, \beta_m(t) = \beta_m, \beta_h(t) = \beta_h$ are constant. In this case, $E_1 = (\bar{A}^*, \bar{M}_s^*, 0, 0, \bar{H}^*, 0, 0, 0)$, where $\bar{A}^* = C[1 - \frac{1}{\mathcal{R}^M}]$, $\bar{M}_s^* = \theta\bar{A}^*/\mu_m$, and $\bar{H}^* = \Lambda_h/\mu_h$. Clearly, E_1 exists if $\mathcal{R}^M > 1$. Here, the system linearized about E_1 provides both $\mathbb{F}(t) \equiv \mathbb{F}$ and $\mathbb{V}(t) \equiv \mathbb{V}$ to be constant matrices. Substituting constant matrices $\mathbb{F}$ and $\mathbb{V}$, we obtain (see also [40, 38])

$$\mathcal{R}_0 = r(L) = r(\mathbb{F}\mathbb{V}^{-1}).$$

By computations, we can obtain that

$$\mathbb{F}\mathbb{V}^{-1} = \begin{pmatrix} 0 & 0 & D\gamma_h/(\gamma_h + \mu_h)(\alpha_h + \mu_h) & D/(\alpha_h + \mu_h) \\ 0 & 0 & 0 & 0 \\ E\gamma_m/\mu_m(\gamma_m + \mu_m) & E/\mu_m & 0 & 0 \\ 0 & 0 & 0 & 0 \end{pmatrix},$$

where $D = \frac{b\beta_m M_s^*}{H^*}$ and $E = b\beta_h$. Then $\mathcal{R}^0$ can be expressed as the following explicit form

$$\mathcal{R}^0 = \sqrt{\frac{DE\gamma_m\gamma_h}{\mu_m(\gamma_m + \mu_m)(\gamma_h + \mu_h)(\alpha_h + \mu_h)}}.$$

Here, $\mathcal{R}^0 = \bar{\mathcal{R}}_0$, which is the basic reproduction number [36] that we derived using the second generation matrix method [38] for constant temperature case.

We have the result about the local stability of the disease-free state $E_1(t)$ as stated in the following theorem.

Lemma 3.7. [40, Theorem 2.2] *The following statements hold.*

- (i) $\mathcal{R}^0 = 1$ if and only if $r(\Phi_{\mathbb{F}(\cdot)-\mathbb{V}(\cdot)}(\tau)) = 1$;
- (ii) $\mathcal{R}^0 > 1$ if and only if $r(\Phi_{\mathbb{F}(\cdot)-\mathbb{V}(\cdot)}(\tau)) > 1$;
- (iii) $\mathcal{R}^0 < 1$ if and only if $r(\Phi_{\mathbb{F}(\cdot)-\mathbb{V}(\cdot)}(\tau)) < 1$.

Thus, the disease-free state $E_1(t)$ is locally asymptotically stable if $\mathcal{R}^0 < 1$, and unstable if $\mathcal{R}^0 > 1$.

3.3. Threshold dynamics. Let $\mathbf{A}(t)$ be a continuous, cooperative, irreducible, and τ -periodic $k \times k$ matrix function. Suppose $\Phi_{\mathbf{A}(\cdot)}(t)$ is the monodromy matrix of the linear ordinary differential system

$$\frac{dx(t)}{dt} = \mathbf{A}(t)x, \quad (3.18)$$

and $r(\Phi_{\mathbf{A}(\cdot)}(\tau))$ is the spectral radius of $\Phi_{\mathbf{A}(\cdot)}(\tau)$. From [1, Lemma 2] (see also [13, Theorem 1.1]), it follows that $\Phi_{\mathbf{A}(\cdot)}(t)$ is a matrix with all entries positive for each $t > 0$. By the Perron-Frobenius theorem, $r(\Phi_{\mathbf{A}(\cdot)}(\tau))$ is the principal eigenvalue of $\Phi_{\mathbf{A}(\cdot)}(\tau)$ in the sense that it is simple and admits a positive eigenvector. Then we have the following result.

Lemma 3.8. ([46, Lemma 2.1]) *Let $\mu = \frac{1}{\tau} \ln r(\Phi_{\mathbf{A}(\cdot)}(\tau))$. Then there exists a positive, τ -periodic function $v(t)$ such that $e^{\mu t}v(t)$ is a solution of (3.18).*

Suppose $P : \mathbb{X} \rightarrow \mathbb{X}$ is the Poincaré map associated with system (2.1), that is,

$$P(x^0) = u(\tau, x^0), \quad \forall x^0 := (A^0, M_s^0, M_e^0, M_i^0, H_s^0, H_e^0, H_i^0, H_r^0) \in \mathbb{X},$$

where $u(t, x^0)$ is the unique solution of system (2.1) with $u(0, x^0) = x^0$. It is easy to see that

$$P^n(x^0) = u(n\tau, x^0), \quad \forall n \geq 0.$$

For convenience, we define $\mathcal{E}_0 = E_0 = (0, 0, 0, 0, H^*, 0, 0, 0)$ and $\mathcal{E}_1 = E_1(0) = (A^*(0), M^*(0), 0, 0, H^*, 0, 0, 0)$. Let

$$\mathbb{X}_0 := \{(A, M_s, M_e, M_i, H_s, H_e, H_i, H_r) \in \mathbb{X} : M_i > 0\}.$$

and

$$\partial\mathbb{X}_0 := \mathbb{X} \setminus \mathbb{X}_0 = \{(A, M_s, M_e, M_i, H_s, H_e, H_i, H_r) \in \mathbb{X} : M_i = 0\}.$$

Lemma 3.9. *Assume that $(A(t), M_s(t), M_e(t), M_i(t), H_s(t), H_e(t), H_i(t), H_r(t))$ is a solution of the system (2.1) with initial value $(A^0, M_s^0, M_e^0, M_i^0, H_s^0, H_e^0, H_i^0, H_r^0) \in \mathbb{X}_0$. Then $(A(t), M_s(t), M_e(t), M_i(t), H_s(t), H_e(t), H_i(t), H_r(t)) \gg 0, \forall t > 0$.*

Proof. Given an initial value $(A^0, M_s^0, M_e^0, M_i^0, H_s^0, H_e^0, H_i^0, H_r^0) \in \mathbb{X}_0$. In view of the fifth equation of system (2.1), it follows that

$$H_s(t) = e^{-\int_0^t \varsigma(s_1) ds_1} \left[\Lambda_h \int_0^t e^{\int_0^{s_2} \varsigma(s_1) ds_1} ds_2 + H_s^0 \right], \quad (3.19)$$

where

$$\varsigma(t) := \mu_h + \frac{b\beta_h(t)M_i(t)}{N_H(t)}. \quad (3.20)$$

Thus, $H_s(t) > 0$, $\forall t > 0$. From the first equation of system (2.1), we see that

$$A(t) = e^{-\int_0^t b(s_1) ds_1} \left[\int_0^t e^{\int_0^{s_2} b(s_1) ds_1} \zeta(s_2) ds_2 + A^0 \right], \quad (3.21)$$

where

$$\begin{cases} \zeta(t) := k\delta(t)N_M \geq 0, \\ b(t) := \frac{k\delta(t)}{C}N_m + \theta(t) + \mu_a(t). \end{cases} \quad (3.22)$$

On the contrary, we assume there exists $t_0 \geq 0$ such that $A(t_0) = 0$. This implies that $A^0 = 0$ and $\zeta(t) := k\delta(t)N_M \equiv 0$ on $[0, t_0]$. This contradicts that $M_i(0) = M_i^0 > 0$. Thus, $A(t) > 0$, $\forall t > 0$. From the second equation of system (2.1), we have

$$M_s(t) = e^{-\int_0^t c(s_1) ds_1} \left[\int_0^t e^{\int_0^{s_2} c(s_1) ds_1} \theta(s_2) A(s_2) ds_2 + M_s^0 \right], \quad (3.23)$$

where

$$c(t) := \frac{b\beta_m(t)H_i(t)}{N_H(t)} + \mu_m(t). \quad (3.24)$$

This implies that $M_s(t) > 0$, $\forall t > 0$.

By [32, Theorem 4.1.1] as generalized to nonautonomous systems, the irreducibility of the cooperative matrix

$$\begin{pmatrix} -(\gamma_m(t) + \mu_m(t)) & 0 & 0 & \frac{b\beta_m(t)M_s(t)}{N_H(t)} \\ \gamma_m(t) & -\mu_m(t) & 0 & 0 \\ 0 & \frac{b\beta_h(t)H_s(t)}{N_H(t)} & -(\gamma_h + \mu_h) & 0 \\ 0 & 0 & \gamma_h & -(\alpha_h + \mu_h) \end{pmatrix} \quad (3.25)$$

implies that $(M_e(t), M_i(t), H_e(t), H_i(t))^T \gg 0$, $\forall t > 0$.

Finally, it follows from the eighth equation in system (2.1) that

$$H_r(t) = e^{-\mu_h t} \left[\alpha_h \int_0^t e^{\mu_h s} H_i(s) ds + H_r^0 \right], \quad (3.26)$$

which implies that $H_r(t) > 0$, $\forall t > 0$. This completes the proof of the lemma. $\square$

Lemma 3.10. *Let $\mathcal{R}^M > 1$ and $\mathcal{R}^0 > 1$. Then for $j = 0, 1$, there exists $\sigma_j > 0$ such that for any $(A^0, M_s^0, M_e^0, M_i^0, H_s^0, H_e^0, H_i^0, H_r^0) \in \mathbb{X}_0$ with*

$$\|(A^0, M_s^0, M_e^0, M_i^0, H_s^0, H_e^0, H_i^0, H_r^0) - \mathcal{E}_j\| \leq \sigma_j,$$

we have

$$\limsup_{n \rightarrow \infty} \text{dist}(P^n(A^0, M_s^0, M_e^0, M_i^0, H_s^0, H_e^0, H_i^0, H_r^0), \mathcal{E}_j) \geq \sigma_j.$$

Proof. Since $\mathcal{R}^0 > 1$, Lemma 3.7 implies that $r(\Phi_{\mathbb{F}(\cdot) - \mathbb{V}(\cdot)}(\tau)) > 1$. Thus, we may choose $\rho_1 > 0$ small enough such that $r(\Phi_{\mathbb{F}_{\rho_1}(\cdot) - \mathbb{V}(\cdot)}(\tau)) > 1$, where

$$\mathbb{F}_{\rho_1}(t) = \begin{pmatrix} 0 & 0 & 0 & \frac{b\beta_m(t)(M^*(t) - \rho_1)}{H^* + 4\rho_1} \\ 0 & 0 & 0 & 0 \\ 0 & \frac{b\beta_h(t)(H^* - \rho_1)}{H^* + 4\rho_1} & 0 & 0 \\ 0 & 0 & 0 & 0 \end{pmatrix}.$$

By the continuity of the solutions with respect to the initial values, there exists a $\sigma_1 > 0$ such that for all $(A^0, M_s^0, M_e^0, M_i^0, H_s^0, H_e^0, H_i^0, H_r^0) \in \mathbb{X}_0$ with

$$\|(A^0, M_s^0, M_e^0, M_i^0, H_s^0, H_e^0, H_i^0, H_r^0) - \mathcal{E}_1\| \leq \sigma_1,$$

there holds $\|u(t, (A^0, M_s^0, M_e^0, M_i^0, H_s^0, H_e^0, H_i^0, H_r^0)) - u(t, \mathcal{E}_1)\| < \rho_1, \forall t \in [0, \tau]$.

We first prove the case $j = 1$, i.e.,

$$\limsup_{n \rightarrow \infty} \text{dist}(P^n(A^0, M_s^0, M_e^0, M_i^0, H_s^0, H_e^0, H_i^0, H_r^0), \mathcal{E}_1) \geq \sigma_1.$$

Assume, by contradiction, that the above conclusion does not hold. Then we have

$$\limsup_{n \rightarrow \infty} \text{dist}(P^n(A^0, M_s^0, M_e^0, M_i^0, H_s^0, H_e^0, H_i^0, H_r^0), \mathcal{E}_1) < \sigma_1,$$

for some $(A^0, M_s^0, M_e^0, M_i^0, H_s^0, H_e^0, H_i^0, H_r^0) \in \mathbb{X}_0$. Without loss of generality, we assume that

$$\text{dist}(P^n(A^0, M_s^0, M_e^0, M_i^0, H_s^0, H_e^0, H_i^0, H_r^0), \mathcal{E}_1) < \sigma_1, \forall n \geq 0.$$

It follows that

$$\|u(t, P^n(A^0, M_s^0, M_e^0, M_i^0, H_s^0, H_e^0, H_i^0, H_r^0)) - u(t, \mathcal{E}_1)\| < \rho_1, \forall t \in [0, \tau], n \geq 0.$$

For any $t \geq 0$, let $t = m\tau + t'$, where $t' \in [0, \tau)$, and m is the largest integer less than or equal to $\frac{t}{\tau}$. Therefore, we have $\|u(t, (A^0, M_s^0, M_e^0, M_i^0, H_s^0, H_e^0, H_i^0, H_r^0)) - u(t, \mathcal{E}_1)\| = \|u(t', P^m(A^0, M_s^0, M_e^0, M_i^0, H_s^0, H_e^0, H_i^0, H_r^0)) - u(t', \mathcal{E}_1)\| < \rho_1$. Note that $(A(t), M_s(t), M_e(t), M_i(t), H_s(t), H_e(t), H_i(t), H_r(t)) = u(t, (A^0, M_s^0, M_e^0, M_i^0, H_s^0, H_e^0, H_i^0, H_r^0))$ and $u(t, \mathcal{E}_1) = E_1(t), \forall t \geq 0$. It then follows that for all $t \geq 0$, we have

$$M_s(t) > M^*(t) - \rho_1, H^* + \rho_1 > H_s(t) > H^* - \rho_1, \rho_1 > H_e(t), \rho_1 > H_i(t), \rho_1 > H_r(t).$$

From the equations of M_e, M_i, H_e and H_i in (2.1), it follows that

$$\begin{cases} \frac{dM_e}{dt} \geq \frac{b\beta_m(t)(M^*(t) - \rho_1)}{H^* + 4\rho_1} H_i - (\gamma_m(t) + \mu_m(t)) M_e, \forall t \geq 0, \\ \frac{dM_i}{dt} = \gamma_m(t) M_e - \mu_m(t) M_i, \forall t \geq 0, \\ \frac{dH_e}{dt} \geq \frac{b\beta_h(t)(H^* - \rho_1)}{H^* + 4\rho_1} M_i - (\gamma_h + \mu_h) H_e, \forall t \geq 0, \\ \frac{dH_i}{dt} = \gamma_h H_e - (\alpha_h + \mu_h) H_i, \forall t \geq 0. \end{cases} \quad (3.27)$$

Since $(A^0, M_s^0, M_e^0, M_i^0, H_s^0, H_e^0, H_i^0, H_r^0) \in \mathbb{X}_0$, it follows from Lemma 3.9 that

$$(M_e(t), M_i(t), H_e(t), H_i(t)) \gg 0, \forall t > 0.$$

Thus, we may fix a $t_1 > 0$ such that $(M_e(t_1), M_i(t_1), H_e(t_1), H_i(t_1)) \gg 0$. By Lemma 3.8, it follows that there exists a positive, τ -periodic function $J(t)$ and $\tilde{\mu} = \frac{1}{\tau} \ln [r(\Phi_{\mathbb{F}_{\rho_1}(\cdot) - \mathbb{V}(\cdot)}(\tau))]$ such that $\tilde{J}(t) := \tilde{b}e^{\tilde{\mu}(t - t_1)} J(t)$ is a solution of

$$\frac{dx(t)}{dt} = (\mathbb{F}_{\rho_1}(t) - \mathbb{V}(t)) x(t),$$

where $\tilde{b}$ satisfies $\tilde{J}(t_1) := \tilde{b}J(t_1) \leq (M_e(t_1), M_i(t_1), H_e(t_1), H_i(t_1))$. The standard comparison theorem (see, e.g., [33, Theorem B.1]) implies that

$$(M_e(t), M_i(t), H_e(t), H_i(t)) \geq \tilde{J}(t), \quad \forall t \geq t_1.$$

In particular, there exists n_1 such that

$$(M_e(n\tau), M_i(n\tau), H_e(n\tau), H_i(n\tau)) \geq \tilde{J}(n\tau), \quad \forall n \geq n_1.$$

Since $\tilde{\mu} > 0$, it follows that $\tilde{J}(n\tau) \rightarrow \infty$ as $n \rightarrow \infty$. Thus, $(M_e(n\tau), M_i(n\tau), H_e(n\tau), H_i(n\tau)) \rightarrow \infty$ as $n \rightarrow \infty$. This contradiction completes the proof of the case $j = 1$.

Next, we will use the fact $\mathcal{R}^M > 1$ to show that the conclusion is also true for the case $j = 0$. Since $\mathcal{R}^M > 1$, Lemma 3.3 implies that $r(\Psi_{\mathbf{F}^M(\cdot) - \mathbf{V}^M(\cdot)}(\tau)) > 1$. Thus, we may choose $\rho_0 > 0$ small enough such that $r(\Psi_{\mathbf{F}_{\rho_0}^M(\cdot) - \mathbf{V}_{\rho_0}^M(\cdot)}(\tau)) > 1$, where

$$\mathbf{F}_{\rho_0}^M(t) = \begin{pmatrix} 0 & k(1 - \frac{\rho_0}{C})\delta(t) \\ 0 & 0 \end{pmatrix}, \quad (3.28)$$

and

$$\mathbf{V}_{\rho_0}^M(t) = \begin{pmatrix} \theta(t) + \mu_a(t) & 0 \\ -\theta(t) & \frac{b\beta_m(t)\rho_0}{H^* - \rho_0} + \mu_m(t) \end{pmatrix}. \quad (3.29)$$

By the continuity of the solutions with respect to the initial values, there exists a $\sigma_0 > 0$ such that for all $(A^0, M_s^0, M_e^0, M_i^0, H_s^0, H_e^0, H_i^0, H_r^0) \in \mathbb{X}_0$ with

$$\|(A^0, M_s^0, M_e^0, M_i^0, H_s^0, H_e^0, H_i^0, H_r^0) - \mathcal{E}_0\| \leq \sigma_0,$$

there holds $\|u(t, (A^0, M_s^0, M_e^0, M_i^0, H_s^0, H_e^0, H_i^0, H_r^0)) - u(t, \mathcal{E}_0)\| < \rho_0, \quad \forall t \in [0, \tau]$.

For the case $j = 0$, we need to prove that

$$\limsup_{n \rightarrow \infty} \text{dist}(P^n(A^0, M_s^0, M_e^0, M_i^0, H_s^0, H_e^0, H_i^0, H_r^0), \mathcal{E}_0) \geq \sigma_0,$$

where, $\text{dist}(A, B)$ is the distance between A and B .

Assume, by contradiction, that the above conclusion does not hold. Then we have

$$\limsup_{n \rightarrow \infty} \text{dist}(P^n(A^0, M_s^0, M_e^0, M_i^0, H_s^0, H_e^0, H_i^0, H_r^0), \mathcal{E}_0) < \sigma_0,$$

for some $(A^0, M_s^0, M_e^0, M_i^0, H_s^0, H_e^0, H_i^0, H_r^0) \in \mathbb{X}_0$. Without loss of generality, we assume that

$$\text{dist}(P^n(A^0, M_s^0, M_e^0, M_i^0, H_s^0, H_e^0, H_i^0, H_r^0), \mathcal{E}_0) < \sigma_0, \quad \forall n \geq 0.$$

It follows that

$$\|u(t, P^n(A^0, M_s^0, M_e^0, M_i^0, H_s^0, H_e^0, H_i^0, H_r^0)) - u(t, \mathcal{E}_0)\| < \rho_0, \quad \forall t \in [0, \tau], \quad n \geq 0.$$

For any $t \geq 0$, let $t = \ell\tau + t''$, where $t'' \in [0, \tau]$, and ℓ is the largest integer less than or equal to $\frac{t}{\tau}$. Therefore, we have $\|u(t, (A^0, M_s^0, M_e^0, M_i^0, H_s^0, H_e^0, H_i^0, H_r^0)) - u(t, \mathcal{E}_0)\| = \|u(t'', P^\ell(A^0, M_s^0, M_e^0, M_i^0, H_s^0, H_e^0, H_i^0, H_r^0)) - u(t'', \mathcal{E}_0)\| < \rho_0$. Note that $(A(t), M_s(t), M_e(t), M_i(t), H_s(t), H_e(t), H_i(t), H_r(t)) = u(t, (A^0, M_s^0, M_e^0, M_i^0, H_s^0, H_e^0, H_i^0, H_r^0))$ and $u(t, \mathcal{E}_0) = \mathcal{E}_0 = E_0, \quad \forall t \geq 0$. It then follows that for all $t \geq 0$, we have

$$A(t) < \rho_0, \quad M_s(t) < \rho_0, \quad \forall t \geq 0.$$

By Lemma 3.1, it follows that there exists a $t_0 > 0$ such that

$$N_H(t) > H^* - \rho_0, \quad \forall t \geq t_0.$$

Then it follows from the equations of A and M_s in (2.1) that

$$\begin{cases} \frac{dA}{dt} \geq k\delta(t) \left(1 - \frac{\rho_0}{C}\right) M_s - (\theta(t) + \mu_a(t))A, & t \geq t_0, \\ \frac{dM_s}{dt} \geq \theta(t)A - \left[\frac{b\beta_m(t)M_s\rho_0}{H^* - \rho_0} + \mu_m(t)\right]M_s, & t \geq t_0. \end{cases} \quad (3.30)$$

Since $(A^0, M_s^0, M_e^0, M_i^0, H_s^0, H_e^0, H_i^0, H_r^0) \in \mathbb{X}_0$, it follows from Lemma 3.9 that

$$(A(t_0), M_s(t_0)) \gg 0.$$

By Lemma 3.8, it follows that there exists a positive, τ -periodic function $Q(t)$ and $\kappa = \frac{1}{\tau} \ln [r(\Psi_{\mathbf{F}^M(\cdot) - \mathbf{V}^M(\cdot)}(\tau))]$ such that $\tilde{Q}(t) := \tilde{d}e^{\kappa(t-t_0)}Q(t)$ is a solution of

$$\frac{dy(t)}{dt} = (\mathbf{F}^M(t) - \mathbf{V}^M(t))y(t),$$

where $\tilde{d}$ satisfies $\tilde{Q}(t_0) := \tilde{d}Q(t_0) \leq (A(t_0), M_s(t_0))$. The standard comparison theorem (see, e.g., [33, Theorem B.1]) implies that

$$(A(t), M_s(t)) \geq \tilde{Q}(t), \quad \forall t \geq t_0.$$

In particular, there exists n_0 such that

$$(A(n\tau), M_s(n\tau)) \geq \tilde{Q}(n\tau), \quad \forall n \geq n_0.$$

Since $\kappa > 0$, it follows that $\tilde{Q}(n\tau) \rightarrow \infty$ as $n \rightarrow \infty$. Thus, $(A(n\tau), M_s(n\tau)) \rightarrow \infty$ as $n \rightarrow \infty$. This contradiction completes the proof of the case $j = 0$. $\square$

Now we prove that $\mathcal{R}^0$ is a threshold index for disease persistence if $\mathcal{R}^M > 1$ as stated in the following theorem.

Theorem 3.2. *Assume that $\mathcal{R}^M > 1$. Then the following statements hold.*

- (i) *If $\mathcal{R}^0 < 1$, then the disease-free periodic state $E_1(t)$ is globally attractive for system (2.1) in the sense that if $(A^0, M_s^0) \neq (0, 0)$, we have*

$$\lim_{t \rightarrow \infty} [(A(t), M_s(t), M_e(t), M_i(t), H_s(t), H_e(t), H_i(t), H_r(t)) - E_1(t)] = (0, 0, 0, 0, 0, 0, 0, 0);$$

- (ii) *If $\mathcal{R}^0 > 1$, there exists an $\eta > 0$ such that for any solution*

$$(A(t), M_s(t), M_e(t), M_i(t), H_s(t), H_e(t), H_i(t), H_r(t))$$

with initial value $(A^0, M_s^0, M_e^0, M_i^0, H_s^0, H_e^0, H_i^0, H_r^0) \in \mathbb{X}_0$ satisfies

$$\liminf_{t \rightarrow \infty} M_i(t) \geq \eta.$$

Further, system (2.1) admits at least one positive τ -periodic solution

$$(\tilde{A}(t), \tilde{M}_s(t), \tilde{M}_e(t), \tilde{M}_i(t), \tilde{H}_s(t), \tilde{H}_e(t), \tilde{H}_i(t), \tilde{H}_r(t)).$$

Proof. Part (i). We first consider the case where $\mathcal{R}^0 < 1$. From Lemma 3.7, it follows that $r(\Phi_{\mathbf{F}(\cdot) - \mathbf{V}(\cdot)}(\tau)) < 1$. Now we choose $\xi_0 > 0$ sufficiently small such that $r(\Phi_{\mathbf{F}_{\xi_0}(\cdot) - \mathbf{V}(\cdot)}(\tau)) < 1$, where

$$\mathbf{F}_{\xi_0}(t) = \begin{pmatrix} 0 & 0 & 0 & \frac{b\beta_m(t)(M^*(t) + \xi_0)}{H^* - \xi_0} \\ 0 & 0 & 0 & 0 \\ 0 & \frac{b\beta_h(t)(H^* + \xi_0)}{H^* - \xi_0} & 0 & 0 \\ 0 & 0 & 0 & 0 \end{pmatrix}.$$

Assume that

$$(A(t), M_s(t), M_e(t), M_i(t), H_s(t), H_e(t), H_i(t), H_r(t))$$

is a nonnegative solution of system (2.1) in $\mathbb{X}$. Note that $N_H(t)$ and $(A(t), N_M(t))$ satisfy (3.3) (Lemma 3.1) and (3.12) (Lemma 3.4), respectively. Then there is a $T > 0$ such that for any $t \geq T$, we have

$$M_s(t) \leq N_M(t) \leq M^*(t) + \xi_0, \quad H_s(t) \leq N_H(t) \leq H^* + \xi_0, \quad N_H(t) \geq H^* - \xi_0.$$

By Lemma 3.8, it follows that there exists a positive, τ -periodic function $v(t)$ and $\mu = \frac{1}{\tau} \ln [r(\Phi_{\mathbb{F}_{\xi_0}(\cdot) - \mathbb{V}(\cdot)}(\tau))]$ such that $\bar{v}(t) := \bar{a}e^{\mu t}v(t)$ is a solution of

$$\frac{dx(t)}{dt} = (\mathbb{F}_{\xi_0}(t) - \mathbb{V}(t))x(t),$$

where $\bar{a}$ satisfies $\bar{v}(T) := \bar{a}v(T) \geq (M_e(T), M_i(T), H_e(T), H_i(T))$.

From the equations of M_e , M_i , H_e and H_i in (2.1), it follows that

$$\begin{cases} \frac{dM_e}{dt} \leq \frac{b\beta_m(t)(M^*(t) + \xi_0)}{H^* - \xi_0} H_i - (\gamma_m(t) + \mu_m(t))M_e, \quad \forall t \geq T, \\ \frac{dM_i}{dt} = \gamma_m(t)M_e - \mu_m(t)M_i, \quad \forall t \geq T, \\ \frac{dH_e}{dt} \leq \frac{b\beta_h(t)(H^* + \xi_0)}{H^* - \xi_0} M_i - (\gamma_h + \mu_h)H_e, \quad \forall t \geq T, \\ \frac{dH_i}{dt} = \gamma_h H_e - (\alpha_h + \mu_h)H_i, \quad \forall t \geq T. \end{cases} \quad (3.31)$$

The standard comparison theorem (see, e.g., [33, Theorem B.1]) implies that

$$(M_e(t), M_i(t), H_e(t), H_i(t)) \leq \bar{v}(t), \quad \forall t \geq T.$$

Since $\mu < 0$, it follows that $\bar{v}(t) \rightarrow 0$ as $t \rightarrow \infty$. Thus, $(M_e(t), M_i(t), H_e(t), H_i(t)) \rightarrow 0$ as $t \rightarrow \infty$. This implies that (A, M_s) is asymptotic to (3.6). By the theory of asymptotically periodic semiflows (see, e.g., [48] or [47, section 3.2]) and Lemma 3.4, it follows that $\lim_{t \rightarrow \infty} [(A(t), M_s(t)) - (A^*(t), M^*(t))] = (0, 0)$. This completes the proof of Part (i).

Part (ii). We next consider the case where $\mathcal{R}^0 > 1$. From Lemma 3.5, it follows that the discrete-time system $\{P^n\}_{n \geq 0}$ admits a global attractor in $\mathbb{X}$. Now we prove that $\{P^n\}_{n \geq 0}$ is uniformly persistent with respect to $(\mathbb{X}_0, \partial\mathbb{X}_0)$. By Lemma 3.9, it follows that $\mathbb{X}$ and $\mathbb{X}_0$ are positively invariant. Clearly, $\partial\mathbb{X}_0$ is relatively closed in $\mathbb{X}$. Let

$$\begin{aligned} M_{\partial} &= \{(A^0, M_s^0, M_e^0, M_i^0, H_s^0, H_e^0, H_i^0, H_r^0) \in \partial\mathbb{X}_0, \\ &\quad : P^n(A^0, M_s^0, M_e^0, M_i^0, H_s^0, H_e^0, H_i^0, H_r^0) \in \partial\mathbb{X}_0, \quad \forall n \geq 0\}. \end{aligned}$$

We are going to prove that

$$M_{\partial} := \{(A^0, M_s^0, M_e^0, M_i^0, H_s^0, H_e^0, H_i^0, H_r^0) \in \mathbb{X} : M_i^0 = 0\}, \quad (3.32)$$

for which, it suffices to prove that for any $(A^0, M_s^0, M_e^0, M_i^0, H_s^0, H_e^0, H_i^0, H_r^0) \in M_{\partial}$, we have $M_i(n\tau) = 0$, $\forall n \geq 0$. If it is not true, there exists an $n_1 \geq 0$ such that

$$M_i(n_1\tau) > 0. \quad (3.33)$$

It is easy to see from A equation of (2.1) that

$$A(t) = e^{-\int_{n_1\tau}^t b(s_1)ds_1} \left[\int_{n_1\tau}^t e^{\int_{n_1\tau}^{s_2} b(s_1)ds_1} \zeta(s_2)ds_2 + A(n_1\tau) \right], \quad (3.34)$$

where $\zeta(t)$ and $b(t)$ are defined in (3.22). Thus, $A(t) > 0$, $\forall t > n_1\tau$. Similarly, from M_s equation of (2.1) we have

$$M_s(t) = e^{-\int_{n_1\tau}^t c(s_1)ds_1} \left[\int_{n_1\tau}^t e^{\int_{n_1\tau}^{s_2} c(s_1)ds_1} \theta(s_2)A(s_2)ds_2 + M_s(n_1\tau) \right], \quad (3.35)$$

where $c(t)$ is defined in (3.24). This implies that $M_s(t) > 0$, $\forall t > n_1\tau$. By [32, Theorem 4.1.1] as generalized to nonautonomous systems, the irreducibility of the cooperative matrix (3.25) implies that

$$(M_e(t), M_i(t), H_e(t), H_i(t)) \gg 0, \forall t > n_1\tau,$$

where the initial value $(M_e(n_1\tau), M_i(n_1\tau), H_e(n_1\tau), H_i(n_1\tau)) > 0$. In particular, we have $(M_e(n\tau), M_i(n\tau), H_e(n\tau), H_i(n\tau)) \gg 0$, $\forall n > n_1$, which contradicts the fact that $(A^0, M_s^0, M_e^0, M_i^0, H_s^0, H_e^0, H_i^0, H_r^0) \in M_\partial$. This implies that (3.32) holds. It is clear that there are two fixed points of P in M_∂ , which are $\mathcal{E}_0 = E_0 = (0, 0, 0, 0, H^*, 0, 0, 0)$ and $\mathcal{E}_1 = E_1(0) = (A^*(0), M^*(0), 0, 0, H^*, 0, 0, 0)$. If $(A(t), M_s(t), M_e(t), M_i(t), H_s(t), H_e(t), H_i(t), H_r(t))$ is a solution of system (2.1) initiating from M_∂ , it follows from system (2.1) and the fact $M_i(t) \equiv 0$ that $(A(t), M_s(t), M_e(t), M_i(t), H_s(t), H_e(t), H_i(t), H_r(t))$ approaches E_0 or $E_1(t)$ as t approaches ∞ .

It follows from Lemma 3.10 that $\{\mathcal{E}_0\} \cup \{\mathcal{E}_1\}$ is an isolated invariant set in $\mathbb{X}$ and $W^s(\mathcal{E}_j) \cap \mathbb{X}_0 = \emptyset$, $j = 0, 1$, where $W^s(\mathcal{E}_j)$ is the stable set of $\mathcal{E}_j$. Note that every orbit in M_∂ approaches to $\{\mathcal{E}_0\} \cup \{\mathcal{E}_1\}$, and $\{\mathcal{E}_0\} \cup \{\mathcal{E}_1\}$ is acyclic in M_∂ . By [47, Theorem 1.3.1], it follows that $\{P^n\}_{n \geq 0}$ is uniformly persistent with respect to $(\mathbb{X}_0, \partial\mathbb{X}_0)$. By [47, Theorem 3.1.1], the solutions of system (2.1) are uniformly persistent with respect to $(\mathbb{X}_0, \partial\mathbb{X}_0)$, that is, there exists an $\eta > 0$ such that for any solution

$$(A(t), M_s(t), M_e(t), M_i(t), H_s(t), H_e(t), H_i(t), H_r(t))$$

with initial value $(A^0, M_s^0, M_e^0, M_i^0, H_s^0, H_e^0, H_i^0, H_r^0) \in \mathbb{X}_0$ satisfies

$$\liminf_{t \rightarrow \infty} M_i(t) \geq \eta.$$

Furthermore, [47, Theorem 1.3.6] implies that P has a fixed point

$$(\tilde{A}(0), \tilde{M}_s(0), \tilde{M}_e(0), \tilde{M}_i(0), \tilde{H}_s(0), \tilde{H}_e(0), \tilde{H}_i(0), \tilde{H}_r(0)) \in \mathbb{X}_0,$$

and hence, $\tilde{M}_i(0) > 0$. By the same arguments as those in Lemma 3.9, one can show that

$$(\tilde{A}(t), \tilde{M}_s(t), \tilde{M}_e(t), \tilde{M}_i(t), \tilde{H}_s(t), \tilde{H}_e(t), \tilde{H}_i(t), \tilde{H}_r(t)) \gg 0.$$

This completes the proof of Part (ii). $\square$

4. Numerical computation. In this section we present some numerical results demonstrating how mean temperature, seasonal temperature variations, and diurnal temperature variations can impact the mosquito reproduction number ($\mathcal{R}^M$) and the infection invasion threshold ($\mathcal{R}^0$). We used Lemma 3.11 to compute $\mathcal{R}^M$ and Lemma 3.17 to compute $\mathcal{R}^0$ numerically as done in previous studies ([37, 40, 19]). Our results show that the value of $\mathcal{R}^M$ is greater than $\mathcal{R}^0$ for every temperature profile. This indicates that $\mathcal{R}^M < 1$ (extinction of mosquito population) implies $\mathcal{R}^0 < 1$ (eradication of dengue), which is practically true as mosquito bites are the only route of dengue transmission.

4.1. Effects of mean temperature, T_0 . We performed computations to study how varying annual mean temperature, T_0 , from 10°C to 45°C affects $\mathcal{R}^M$ and $\mathcal{R}^0$ (Fig. 4.1). On increasing T_0 , both $\mathcal{R}^M$ and $\mathcal{R}^0$ increase, reach the corresponding maximum values and then decrease, with $\mathcal{R}^M < 1$ and $\mathcal{R}^0 < 1$ for extremely low mean temperatures as well as extremely high mean temperatures. Therefore, there exist optimal ranges of the mean temperature for both persistence of mosquito population and persistence of dengue fever. However, the interval of the mean temperature for mosquito persistence is larger than that for the dengue persistence. For example, in our computation (Fig. 4.1), mosquito persists (i.e., $\mathcal{R}^M > 1$) for $13.5^\circ\text{C} \leq T_0 \leq 44.5^\circ\text{C}$, while dengue persists (i.e., $\mathcal{R}^0 > 1$) for $16.5^\circ\text{C} \leq T_0 \leq 36.5^\circ\text{C}$. Note that there are small ranges of the mean temperature during which mosquito persists, but dengue does not persist.

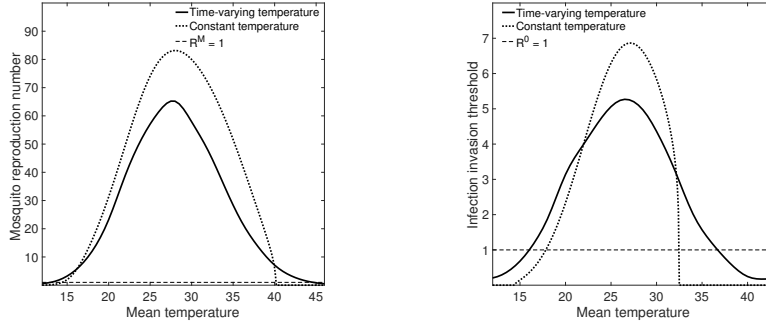


FIGURE 4.1. Mosquito reproduction number ($\mathcal{R}^M$) [Left] and infection invasion threshold ($\mathcal{R}^0$) [right] for different values of the mean temperature (T_0) with amplitudes of seasonal temperature and diurnal temperature fixed at $\epsilon_m = 5^\circ\text{C}$ and $\epsilon_d = 5^\circ\text{C}$, respectively. For comparison purposes, $\mathcal{R}^M$ and $\mathcal{R}^0$ for the constant temperature (i.e., $\epsilon_m = \epsilon_d = 0^\circ\text{C}$) are also plotted.

For comparison purposes, we also computed both the mosquito reproduction number and the infection invasion threshold for the constant temperature (Figure 4.1). For the parameter range considered in this study, the mosquito population hardly persists for temperatures maintained constant at values greater than 40°C . However, for the time-varying temperature, the mosquito population may persist also for the mean temperatures slightly higher than 40°C . It should be noted that for the time-varying periodic temperature, even though the mean temperature is 40°C , the temperature in our base case computation can reach as low as 30°C due to the seasonal and diurnal variations. Therefore, the time-varying temperature provides the values of $\mathcal{R}^M$ and $\mathcal{R}^0$ different from their values with constant temperature. Our estimates show that the constant temperature underestimates $\mathcal{R}^M$ and $\mathcal{R}^0$ for low and high mean temperatures while it overestimates for the middle temperature range.

4.2. Effects of seasonal temperature variation, ϵ_m . In this subsection, we use the parameter ϵ_m , the amplitude of the seasonal temperature, to evaluate the

effects of seasonal temperature variation on the mosquito reproduction number and the infection invasion threshold. We compute $\mathcal{R}^M$ (Fig. 4.2, left column) and $\mathcal{R}^0$ (Fig. 4.2, right column) for various values of ϵ_m with all other parameters fixed. As we discussed above, since the values of $\mathcal{R}^M$ and $\mathcal{R}^0$ may highly depend on the mean temperature with maximum values occurring at some temperature, we consider three cases: a lower mean temperature ($T_0 = 16^\circ\text{C}$) (Fig. 4.2, top row), an optimal mean temperature ($T_0 = 28^\circ\text{C}$) (Fig. 4.2, middle row), and a higher mean temperature ($T_0 = 38^\circ\text{C}$) (Fig. 4.2, bottom row).

For the amplitude of seasonal temperature considered, the mosquito reproduction number mostly remains larger than 1 (Fig. 4.2, right column). This shows that the mosquito population persists for this range of temperature as observed in reality. We observed that in each of the three mean temperatures considered, there is a decreasing trend of $\mathcal{R}^M$ for an increasing amplitude of the seasonal temperature (Fig. 4.2, right column). This shows that in places, where the temperature remains relatively stable over the seasons, the growth of mosquito population is favored, compared to the places with large seasonal variation of temperature. This effect is mainly pronounced in the case of the optimal mean temperature ($T_0 = 28^\circ\text{C}$) (Fig. 4.2, middle row). At $T_0 = 28^\circ\text{C}$, $\mathcal{R}^M$ decreases from 65 to 13 when ϵ_m increases from 5°C to 15°C , while at $T_0 = 16^\circ\text{C}$ and $T_0 = 38^\circ\text{C}$, the change of $\mathcal{R}^M$ is from 4.9 to 2 and from 13.6 to 6, respectively.

Computed values of $\mathcal{R}^0$ for varying ϵ_m (Fig. 4.2, left column) indicate that $\mathcal{R}^0$ can be less than 1 for some values of ϵ_m . Therefore, the seasonal variation of the temperature can be a determinant factor for the dengue epidemic to die out ($\mathcal{R}^0 < 1$) or to persist ($\mathcal{R}^0 > 1$). In general, a larger variation of seasonal temperature provides a smaller value of the infection invasion threshold. For example, $\mathcal{R}^0 < 1$ for $\epsilon_m > 11^\circ\text{C}$, 16°C , and 18.5°C at the mean temperature $T_0 = 16^\circ\text{C}$, $T_0 = 28^\circ\text{C}$, and $T_0 = 38^\circ\text{C}$, respectively. However, note that for $T_0 = 16^\circ\text{C}$ and $T_0 = 38^\circ\text{C}$, smaller amplitudes also make $\mathcal{R}^0 < 1$. These results indicate that the places with a larger variation in seasonal temperature has a less likelihood for a dengue epidemic to occur.

4.3. Effects of diurnal temperature variation, ϵ_d . We now vary ϵ_d , the amplitude of diurnal temperature, from 5°C to 25°C , and compute the mosquito reproduction number ($\mathcal{R}^M$) (Fig. 4.3, left column) and the infection invasion threshold $\mathcal{R}^0$ (Fig. 4.2, right column) for those values of ϵ_m . Again, we consider three different seasonal mean temperature, $T_0 = 16^\circ\text{C}$ (Fig. 4.3, top row), $T_0 = 28^\circ\text{C}$ (Fig. 4.3, middle row), and $T_0 = 38^\circ\text{C}$ (Fig. 4.3, bottom row). Our results show that the patterns of $\mathcal{R}^M$ and $\mathcal{R}^0$ (Fig. 4.3) for an increasing ϵ_d are similar to those observed for an increasing ϵ_m .

An increase in diurnal temperature variation decreases the mosquito reproduction number with a bigger effect seen in the mean temperature corresponding to the peak $\mathcal{R}^M$ (i.e. $T_0 = 28^\circ\text{C}$). In our calculation, the increase in ϵ_d by 10°C (from 5°C to 15°C) caused a decrease of the mosquito reproduction number by 3 (from 5 to 2), 55 (from 65 to 10), and 11 (from 13 to 2) when the mean temperature was set to $T_0 = 16^\circ\text{C}$, 28°C , and 38°C , respectively. Thus, places with higher diurnal temperature variation are less favorable for the growth of mosquito population. It is worth noting that at $T_0 = 38^\circ\text{C}$, a higher amplitude of diurnal temperature,

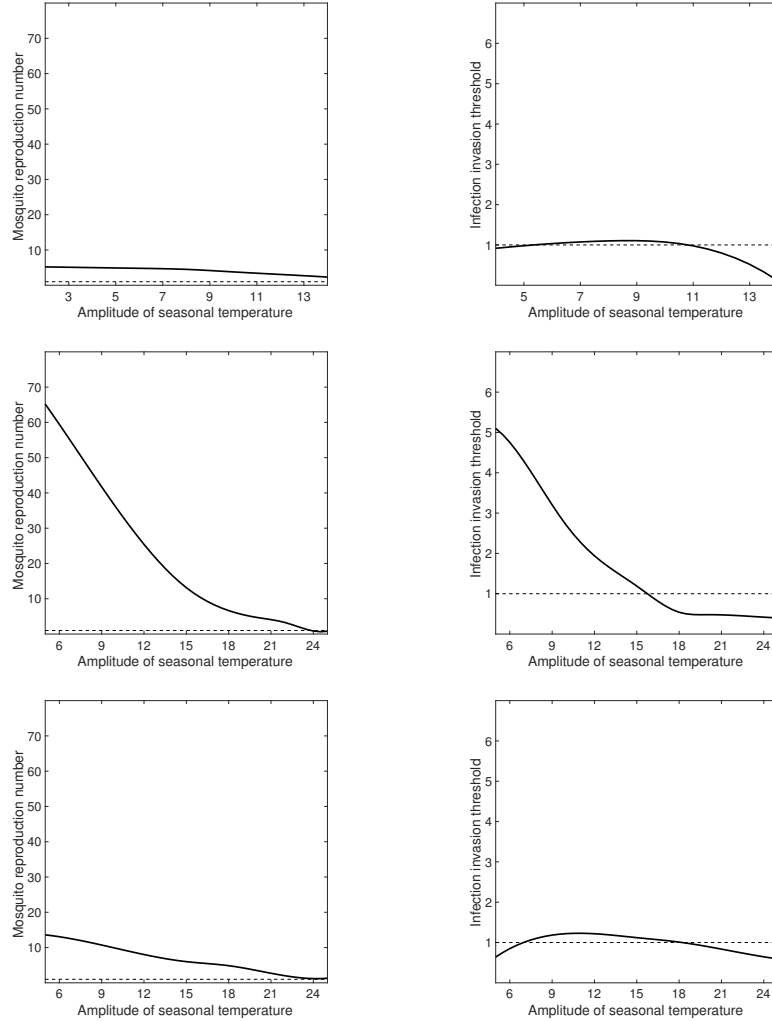


FIGURE 4.2. Mosquito reproduction number ($\mathcal{R}^M$) [left column] and infection invasion threshold ($\mathcal{R}^0$) [right column] for different values of the amplitudes of seasonal temperature (ϵ_m) with the amplitude of diurnal temperature fixed at $\epsilon_d = 5$ °C and the mean temperature fixed at $T_0 = 16$ °C [top row], $T_0 = 28$ °C [middle row], and $T_0 = 38$ °C [bottom row].

for example, $\epsilon_d > 20$ °C, can bring $\mathcal{R}^M$ to a value less than 1, resulting in the extinction of mosquito population.

Similarly, our results show that higher diurnal temperature can bring the infection invasion threshold, $\mathcal{R}^0$, to a value less than 1, avoiding dengue epidemics. According to our computations, the dengue can not persist for amplitude of diurnal temperature, ϵ_d , greater than 13.5 °C, 19.5 °C, and 13.5 °C, for the mean temperature $T_0 = 16$ °C, 28 °C, and 38 °C, respectively. Therefore, places with

environmental temperature with higher diurnal fluctuation are less vulnerable to dengue epidemics.

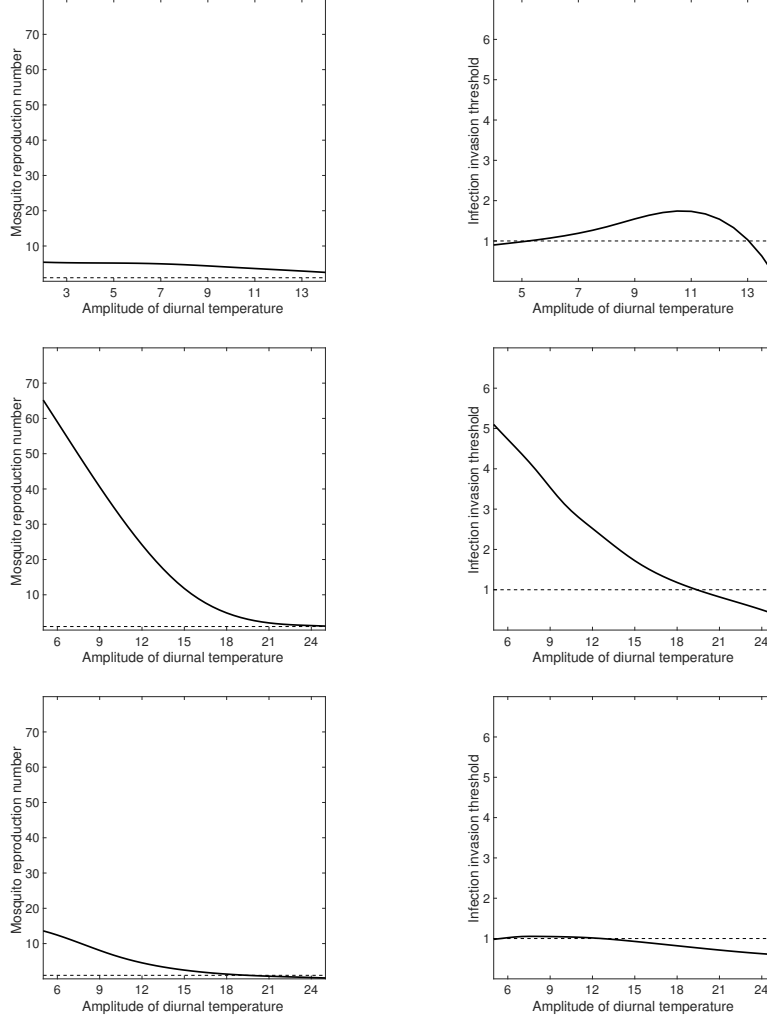


FIGURE 4.3. Mosquito reproduction number ($\mathcal{R}^M$) [left column] and infection invasion threshold ($\mathcal{R}^0$) [right column] for different values of the amplitudes of diurnal temperature (ϵ_d) with the amplitude of seasonal temperature fixed at $\epsilon_m = 5$ °C and the mean temperature fixed at $T_0 = 16$ °C [top row], $T_0 = 28$ °C [middle row], and $T_0 = 38$ °C [bottom row].

5. Discussion and conclusion. It is known that the environmental temperature can have a substantial impact on the life cycle of mosquito and the mosquito-human-mosquito transmission cycle of dengue virus [4, 35, 24, 9, 17, 45, 43]. Because of complexity in the variation of environmental temperature, especially existence of

diurnal temperature fluctuations on top of the seasonal variations, there remains much uncertainty on the understanding of the role of temperature on mosquito population and dengue transmission [17, 28]. The major objective of this study was to develop a mathematical model to evaluate the impact of seasonal and diurnal temperature variation on the persistence of mosquito vectors and dengue.

Using techniques from the dynamical system theory, we used our nonautonomous model to establish two thresholds, the mosquito reproduction number ($\mathcal{R}^M$) and the infection invasion threshold ($\mathcal{R}^0$), which fully determine whether the mosquito population and dengue, respectively, persist or die out in a community. Specifically, $\mathcal{R}^M > 1$ implies the persistence of mosquito population and $\mathcal{R}^0 > 1$ implies the persistence of dengue. Importantly, the formulated expressions show that both of $\mathcal{R}^M$ and $\mathcal{R}^0$ depend on seasonal and diurnal temperature variations, highlighting the importance of considering these factors in the study of mosquito abundance and dengue spread.

Analysis of threshold dynamics and numerical computations of the threshold values provide some interesting results related to mosquito vectors and dengue epidemics. First, $\mathcal{R}^M$ is always greater than $\mathcal{R}^0$, indicating that a certain temperature can result in the persistence of mosquitos while avoiding dengue epidemics, as observed in real life situations. This also indicates eradicating the mosquito population can be much difficult compared to eradicating the dengue. Therefore, relying on only mosquito population control may not be enough for the successful control of dengue. Second, we identified that there exists a certain range of annual mean temperature for the persistence of mosquito population, i.e., the mosquito population can not persist when the average environmental temperature is too low or too high. Similarly, the dengue persistence is favored for a certain range of annual mean temperature. The temperature range (interval) for the persistence of dengue is subset of the temperature range (interval) for the persistence of mosquito population. These temperature intervals provide the ranges of temperature for which mosquitos persist but the dengue epidemic is avoided.

Next, our results show that both seasonal and diurnal temperature variations are critical for the persistence of mosquito population ($\mathcal{R}^M > 1$) as well as for the persistence of dengue ($\mathcal{R}^0 > 1$). This explains why only the mean temperature was unable to describe the observed epidemics in some places, such as Thailand, where the epidemics are correlated mainly with diurnal temperature variations [17, 8, 20, 29, 30]. In general, our numerical estimates show that a sufficiently large seasonal or diurnal temperature variation can result in $\mathcal{R}^M < 1$ and $\mathcal{R}^0 < 1$, implying that places with larger temperature variations suffer less from the mosquito population burden and dengue epidemics.

We acknowledge the several limitations of our study. Our computations are based on the parameters estimated using limited data sets. Therefore, we note that our computations should be considered primarily for the purpose of qualitative results, and may need to be improved for quantitative applications in real life. More data sets, particularly those related to diurnal temperature variations, can help improve the calculation of $\mathcal{R}^M$ and $\mathcal{R}^0$. We primarily focused on the threshold dynamics predicted by the model. However, it might be important to study detailed temporal dynamics of the dengue, especially for the case when $\mathcal{R}^0 > 1$. For this, the future work with numerical comparison of the model prediction with real data on dengue

cases will strengthen the validity of our model predictions. We are also unable to explicitly formulate the endemic equilibrium, which requires more theoretical and higher computational exercises. Furthermore, models that combine spatial variation along with the temporal variation of the environmental temperature may be needed to more accurately describe the rapid worldwide spread of dengue.

In summary, the model developed here is capable of capturing the effects of diurnal and seasonal temperature variations on the dynamics of mosquito population and dengue transmission. As revealed in the results from our model, in addition to the seasonal temperature variation, the diurnal temperature variation also plays a significant role in the persistence of mosquito vectors and the persistence of dengue. Thus, both seasonal as well as diurnal temperature variations should be considered in the study of mosquito population as well as dengue transmission, control, and prevention.

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