Habitat fragmentation promotes malaria persistence

Daozhou Gao¹ · P. van den Driessche² · Chris Cosner³

Abstract Based on a Ross–Macdonald type model with a number of identical patches, we study the role of the movement of humans and/or mosquitoes on the persistence of malaria and many other vector-borne diseases. By using a theorem on line-sum symmetric matrices, we establish an eigenvalue inequality on the product of a class of nonnegative matrices and then apply it to prove that the basic reproduction number of the multipatch model is always greater than or equal to that of the single patch model. Biologically, this means that habitat fragmentation or patchiness promotes disease outbreaks and intensifies disease persistence. The risk of infection is minimized when the distribution of mosquitoes is proportional to that of humans. Numerical examples for the two-patch submodel are given to investigate how the multipatch reproduction number varies with human and/or mosquito movement. The reproduction number can surpass any given value whenever an appropriate travel pattern is chosen. Fast human and/or mosquito movement decreases the infection risk, but may increase the total number of infected humans.

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1 Introduction

Vector-borne diseases are illness caused by pathogens, which are transmitted to humans or animals by the bites of infected vectors such as mosquitoes (e.g., malaria, dengue fever, Rift Valley fever, and Zika virus disease), ticks (e.g., Lyme disease and babesiosis), aquatic snails (e.g., schistosomiasis), fleas (e.g., plague), bugs (e.g., Chagas disease), and sandflies (e.g., onchocerciasis). They are responsible for over 17% of the estimated global burden of all infectious diseases (World Health Organization 2017). For example, malaria alone caused an estimated 219 million cases and approximately 435,000 deaths worldwide in 2017, though the mortality rates have reduced by about 60% since 2000 (World Health Organization 2018). Rift Valley fever results in significant economic costs through human morbidity and loss of livestock. The 2015-16 Zika virus outbreak caused up to one million suspected cases and thousands of confirmed microcephaly cases in Brazil (Pan American Health Organization 2017).

Mathematical modeling and analysis of vector-borne diseases, with a long history of development and application, have attracted considerable attention among governmental agencies and institutional researchers (Mandal et al. 2011; Reiner et al. 2013). The original mathematical model for malaria transmission was proposed by Ross (1911) in 1911 and later extended by MacDonald (1957) in the 1950s. In this seminal work, the malaria transmission cycle is depicted in Figure 1.

![Flowchart of the Ross–Macdonald model for malaria. The variables and parameters are defined in the text.](image-url)
Both humans and mosquitoes are either susceptible or infectious and their respective total population sizes, \( H \) and \( V \), are constant. The rates of change of the number of infectious humans and infectious mosquitoes, \( h(t) \) and \( v(t) \), are described by a system of two ordinary differential equations as follows:

\[
\begin{align*}
\frac{dh}{dt} &= a \frac{v}{H} (H - h) - \gamma h, \\
\frac{dv}{dt} &= a \frac{h}{H} (V - v) - \mu v,
\end{align*}
\]

where \( H - h \) and \( V - v \) are respectively the number of susceptible humans and susceptible mosquitoes, \( a \) is the rate of biting on humans by a single mosquito, \( \gamma \) is the rate at which infectious humans recover, \( \mu \) is the birth rate and the mortality rate of mosquitoes, \( b \) and \( c \) are the transmission probabilities from an infectious mosquito to a susceptible human and from an infectious human to a susceptible mosquito per bite, respectively. The reader may refer to the paper by Smith and McKenzie (2004) for a detailed derivation and some results on the model.

Obviously the origin is the disease-free equilibrium of the so called Ross–Macdonald model (1). We can use the next generation matrix method (Diekmann et al. 1990; van den Driessche and Watmough 2002) to define a basic reproduction number for the average number of secondary infections produced by a typical infectious individual (human or mosquito) during the entire infectious period provided that everyone else of both populations are susceptible. The disease will disappear if the reproduction number is less than or equal to unity and will eventually stabilize at an endemic equilibrium if the reproduction number is greater than one. The Ross–Macdonald model reflects the essential feature of malaria transmission process, namely, the transmission from infected mosquitoes to susceptible humans and from infected humans to susceptible mosquitoes. The model and its threshold quantity play a critical role in the World Health Organization’s Global Malaria Eradication Programme (1955-1969) (Smith et al. 2012). It is now widely accepted as a solid framework for the study of the transmission dynamics of malaria and many other mosquito-borne or vector-borne diseases like West Nile virus (Bowman et al. 2005; Chen et al. 2016), dengue fever (Abdelrazec et al. 2016; Feng and Velasco-Hernández 1997), yellow fever (Codeço et al. 2007), and Zika (Gao et al. 2016; Kucharski et al. 2016). Interestingly, Ross received a Nobel Prize in Physiology or Medicine for his discovery of the life cycle of the malarial parasite in 1902, but he considered his epidemiological mathematics as his greatest contribution.

Since the Ross–Macdonald model is the earliest and simplest malaria model, it inevitably has some major limitations due to failure to take many ecological and epidemiological factors into account. Over the last few decades, a large number of studies on mathematical models of malaria have been done by adding factors such as superinfection, extrinsic incubation period of malaria parasites in mosquitoes (10 days or longer), age structure (children are more susceptible than adults), acquired immunity and vital dynamics in humans, environmental factors (temperature, humidity and rain are important for the
survival of mosquitoes and the development of parasites), treatment and drugesoance, a hypothetical vaccine to the model (Mandal et al. 2011; Reiner et al. 2013; Smith et al. 2012). Among these extensions, a few efforts have been made to incorporate spatial heterogeneity in discrete or continuous space (Arino et al. 2012; Auger et al. 2008; Bai et al. 2018; Cosner et al. 2009; Gao and Ruan 2012; Lou and Zhao 2011). Both observation data and theoretical research suggest that human movement may strengthen the spread and persistence of malaria around the world (Cosner et al. 2009; Gao and Ruan 2012; Khuu et al. 2017). We refer the readers to two review articles by Cosner (2015) and Gao and Ruan (2014).

In this paper, we will study the effect of human and/or mosquito movement on the persistence of malaria in a fragmented environment with identical patches, i.e., there is no epidemiological or demographic difference among patches in case they are isolated. Such a tough restriction enables us to exclusively focus on the movement itself with no interference from spatial heterogeneities.

In the next section, we present a generalized Ross–Macdonald model where population dispersal among identical patches is considered and summarize the global stability result on it. Section 3 is devoted to the main results and their proofs for comparing the basic reproduction numbers of the single patch model and the multipatch model. Some numerical examples are given in Section 4. Finally we discuss the biological meaning of our results, their relevance to other studies, and future research questions.

2 Model Formulation

We begin by formulating a simple multipatch malaria model where the model of each patch in isolation is exactly the same as the Ross–Macdonald model (1) and humans and mosquitoes move between \( n \) identical patches. In patch \( i \), let \( H_i(t) \) and \( V_i(t) \) be the total human and mosquito populations at time \( t \), respectively; \( h_i(t) \) and \( v_i(t) \) be the numbers of infectious humans and infectious mosquitoes at time \( t \), respectively. Then the multipatch Ross–Macdonald model takes the form

\[
\begin{align*}
\frac{dH_i}{dt} &= \sum_{j=1}^{n} c_{ij} H_j, \quad 1 \leq i \leq n, \\
\frac{dV_i}{dt} &= \sum_{j=1}^{n} d_{ij} V_j, \quad 1 \leq i \leq n, \\
\frac{dh_i}{dt} &= ab \frac{v_i}{H_i} (H_i - h_i) - \gamma h_i + \sum_{j=1}^{n} c_{ij} h_j, \quad 1 \leq i \leq n, \\
\frac{dv_i}{dt} &= ac \frac{h_i}{H_i} (V_i - v_i) - \mu v_i + \sum_{j=1}^{n} d_{ij} v_j, \quad 1 \leq i \leq n,
\end{align*}
\]

with nonnegative initial conditions

\[ (H_1(0), \ldots, H_n(0), V_1(0), \ldots, V_n(0), h_1(0), \ldots, h_n(0), v_1(0), \ldots, v_n(0)) \]

satisfying \( \sum_{i=1}^{n} H_i(0) = H > 0 \) and \( \sum_{i=1}^{n} V_i(0) = V > 0 \).
The parameters $c_{ij} \geq 0$ and $d_{ij} \geq 0$ are the movement rate of humans and mosquitoes from patch $j$ to patch $i$ for $i \neq j$, respectively; $-c_{ii} = \sum_{j=1, j \neq i}^{n} c_{ji}$ and $-d_{ii} = \sum_{j=1, j \neq i}^{n} d_{ji}$ are the emigration rates of humans and mosquitoes in patch $i$, respectively. Thus the human and mosquito travel rate matrices $C = (c_{ij})_{n \times n}$ and $D = (d_{ij})_{n \times n}$ are Laplacian matrices. Unless otherwise indicated, we assume throughout this paper that $C$ and $D$ are irreducible such that $n$ patches cannot be separated into two disconnected parts. A square matrix is called quasi-positive, Metzler or essentially nonnegative if all its off-diagonal entries are nonnegative. The assumptions on the signs of $c_{ij}$ and $d_{ij}$ for $i \neq j$ mean that matrices $C$ and $D$ are quasi-positive, and the assumptions on $c_{ii}$ and $d_{ii}$ mean that $C$ and $D$ have zero column sums. The following lemma is part of Corollary 4.3.2 in Smith (1995) and Theorem 6.2.7 in Berman and Plemmons (1979). It guarantees the existence and uniqueness of positive equilibrium for the human and mosquito movement models and the validity of the definition of the multipatch basic reproduction number.

**Lemma 1** Let $C = (c_{ij})_{n \times n}$ be an irreducible quasi-positive matrix satisfying

$$\sum_{i=1}^{n} c_{ij} = 0 \text{ for } j = 1, \ldots, n \text{ and } \delta C = (\delta_{ij} \gamma_{i})_{n \times n} - C \text{ with } \gamma_{i} > 0 \text{ for } i = 1, \ldots, n. \text{ Here } \delta_{ij} \text{ is the Kronecker delta, i.e., } 1 \text{ when } i = j \text{ and } 0 \text{ otherwise.}$

Then $C$ has a simple positive right eigenvector corresponding to the eigenvalue zero; $\delta C^{-1}$ exists and is positive.

The equations for the total human and mosquito populations in model (2) are decoupled from the remaining equations. It follows from Lemma 1 that the model (2) has a unique disease-free equilibrium

$$E_0 = (H_1^*, \ldots, H_n^*, V_1^*, \ldots, V_n^*, 0, \ldots, 0, 0, \ldots, 0),$$

where $(H_1^*, \ldots, H_n^*)$ and $(V_1^*, \ldots, V_n^*)$ are the unique positive solutions to

$$\sum_{j=1}^{n} c_{ij} H_j = 0, \quad i = 1, \ldots, n, \quad \sum_{i=1}^{n} H_i = \sum_{i=1}^{n} H_i(0) = H,$$

and

$$\sum_{j=1}^{n} d_{ij} V_j = 0, \quad i = 1, \ldots, n, \quad \sum_{i=1}^{n} V_i = \sum_{i=1}^{n} V_i(0) = V,$$

respectively; see Lemma 1 in Cosner et al. (2009). It is worth noting that $(H_1^*, \ldots, H_n^*)^T$ and $(V_1^*, \ldots, V_n^*)^T$ are respectively the positive right eigenvectors of $C$ and $D$ corresponding to the zero eigenvalue. Indeed, they are respectively a positive multiple of the positive vectors

$$(-1)^{n-1}(C_{11}, \ldots, C_{nn})^T \text{ and } (-1)^{n-1}(D_{11}, \ldots, D_{nn})^T,$$

normalized by the total human and mosquito population sizes, where $C_{ii}$ and $D_{ii}$ denote the $(i, i)$ cofactor of $C$ and $D$, respectively (Gao and Dong 2019). Explicit expressions for $C_{ii}$ and $D_{ii}$ can be obtained through Kirchhoff’s Matrix Tree Theorem (see Moon (1970)).
Using the next generation matrix method (Diekmann et al. 1990; van den Driessche and Watmough 2002), the new infection and disease transition matrices of the model (2) are respectively
\[
F = \begin{pmatrix} 0 & \mathcal{A} \\ \mathcal{B} & 0 \end{pmatrix} \quad \text{and} \quad V = \begin{pmatrix} \mathcal{C} & 0 \\ 0 & \mathcal{D} \end{pmatrix},
\]
where \( \mathcal{A} = abI_n \), \( \mathcal{B} = ac(\delta_{ij}V_1^*/H_1^*)_{n \times n} \), \( \mathcal{C} = \gamma I_n - C \), and \( \mathcal{D} = \mu I_n - D \). The \( n \times n \) identity matrix is denoted by \( I_n \). It follows from Proposition 2.1 in Iggidr et al. (2016) that the next generation matrix
\[
FV^{-1} = \begin{pmatrix} 0 & \mathcal{A} \mathcal{D}^{-1} \\ \mathcal{B} \mathcal{C}^{-1} \mathcal{D}^{-1} & 0 \end{pmatrix}
\]
is irreducible if and only if \( \mathcal{A} \mathcal{D}^{-1} \mathcal{B} \mathcal{C}^{-1} \) and \( \mathcal{B} \mathcal{C}^{-1} \mathcal{D}^{-1} \mathcal{A} \) are irreducible.

By Lemma 1, the irreducibilities of \( C \) and \( D \) imply that both \( \mathcal{C}^{-1} \) and \( \mathcal{D}^{-1} \) exist and are positive. Thus, \( \mathcal{A} \mathcal{D}^{-1} \mathcal{B} \mathcal{C}^{-1} \) and \( \mathcal{B} \mathcal{C}^{-1} \mathcal{D}^{-1} \mathcal{A} \) are positive and irreducible. The basic reproduction number of the \( n \)-patch model (2) is
\[
R_0(n) = \rho(FV^{-1}) = \rho \left( \begin{array}{cc} 0 & \mathcal{A} \mathcal{D}^{-1} \\ \mathcal{B} \mathcal{C}^{-1} \mathcal{D}^{-1} & 0 \end{array} \right) = \sqrt{\rho(\mathcal{A} \mathcal{D}^{-1} \mathcal{B} \mathcal{C}^{-1})},
\]
where \( \rho \) is the spectral radius of a square matrix. In particular, if \( n = 1 \) then the basic reproduction number of the single patch model (1) is
\[
R_0(1) = \sqrt{\frac{a^2bcV}{\gamma \mu H}}.
\]

By the theory of monotone dynamical systems (Smith 1995), it is shown that the disease dynamics of system (2) are completely determined by its basic reproduction number even if the model parameters \( a, b, c, \gamma \) and \( \mu \) are location-dependent.

**Theorem 1 (Cosner et al. 2009)** For system (2), if \( R_0(n) \leq 1 \) then the disease-free equilibrium, \( E_0 \), is globally stable among nonnegative solutions; if \( R_0(n) > 1 \) then there is a unique positive equilibrium which is globally stable among positive solutions.

In order to eradicate malaria, it follows that we need to reduce \( R_0(n) \) to be less than one by implementing suitable control measures such as vector control and insecticide-treated bednets that increase or decrease certain parameter values. Obviously, \( R_0(n) \) is monotone increasing in terms of \( a, b \) and \( c \), and monotone decreasing with respect to \( \gamma \) and \( \mu \). The classification of the relationship between \( R_0(n) \) and travel rate \( c_{ij} \) or \( d_{ij} \) is a challenging question. We will investigate the effect of population dispersal or patchiness on disease persistence by comparing the basic reproduction numbers of the single patch model (1) and the \( n \)-patch model (2), i.e., \( R_0(1) \) versus \( R_0(n) \).

For model (2) with two identical patches connected by human movement, Gao and Ruan (2014) explicitly solved \( R_0(2) \) and showed that \( R_0(2) \geq R_0(1) \).
This implies that human movement always facilitates malaria transmission in an environment with two identical patches. However, solving $R_0(n)$ or the spectral radius of the $n \times n$ matrix $D^{-1}BC^{-1}$ becomes extremely difficult or even impossible when three or more identical patches are concerned. In what follows, we show that the inequality $R_0(n) \geq R_0(1)$ still holds for the multi-patch Ross–Macdonald model with an arbitrary number of patches connected by movement of humans, mosquitoes or both.

3 Main Results

Before stating the main results and their proofs, we prove a lemma and establish a general result on the spectral radius of a class of nonnegative matrices.

A square matrix $A = (a_{ij})_{n \times n}$ is called line-sum-symmetric if for every $1 \leq i \leq n$, the sum of the entries in the $i$-th row of $A$ equals the sum of the entries in the $i$-th column of $A$, i.e., $\sum_{j=1}^{n} a_{ij} = \sum_{j=1}^{n} a_{ji}$ for $1 \leq i \leq n$. The following result will be used to prove the second lemma below.

**Lemma 2** (Eaves et al. 1985) Let $A = (a_{ij})_{n \times n}$ be an $n \times n$ nonnegative matrix. Then $A$ is line-sum-symmetric if and only if

$$\sum_{i,j=1}^{n} a_{ij} \frac{x_i}{x_j} \geq \sum_{i,j=1}^{n} a_{ij}$$

for all $x_i > 0$ and $1 \leq i \leq n$. Moreover, if $A$ is irreducible and line-sum-symmetric, equality holds if and only if all the coordinates of $x = (x_1, \ldots, x_n)$ coincide, i.e., $x_i = x_j$ for any $1 \leq i, j \leq n$.

**Lemma 3** Let $A = (a_{ij})_{n \times n}$ be an irreducible quasi-positive matrix satisfying $\sum_{i=1}^{n} a_{ij} = 0$ for $j = 1, \ldots, n$; $(w_1, \ldots, w_n)^T$ be a right positive eigenvector of $A$ corresponding to the eigenvalue zero; $\bar{w} = \frac{1}{n} \sum_{i=1}^{n} w_i$, the average of $w_1, \ldots, w_n$; $M = \text{diag}\{w_1, \ldots, w_n\}$ and $N = rI_n - A$ with $r > 0$. Assume that $x = (x_1, \ldots, x_n)^T$ and $y = (y_1, \ldots, y_n)^T$ are two positive vectors, and $\lambda$ is a positive constant. The following statements are valid:

1. if $M^{-1}N^{-1}x = \lambda y$ then $\lambda \geq \frac{1}{nr\bar{w}} \sum_{i=1}^{n} \frac{x_i}{y_i}$ with equality if and only if

$$y_1 = \cdots = y_n \text{ and } \frac{x_1}{y_1} w_1 = \cdots = \frac{x_n}{y_n} w_n = r\lambda; \quad (5)$$

2. if $MN^{-1}x = \lambda y$ then $\lambda \geq \frac{1}{nrw_2} \sum_{i=1}^{n} \frac{x_i}{y_i} w_i^2$ with equality if and only if

$$\frac{y_1^2}{w_1^2} = \cdots = \frac{y_n^2}{w_n^2} \text{ and } \frac{x_1}{y_1} w_1 = \cdots = \frac{x_n}{y_n} w_n = r\lambda; \quad (6)$$
(3) if $N^{-1}M^{-1}x = \lambda y$ then $\lambda \geq \frac{1}{nr\bar{w}} \sum_{i=1}^{n} x_i w_i$ with equality if and only if

$$\frac{y_1}{w_1} = \cdots = \frac{y_n}{w_n} \quad \text{and} \quad \frac{x_1}{y_1} \frac{1}{w_1} = \cdots = \frac{x_n}{y_n} \frac{1}{w_n} = r\lambda; \quad (7)$$

(4) if $N^{-1}Mx = \lambda y$ then $\lambda \geq \frac{1}{nr\bar{w}} \sum_{i=1}^{n} x_i w_i^2$ with equality if and only if

$$\frac{y_1}{w_1} = \cdots = \frac{y_n}{w_n} \quad \text{and} \quad \frac{x_1}{y_1} \frac{1}{w_1} = \cdots = \frac{x_n}{y_n} \frac{w_n}{w_n} = r\lambda. \quad (8)$$

Proof The first equation $M^{-1}N^{-1}x = \lambda y$ is equivalent to $-\frac{1}{\lambda}x = -NM^{-1}y$, or explicitly,

$$-\frac{1}{\lambda} \begin{pmatrix} x_1 \\ \vdots \\ x_n \end{pmatrix} = \begin{pmatrix} w_1 & \cdots & 0 \\ \vdots & \ddots & \vdots \\ 0 & \cdots & w_n \end{pmatrix} + \begin{pmatrix} a_{11}w_1 & \cdots & a_{1n}w_n \\ \vdots & \ddots & \vdots \\ a_{n1}w_1 & \cdots & a_{nn}w_n \end{pmatrix} \begin{pmatrix} y_1 \\ \vdots \\ y_n \end{pmatrix}. \quad (9)$$

Since both the row sums and column sums of $AM = (a_{ij}w_j)_{n \times n}$ are zero, adding $kI_n$ with $k$ sufficiently large to that matrix gives a nonnegative irreducible and line-sum-symmetric matrix. The $i$-th row of (9) can then be written as

$$-\frac{1}{\lambda} x_i + ky_i = -rw_i y_i + \sum_{j=1}^{n} (a_{ij}w_j + \delta_{ij}k)y_j$$

or

$$-\frac{1}{\lambda} \frac{x_i}{y_i} + k + rw_i = \sum_{j=1}^{n} (a_{ij}w_j + \delta_{ij}k) \frac{y_j}{y_i}, \quad (10)$$

for $i = 1, \ldots, n$. It follows from Lemma 2 that summing (10) over $i$ gives

$$-\frac{1}{\lambda} \sum_{i=1}^{n} \frac{x_i}{y_i} + nk + r \sum_{i=1}^{n} w_i = \sum_{i,j=1}^{n} \frac{a_{ij}w_j + \delta_{ij}k}{y_i} \frac{y_j}{y_i} \geq \sum_{i,j=1}^{n} a_{ij}w_j + \sum_{i,j=1}^{n} \delta_{ij}k = nk.$$ 

So

$$\lambda \geq \frac{1}{nr\bar{w}} \sum_{i=1}^{n} \frac{x_i}{y_i}$$

with equality if and only if $y_1 = \cdots = y_n$. But then (10) gives

$$-\frac{1}{\lambda} \frac{x_i}{y_i} + k + rw_i = \sum_{j=1}^{n} (a_{ij}w_j + \delta_{ij}k) = k,$$

which is impossible unless

$$\frac{x_1}{y_1} \frac{1}{w_1} = \cdots = \frac{x_n}{y_n} \frac{1}{w_n} = r\lambda. \quad (11)$$
On the other hand, (11) implies that
\[
\frac{1}{nrw} \sum_{i=1}^{n} \frac{x_i}{y_i} = \frac{1}{nrw} \sum_{i=1}^{n} (r\lambda w_i) = \frac{r\lambda}{nrw} \sum_{i=1}^{n} w_i = \frac{r\lambda}{nrw} n\bar{w} = \lambda,
\]
proving the equality case and completing the proof of part (1).

The three equations
\[
MN^{-1}x = \lambda y, \quad N^{-1}M^{-1}x = \lambda y, \quad \text{and} \quad N^{-1}Mx = \lambda y
\]
can be rewritten respectively as
\[
M^{-1}N^{-1}\bar{x} = \lambda \bar{y}, \quad M^{-1}N^{-1}\bar{x} = \lambda \bar{y}, \quad \text{and} \quad M^{-1}N^{-1}\bar{x} = \lambda \bar{y},
\]
where
\[
\bar{x} = x, \quad \bar{y} = M^{-2}y, \quad \bar{x} = M^{-1}x, \quad \bar{y} = M^{-1}y, \quad \bar{x} = Mx, \quad \text{and} \quad \bar{y} = My.
\]

Using these, parts (2)-(4) can be deduced from part (1).

**Theorem 2** For \(k = 1, \ldots, p\), let \(A_k = (a_{ijk})_{n \times n}\) be an irreducible quasi-positive matrix satisfying \(\sum_{i=1}^{n} a_{ijk} = 0\) for \(j = 1, \ldots, n\); \((w_{1k}, \ldots, w_{nk})^T\)
be a right positive eigenvector of \(A_k\) corresponding to the eigenvalue zero;
\(\bar{w}_k = \frac{1}{n} \sum_{i=1}^{n} w_{ik}\), the average of \(w_{1k}, \ldots, w_{nk}\); \(M_k = \text{diag}\{w_{1k}, \ldots, w_{nk}\}\) and
\(N_k = r_k I_n - A_k\) with \(r_k > 0\); \(W_k = M_k^{-1}N_k^{-1}\) or \(N_k^{-1}M_k^{-1}\). Then
\[
\rho \left( \prod_{k=1}^{p} W_k \right) \geq \prod_{k=1}^{p} \frac{1}{r_k \bar{w}_k}
\]
with equality if and only if \(w_{1k} = \cdots = w_{nk}\) for \(k = 1, \ldots, p\), or equivalently,
\(\sum_{j=1}^{n} a_{ijk} = 0\) for \(i = 1, \ldots, n\) and \(k = 1, \ldots, p\).

Additionally, if \(\bar{W}_1 = M_1 N_1^{-1}\) or \(N_1^{-1}M_1\), and \(W_2 = M_2^{-1}N_2^{-1}\) or \(N_2^{-1}M_2^{-1}\), then we have
\[
\rho(\bar{W}_1 W_2) = \rho(W_2 \bar{W}_1) \geq \frac{\bar{w}_{1}}{r_1 r_2 \bar{w}_2}
\]
with equality if and only if
(i) \(w_{11}/w_{12} = \cdots = w_{n1}/w_{n2}\), or equivalently, the right positive eigenvectors
associated with the eigenvalue zero of \(A_1 \) and \(A_2\) are proportional, provided
that \(\bar{W}_1 = M_1 N_1^{-1}\) and \(W_2 = N_2^{-1}M_2^{-1}\), or \(\bar{W}_1 = N_1^{-1}M_1\) and \(W_2 = M_2^{-1}N_2^{-1}\);
(ii) \(w_{1k} = \cdots = w_{nk}\) for \(k = 1, 2\), or equivalently, \(\sum_{j=1}^{n} a_{ijk} = 0\) for \(i = 1, \ldots, n\) and \(k = 1, 2\), provided that \(\bar{W}_1 = M_1 N_1^{-1}\) and \(W_2 = M_2^{-1}N_2^{-1}\), or
\(\bar{W}_1 = N_1^{-1}M_1\) and \(W_2 = N_2^{-1}M_2^{-1}\).
Proof Since \((w_{1k}, \ldots, w_{nk})^T\) and \(N_k^{-1}\) are positive by Lemma 1, it follows that \(W_k\) is positive and the \(pn \times pn\) matrix

\[
W = \begin{pmatrix}
0 & W_1 & 0 & \cdots & 0 \\
0 & 0 & W_2 & \cdots & 0 \\
\vdots & \vdots & \vdots & \ddots & \vdots \\
0 & 0 & 0 & \cdots & W_{p-1} \\
W_p & 0 & 0 & \cdots & 0
\end{pmatrix}
\]

is nonnegative and irreducible (Iggidr et al. 2016). By the Perron–Frobenius theorem (Horn and Johnson 2013), the spectral radius of matrix \(W\) is a simple eigenvalue of matrix \(W\) associated with a positive eigenvector \(v = (v_1, \ldots, v_p)^T\) for \(k = 1, \ldots, p\). That is,

\[
Wv = \lambda v \text{ and } \lambda \equiv \rho(W),
\]

or explicitly,

\[
W_k v_{k+1} = \lambda v_k, \text{ for } k = 1, \ldots, p, \text{ where } v_{p+1} = v_1.
\] (12)

Thus

\[
\left( \prod_{k=1}^{p} W_k \right) v_1 = \left( \prod_{k=1}^{p} W_k \right) v_{p+1} = \lambda^p v_1 \text{ and } \rho \left( \prod_{k=1}^{p} W_k \right) = \lambda^p.
\]

Since by assumption \(W_k = M_k^{-1}N_k^{-1}\) or \(N_k^{-1}M_k^{-1}\), it follows from part (1) or (3) of Lemma 3 that (12) implies

\[
\lambda \geq \frac{1}{n r_k \bar{w}_k} \sum_{i=1}^{n} \frac{v_i(k+1)}{v_{ik}}
\]

with equality if and only if

\[
v_1k = \cdots = v_{nk} \text{ or } \frac{v_1k}{w_1k} = \cdots = \frac{v_{nk}}{w_{nk}},
\] (13)

and

\[
\frac{v_1(k+1)}{v_1k} \frac{1}{w_1k} = \cdots = \frac{v_n(k+1)}{v_nk} \frac{1}{w_{nk}} = r_k \lambda,
\] (14)

for \(k = 1, \ldots, p\). Therefore, by a generalized Hölder inequality (Evans 1998),

\[
\lambda^p \geq \prod_{k=1}^{p} \left( \frac{1}{n r_k \bar{w}_k} \sum_{i=1}^{n} \frac{v_i(k+1)}{v_{ik}} \right) = \left( \prod_{k=1}^{p} \frac{1}{n r_k \bar{w}_k} \right) \left( \prod_{k=1}^{p} \left( \sum_{i=1}^{n} \frac{v_i(k+1)}{v_{ik}} \right) \right)^{1/p} = \left( \prod_{k=1}^{p} \frac{1}{n r_k \bar{w}_k} \right) \left( \sum_{i=1}^{n} \frac{v_{i1}}{v_{i1}} \times \cdots \times \frac{v_{ip}}{v_{i(p-1)}} \times \frac{v_{i1}}{v_{ip}} \right)^{1/p} = \left( \prod_{k=1}^{p} \frac{1}{n r_k \bar{w}_k} \right) n^p = \prod_{k=1}^{p} \frac{1}{r_k \bar{w}_k},
\]
proving the inequality statement of the theorem. The second inequality above is an equality if and only if there exist positive constants \( m_1, \ldots, m_p \) such that

\[
m_1 \frac{v_{i2}}{v_{i1}} = \cdots = m_k \frac{v_{i(k+1)}}{v_{ik}} = \cdots = m_p \frac{v_{ip}}{v_{i(p-1)}} = m_p \frac{v_{11}}{v_{ip}},
\]

for \( i = 1, \ldots, n \).

Suppose that \( \lambda^p = \prod_{k=1}^p \frac{1}{r_k w_k} \). Then (13)-(15) hold. We claim that

\[
v_{1k} = \cdots = v_{nk}, \quad \text{for } k = 1, \ldots, p
\]

and hence it follows from (14) that \( w_{1k} = \cdots = w_{nk} = \bar{w}_k \) for \( k = 1, \ldots, p \), which means that \( \mathbf{1} = (1, \ldots, 1)^T \) is a right eigenvector of \( A_k \) associated with the eigenvalue zero. In fact, assume from (13) that

\[
\frac{v_{1k}}{w_{1k}} = \cdots = \frac{v_{nk_0}}{w_{nk_0}},
\]

for some \( k_0 \in \{1, \ldots, p\} \), then (15) gives

\[
\frac{v_{i(k_0+1)}}{v_{ik_0}} = \frac{m_{k_0-1} v_{ik_0}}{m_{k_0} v_{i(k_0-1)}}, \quad i = 1, \ldots, n, \quad \text{with } m_0 = m_p \quad \text{and } v_0 = v_p
\]

implying from (14) that

\[
\frac{m_{k_0-1} v_{ik_0}}{m_{k_0} v_{i(k_0-1)} w_{ik_0}} = \cdots = \frac{m_{k_0-1} v_{nk_0}}{m_{k_0} v_{n(k_0-1)} w_{nk_0}}
\]

and hence by (16), \( v_{1(k_0-1)} = \cdots = v_{n(k_0-1)} \). The proof is complete if \( v_{ik}/w_{ik} = \cdots = v_{nk}/w_{nk} \) holds for all \( k \). Otherwise, without loss of generality, suppose that \( v_{11} = \cdots = v_{n3} \) and \( p \geq 3 \). If \( v_{13} = \cdots = v_{n3} \), then by (15),

\[
m_1 \frac{v_{i2}}{v_{i1}} = m_2 \frac{v_{i3}}{v_{i2}}, \quad i = 1, \ldots, n
\]

implies that \( v_{12} = \cdots = v_{n2} \); else by (13), \( v_{13}/w_{13} = \cdots = v_{n3}/w_{n3} \) and by (16), this also implies that \( v_{12} = \cdots = v_{n2} \). The case \( p = 2 \) can be similarly proved.

On the other hand, if \( \sum_{j=1}^n a_{ijk} = 0 \) for \( i = 1, \ldots, n \) and \( k = 1, \ldots, p \), then \( \mathbf{1} \) is a right eigenvector of matrices \( A_k \) and \( N_k \) corresponding to the eigenvalues zero and \( r_k \), respectively, and \( M_k = \bar{w}_k I_n \). Thus,

\[
\left( \prod_{k=1}^p W_k \right) \mathbf{1} = \left( \prod_{k=1}^p \left( \frac{1}{w_k} N_k^{-1} \right) \right) \mathbf{1} = \left( \prod_{k=1}^p \frac{1}{w_k} \right) \left( \prod_{k=1}^p N_k^{-1} \right) \mathbf{1}
\]

\[
= \left( \prod_{k=1}^p \frac{1}{w_k} \right) \left( \prod_{k=1}^{p-1} N_k^{-1} \right) \left( \frac{1}{r_p} \mathbf{1} \right) = \left( \prod_{k=1}^p \frac{1}{r_k w_k} \right) \mathbf{1},
\]

or

\[
= \cdots = \left( \prod_{k=1}^p \frac{1}{w_k} \right) \cdots \left( \prod_{k=2}^p \frac{1}{r_k} \right) \mathbf{1} = \left( \prod_{k=1}^p \frac{1}{r_k w_k} \right) \mathbf{1},
\]

and hence by (16), \( v_{1(k_0-1)} = \cdots = v_{n(k_0-1)} \). The proof is complete if \( v_{ik}/w_{ik} = \cdots = v_{nk}/w_{nk} \) holds for all \( k \). Otherwise, without loss of generality, suppose that \( v_{11} = \cdots = v_{n3} \) and \( p \geq 3 \). If \( v_{13} = \cdots = v_{n3} \), then by (15),

\[
m_1 \frac{v_{i2}}{v_{i1}} = m_2 \frac{v_{i3}}{v_{i2}}, \quad i = 1, \ldots, n
\]

implies that \( v_{12} = \cdots = v_{n2} \); else by (13), \( v_{13}/w_{13} = \cdots = v_{n3}/w_{n3} \) and by (16), this also implies that \( v_{12} = \cdots = v_{n2} \). The case \( p = 2 \) can be similarly proved.

On the other hand, if \( \sum_{j=1}^n a_{ijk} = 0 \) for \( i = 1, \ldots, n \) and \( k = 1, \ldots, p \), then \( \mathbf{1} \) is a right eigenvector of matrices \( A_k \) and \( N_k \) corresponding to the eigenvalues zero and \( r_k \), respectively, and \( M_k = \bar{w}_k I_n \). Thus,
which means that $\rho(\prod_{k=1}^p W_k) = \prod_{k=1}^p \frac{1}{r_k w_k}$, completing the equality statement.

Now consider the case $p = 2$. If $\tilde{W}_1 = M_1 N_1^{-1}$ or $N_1^{-1} M_1$, and $W_2 = M_2^{-1} N_2^{-1}$ or $N_2^{-1} M_2^{-1}$, then using the same approach as above and Lemma 3,

$$\lambda \geq \frac{1}{n r_1 \bar{w}_1} \sum_{i=1}^n \left( \frac{v_{i2}}{v_{i1}} \right) (w_{i1})^2 \text{ and } \lambda \geq \frac{1}{n r_2 \bar{w}_2} \sum_{i=1}^n \frac{v_{i1}}{v_{i2}},$$

which imply that

$$\lambda^2 \geq \left( \frac{1}{n r_1 \bar{w}_1} \sum_{i=1}^n \left( \frac{v_{i2}}{v_{i1}} \right) (w_{i1})^2 \right) \left( \frac{1}{n r_2 \bar{w}_2} \sum_{i=1}^n \frac{v_{i1}}{v_{i2}} \right)$$

$$= \frac{1}{n^2 r_1 r_2 \bar{w}_1 \bar{w}_2} \left( \sum_{i=1}^n \left( \frac{v_{i2}}{v_{i1}} \right) (w_{i1})^2 \right) \left( \sum_{i=1}^n \frac{v_{i1}}{v_{i2}} \right)$$

$$\geq \frac{1}{n^2 r_1 r_2 \bar{w}_1 \bar{w}_2} \sum_{i=1}^n \left( \frac{v_{i2}^2}{v_{i1}^2} \right) \left( \frac{w_{i1}^2}{v_{i2}^2} \right) \geq \frac{1}{n^2 r_1 r_2 \bar{w}_1 \bar{w}_2} \sum_{i=1}^n \frac{w_{i1}^2}{(n \bar{w}_1)^2} = \frac{\bar{w}_1}{r_1 r_2 \bar{w}_2}$$

by the Cauchy-Schwarz inequality. The equality conditions are proved in the following two cases.

(i) Let $\tilde{W}_1 = M_1 N_1^{-1}$ and $W_2 = N_1^{-1} M_2^{-1}$, or $\tilde{W}_1 = N_1^{-1} M_1$ and $W_2 = M_2^{-1} N_2^{-1}$. Suppose that $w_{i1}/w_{i2} = \bar{w}_1/\bar{w}_2$ for $i = 1, \ldots, n$. Then $w_1 = (w_{11}, \ldots, w_{1n})$ is an eigenvector of matrices $A_1$, $A_2$, $N_1$ and $N_2$, associated with the eigenvalues zero, zero, $r_1$, and $r_2$, respectively. It follows from $N_1^{-1} N_2^{-1} w_1 = \frac{1}{r_1 r_2} w_1$ and (17) that $\lambda^2 = \rho(\tilde{W}_1 W_2) = \frac{\bar{w}_1}{r_1 r_2 \bar{w}_2}$.

(ii) Let $\tilde{W}_1 = M_1 N_1^{-1}$ and $W_2 = M_2^{-1} N_2^{-1}$. Then the equality $\lambda^2 = \frac{\bar{w}_1}{r_1 r_2 \bar{w}_2}$ implies

$$\frac{v_{11}}{w_{11}} = \cdots = \frac{v_{n1}}{w_{n1}} \text{ and } \frac{v_{12}}{v_{11}} w_{11} = \cdots = \frac{v_{n2}}{v_{n1}} w_{n1} = r_1 \lambda,$$

$$\frac{v_{12}}{w_{12}} = \cdots = \frac{v_{n2}}{w_{n2}} \text{ and } \frac{v_{11}}{v_{12}} w_{12} = \cdots = \frac{v_{n1}}{v_{n2}} w_{n2} = r_2 \lambda,$$

$$\frac{m_1 v_{12}^2}{v_{11}^2} = m_2 \frac{v_{11}^2}{v_{12}^2} \Rightarrow \frac{v_{11}}{v_{12}} w_{12} = \frac{m_1}{m_2}, \; i = 1, \ldots, n.$$  

The first equations in (18a) and (18b) give

$$\frac{v_{11}}{v_{12}} w_{12} = \cdots = \frac{v_{n1}}{v_{n2}} w_{n2}.$$
which implies \( w_{11} = \cdots = w_{n1} \) by (18c) and therefore by the second equations in (18a) and (18b), \( w_{12} = \cdots = w_{n2} \).

Let \( \bar{W}_1 = N_1^{-1}M_1 \) and \( \bar{W}_2 = N_2^{-1}M_2^{-1} \). Then by (17),

\[
\bar{w}_1/(r_1 r_2 \bar{w}_2) = \lambda^2 \equiv \rho(\bar{W}_1 W_2) = \rho(N_1^{-1}M_1 N_2^{-1}M_2^{-1})
\]

\[
= \rho(M_1 N_2^{-1}M_2^{-1}N_1^{-1}) = (\bar{w}_1/\bar{w}_2)^2 \rho(M_2 N_2^{-1}M_1^{-1}N_1^{-1})
\]

implies that \( \rho(M_2 N_2^{-1}M_1^{-1}N_1^{-1}) = \bar{w}_2/(r_1 r_2 \bar{w}_1) \). This case can then proceed as above.

On the other hand, suppose that \( w_{ik} = \bar{w}_k \) for \( i = 1, \ldots, n \) and \( k = 1, 2 \); it follows from \( N_1^{-1}N_2^{-1}1 = \frac{1}{r_1 r_2 1} \) that \( \lambda^2 \equiv \rho(\bar{W}_1 W_2) = \frac{\bar{w}_1}{r_1 r_2 \bar{w}_2} \).

Now let us return to the multipatch Ross–Macdonald model (2) in an environment with \( n \) identical patches formulated in Section 2, using the notation and definition of \( R_0(n) \) and \( R_0(1) \) given there in (3) and (4).

**Theorem 3** Consider model (2) with \( n \) identical patches connected by human and mosquito movement, i.e., \( C = (c_{ij})_{n \times n} \) and \( D = (d_{ij})_{n \times n} \) are irreducible. Then the basic reproduction number \( R_0(n) \) for the \( n \)-patch model (2) can be estimated against the basic reproduction number \( R_0(1) \) for the single patch model (1) according to

\[
R_0(n) \geq R_0(1)
\]

with equality if and only if the mosquito to human ratio in each patch remains the same under movement, i.e., \( V_i^* / H_i^* = V/H \) for \( i = 1, \ldots, n \), or equivalently, human and mosquito movement rate matrices \( C \) and \( D \) have the same eigenspace associated with the eigenvalue zero.

**Proof** With the irreducibilities of travel rate matrices \( C \) and \( D \), we have

\[
R_0^2(n) = a^2bc \cdot \rho(\mathcal{B}_1^{-1} \mathcal{B}_2^{-1} \mathcal{C}^{-1}),
\]

where \( \mathcal{B}_1 = (\delta_{ij} V_i^*)_{n \times n} \), \( \mathcal{B}_2 = (\delta_{ij} H_i^*)_{n \times n} \), \( \mathcal{C} = \gamma I_n - C \), and \( \mathcal{D} = \mu I_n - D \).

Take \( \bar{W}_1 = N_1^{-1}M_1 \) and \( \bar{W}_2 = N_2^{-1}M_2^{-1} \) where \( M_1 = \mathcal{B}_1 \), \( N_1 = \mathcal{D} \), \( M_2 = \mathcal{B}_2 \) and \( N_2 = \mathcal{C} \). Then by Theorem 3.3 for \( p = 2 \),

\[
R_0^2(n) = a^2bc \cdot \rho(\bar{W}_1 W_2) \geq a^2bc \cdot \frac{V/n}{\gamma \mu H/n} = a^2bcV \gamma \mu H/n = R_0^2(1).
\]

The equality case is immediately proved by using the second case of (i) in Theorem 2.

**Remark 1** The equalities \( H_i^* = H/n \) and \( V_i^* = V/n \) for \( 1 \leq i \leq n \) hold if and only if the human and mosquito travel rate matrices \( C \) and \( D \) are line-sum symmetric. A square matrix is line-sum symmetric if it is symmetric, but not vice versa. Thus \( R_0(n) = R_0(1) \) whenever both \( C \) and \( D \) are symmetric.

In what follows, we show that the estimation \( R_0(n) \geq R_0(1) \) remains valid when only humans or mosquitoes move between patches.
Corollary 1 For model (2), the following statements are valid:

(1) If the $n$ identical patches are connected by human movement (i.e., $C = (c_{ij})_{n \times n}$ is irreducible and $D = (d_{ij})_{n \times n} = 0_{n \times n}$) and mosquitoes are initially present in all patches (i.e., $V_i(0) > 0$ for $i = 1, \ldots, n$), then

$$R_0(n) \geq R_0(1)$$

with equality if and only if $(V_1(0), \ldots, V_n(0))^T$ is a right positive eigenvector of $C$ associated with the zero eigenvalue.

(2) If the $n$ identical patches are connected by mosquito movement (i.e., $C = (c_{ij})_{n \times n} = 0_{n \times n}$ and $D = (d_{ij})_{n \times n}$ is irreducible) and humans are initially present in all patches (i.e., $H_i(0) > 0$ for $i = 1, \ldots, n$), then

$$R_0(n) \geq R_0(1)$$

with equality if and only if $(H_1(0), \ldots, H_n(0))^T$ is a right positive eigenvector of $D$ associated with the zero eigenvalue.

Proof Suppose only humans move. It follows $D = \mu I_n, B_1 = (\delta_{ij} V_i(0))_{n \times n}$ and $B_2 = (\delta_{ij} H_i^*)_{n \times n}$ and hence

$$R_0^D(n) = \rho(\mathcal{A}D^{-1}B_2^{-1}C^{-1}) = a^2/c\mu \cdot \rho(B_1B_2^{-1}C^{-1}).$$

By the Perron–Frobenius theorem, the positive matrix $B_1B_2^{-1}C^{-1}$ has a positive right eigenvector, denoted by $w$, corresponding to the spectral radius $\rho(B_1B_2^{-1}C^{-1})$, i.e.,

$$B_1B_2^{-1}C^{-1}w = B_1B_2^{-1}C^{-1} \iff B_2^{-1}C^{-1}w = \rho(B_1B_2^{-1}C^{-1})B_1^{-1}w.$$

Using the first part of Lemma 3, we have

$$\rho(B_1B_2^{-1}C^{-1}) \geq \frac{1}{\gamma \sum_{i=1}^n \frac{w_i}{H_i^*}} \sum_{i=1}^n \frac{w_i}{V_i(0)} = \frac{V}{\gamma H}$$

with equality if and only if

$$\frac{w_1}{V_1(0)} = \cdots = \frac{w_n}{V_n(0)} \quad \text{and} \quad \frac{V_1(0)}{H_1^*} = \cdots = \frac{V_n(0)}{H_n^*} = \gamma \rho(B_1B_2^{-1}C^{-1}).$$

Now suppose only mosquitoes move. If follows $C = \gamma I_n, B_1 = (\delta_{ij} V_i^*)_{n \times n}$ and $B_2 = (\delta_{ij} H_i(0))_{n \times n}$ and hence

$$R_0^C(n) = \rho(\mathcal{A}D^{-1}B_2^{-1}C^{-1}) = a^2/c\gamma \cdot \rho(D^{-1}B_1B_2^{-1}).$$

Again by the Perron–Frobenius theorem, the positive matrix $D^{-1}B_1B_2^{-1}$ has a positive right eigenvector, denoted by $w$, corresponding to the spectral radius $\rho(D^{-1}B_1B_2^{-1})$, i.e.,

$$D^{-1}B_1B_2^{-1}w = D^{-1}B_1(B_2^{-1}w) = \rho(D^{-1}B_1B_2^{-1})w.$$
Applying the fourth part of Lemma 3 and the Cauchy-Schwarz inequality, we obtain
\[
\rho^{(D^{-1}B_1B_2^{-1})} \geq \frac{1}{\mu} \sum_{i=1}^{n} \frac{w_i/H_i(0)}{V_i^*} \geq \frac{\sum_{i=1}^{n} V_i^*}{\mu \sum_{i=1}^{n} H_i(0)} = \frac{V}{\mu H}
\]
with equality if and only if
\[
\frac{w_1}{V_1^*} = \cdots = \frac{w_n}{V_n^*}
\]
and
\[
\frac{w_1/H_1(0)}{w_1} = \cdots = \frac{w_n/H_n(0)}{w_n} = \mu \rho^{(D^{-1}B_1B_2^{-1})}.
\]

The proofs for the estimation \( R_0(n) \geq R_0(1) \) and the condition for equality are complete.

**Remark 2** The lower bound of \( R_0(n) \) is always achievable. In fact, given a positive vector \( x = (x_1, \ldots, x_n)^T \), there exist some travel rate matrices, e.g.,
\[
-x_1^{-1} x_1 x_1 \cdots x_1
\]
\[
\begin{pmatrix}
  x_1 x_1 & \cdots & x_1 \\
  x_2 x_2 & \cdots & x_2 \\
  \vdots & \vdots & \vdots \\
  x_n x_n & \cdots & x_n
\end{pmatrix}
\]
and
\[
\begin{pmatrix}
  -x_1^{-1} & -x_2^{-1} & 0 & \cdots & 0 \\
  0 & -x_2^{-1} & -x_3^{-1} & \cdots & 0 \\
  \vdots & \vdots & \vdots & \vdots & \vdots \\
  0 & 0 & \cdots & -x_n^{-1}
\end{pmatrix}
\]
having \( x \) as its right eigenvector corresponding to the eigenvalue zero.

It follows from Theorem 3 and Corollary 1 that habitat fragmentation, e.g., a large area of habitat split into some patches, may intensify malaria persistence and promote disease outbreaks. The assumption that humans and mosquitoes are homogeneously mixed or evenly distributed could underestimate the basic reproduction number. In other words, the habitat connectivity of isolated identical patches with the same initial number of humans and mosquitoes tends to increase the risk of infection. It is worth pointing out that Dye and Hasibeder (1986) and Hasibeder and Dye (1988) established similar results based on a spatial malaria model using Lagrangian approach (mimicking commuting behavior) instead of Eulerian approach (mimicking migration) (Bichara and Castillo-Chavez 2016; Cosner et al. 2009).

The inequality \( R_0(n) \geq R_0(1) \) may fail when the incidence rates are not standard, or some patches are host free (Auger et al. 2008), or the travel rates of the susceptible and the infectious humans are not the same (see Appendix), or the model structure is more complicated, or a directly transmitted disease is considered. More specifically, Gao and Ruan (2012) proposed a multipatch malaria model with SEIRS structure for humans and SEI structure for mosquitoes and presented a numerical example where human movement leads to disease extinction in all identical patches, even though the disease persists in each isolated patch. For an SIS patch model with standard incidence, Gao and Ruan (2011) proved that the multipatch basic reproduction number is between the maximum and minimum of the basic reproduction numbers of all patches in isolation. Thus, the single patch and multipatch basic reproduction numbers for the SIS model are equal when all patches are identical.
Consider a malaria model with \( n \) identical patches similar to (2), but with bilinear incidence \( \alpha(H_i - h_i)v_i \) and \( \beta(V_i - v_i)h_i \) (see e.g., Gao et al. (2013)) instead of normalized incidence \( ab(H_i - h_i)v_i/H_i \) and \( ac(V_i - v_i)h_i/H_i \), respectively. The basic reproduction numbers of this new multipatch model and the corresponding single patch model are respectively

\[
\mathcal{R}_0(n) = \sqrt{\rho(s\tilde{D}^{-1}\tilde{F}\tilde{C}^{-1})} \quad \text{and} \quad \mathcal{R}_0(1) = \sqrt{\alpha\beta V H/(\gamma \mu)},
\]

where \( s\tilde{D} = (\delta_{ij}\alpha H_i^*)_{n \times n}, \tilde{F} = (\delta_{ij}\beta V_i^*)_{n \times n}, \tilde{C} = \gamma I_n - C, \) and \( \tilde{D} = \mu I_n - D \).

For an example with two patches, setting \( \alpha = \beta = \gamma = \mu = H = V = 1, \quad c_{12} = d_{21} = 1 \) and \( c_{21} = d_{12} = 2 \), it follows that \( \mathcal{R}_0(2) = 0.2073 < \mathcal{R}_0(1) = 1 \).

Consider model (2) with two identical patches connected by mosquito movement and the second patch is host free (i.e., \( V_1^* = V \) and \( V_2^* = 0 \), all vectors are confined in the first patch), then

\[
\mathcal{R}_0^2(2) = \frac{a^2bcV}{\gamma \mu H} \left( c_{12} + c_{21} \right) \left( \gamma + c_{12} + c_{21} \right) > \mathcal{R}_0^2(1) = \frac{a^2bcV}{\gamma \mu H}.
\]

However, if two identical patches are connected by mosquito movement and the second patch is host free (i.e., \( H_1^* = H \) and \( H_2^* = 0 \)), then

\[
\mathcal{R}_0^2(2) = \frac{a^2bcV}{\gamma \mu H} (d_{12}(\mu + d_{12})(\mu + d_{12} + d_{21})) < \mathcal{R}_0^2(1) = \frac{a^2bcV}{\gamma \mu H}.
\]

Thus, the impact of habitat fragmentation on disease spread becomes complicated when hosts and/or vectors are not present in some patches.

So far, we have established a lower bound for the basic reproduction number of model (2). An upper bound that depends on the maximal ratio of mosquitoes to humans in each patch can be obtained as follows.

**Proposition 1** Consider model (2) with \( n \) identical patches connected by human and mosquito movement, i.e., \( C = (c_{ij})_{n \times n} \) and \( D = (d_{ij})_{n \times n} \) are irreducible. Then

\[
\frac{a^2bc}{\gamma \mu} \min_{1 \leq i \leq n} \frac{V_i^*}{H_i^*} \leq \mathcal{R}_0^2(1) \leq \mathcal{R}_0^2(n) \leq \frac{a^2bc}{\gamma \mu} \max_{1 \leq i \leq n} \frac{V_i^*}{H_i^*}.
\]

**Proof** Similar to the proof of Theorem 3.1 in Gao (2019), without loss of generality, assume that \( V_1^*/H_1^* \leq \cdots \leq V_n^*/H_n^* \). Then

\[
\frac{V_i^*}{H_i^*} I_n \leq \mathcal{B}_1 \mathcal{B}_2^{-1} \leq \frac{V_n^*}{H_n^*} I_n
\]

\[
\Leftrightarrow \frac{V_i^*}{H_i^*} \mathcal{C}^{-1} \mathcal{D}^{-1} \leq \mathcal{B}_1 \mathcal{B}_2^{-1} \mathcal{C}^{-1} \mathcal{D}^{-1} \leq \frac{V_n^*}{H_n^*} \mathcal{C}^{-1} \mathcal{D}^{-1}
\]

\[
\Rightarrow \rho \left( \frac{V_i^*}{H_i^*} \mathcal{C}^{-1} \mathcal{D}^{-1} \right) = \frac{V_i^*}{\gamma \mu H_i^*} \leq \rho(\mathcal{B}_1 \mathcal{B}_2^{-1} \mathcal{C}^{-1} \mathcal{D}^{-1}) \leq \rho \left( \frac{V_n^*}{H_n^*} \mathcal{C}^{-1} \mathcal{D}^{-1} \right) = \frac{V_n^*}{\gamma \mu H_n^*},
\]

due to the fact that \( \rho(\mathcal{C}^{-1} \mathcal{D}^{-1}) = 1/(\gamma \mu) \). \( \square \)
To what extent would human and/or mosquito movement increase the multipatch basic reproduction number? In particular, does there exist an upper bound of \( R_0(n) \) that is independent of travel rate matrices \( C \) and \( D \)? We will consider this point in the next section.

4 Numerical Examples

In this section, we perform some numerical simulations for the model (2) with two identical patches to explore how human and/or mosquito movement affects the basic reproduction number \( R_0(2) \) and disease prevalence. For illustration, the choice of parameter values does not strictly follow the epidemiology and ecology of malaria.

Example 1 Bound of the reproduction number. To see whether the multipatch reproduction number has a uniform bound from above for any travel pattern, we consider a two-patch case where all parameters are set to one except human and mosquito movement rates. Then

\[
R_0(2) = \sqrt{\rho(\mathcal{B}_1 \mathcal{B}_2^{-1} \mathcal{C}^{-1} \mathcal{D}^{-1})} \quad \text{and} \quad R_0(1) = 1,
\]

where \( \mathcal{B}_1 = (\delta_{ij} V_i^*)_{2 \times 2}, \mathcal{B}_2 = (\delta_{ij} H_i^*)_{2 \times 2}, \mathcal{C} = I_2 - (c_{ij})_{2 \times 2}, \mathcal{D} = I_2 - (d_{ij})_{2 \times 2} \) and

\[
H_1^* = \frac{c_{12}}{c_{12} + c_{21}}, \quad H_2^* = \frac{c_{21}}{c_{12} + c_{21}}, \quad V_1^* = \frac{d_{12}}{d_{12} + d_{21}}, \quad V_2^* = \frac{d_{21}}{d_{12} + d_{21}}.
\]

Case 1. We choose the travel rates as follows: \( c_{12} = 1, c_{21} = \phi, d_{12} = 1 \) and \( d_{21} = \psi \) with \( (\phi, \psi) \in \text{Int} \mathbb{R}_+^2 \). Denote \( \Gamma = \psi(1 + \psi) + \phi(4 + 3\psi + \psi^2) \). The basic reproduction number of model (2) is

\[
R_0(2) = \sqrt{(1 + \phi)\left(\Gamma + \sqrt{\frac{T^2 - 4\phi(2 + \phi)(2 + \psi)}{2\phi(2 + \phi)(1 + \psi)(2 + \psi)}}\right)} \geq 1
\]

with equality if and only if \( \phi = \psi \). Denote \( \Gamma_\infty = 4 + 3\phi + \psi^2 \). Direct calculations yield

\[
\lim_{\phi \to 0^+} R_0(2) = +\infty \quad \text{and} \quad \lim_{\phi \to +\infty} R_0(2) = \sqrt{\frac{\Gamma_\infty + \sqrt{T^2 - 4\psi(2 + \psi)}}{2(1 + \psi)(2 + \psi)}},
\]

and

\[
\lim_{\psi \to 0^+} R_0(2) = \sqrt{\frac{2 + 2\phi}{2 + \phi}} \quad \text{and} \quad \lim_{\psi \to +\infty} R_0(2) = \frac{1 + \phi}{\sqrt{\phi(2 + \phi)}}.
\]

Case 2. We choose the travel rates as follows: \( c_{12} = 1, c_{21} = \phi, d_{12} = \psi \) and \( d_{21} = 1 \) with \( (\phi, \psi) \in \text{Int} \mathbb{R}_+^2 \). Denote \( \Lambda = 1 + \phi(1 + \psi)^2 \). The basic reproduction number of model (2) now becomes

\[
R_0(2) = \sqrt{(1 + \phi)(\Lambda + \sqrt{\frac{T^2 - \phi(2 + \phi)(2 + \psi)}{\phi(2 + \phi)(1 + \psi)(2 + \psi)}})} \geq 1
\]
with equality if and only if $\phi \psi = 1$. Again direct calculations yield

$$\lim_{\phi \to 0^+} R_0(2) = +\infty \quad \text{and} \quad \lim_{\phi \to +\infty} R_0(2) = \sqrt{\frac{(1 + \psi)^2 + \sqrt{(1 + \psi)^4 - \psi(2 + \psi)}}{(1 + \psi)(2 + \psi)}},$$

and

$$\lim_{\psi \to 0^+} R_0(2) = \frac{1 + \phi}{\sqrt{\phi(2 + \phi)}} \quad \text{and} \quad \lim_{\psi \to +\infty} R_0(2) = \sqrt{\frac{2 + 2\phi}{2 + \phi}}.$$

The changes of $R_0(2)$ versus relative travel rates $\phi$ and $\psi$ for Case 1 and Case 2 are plotted in Figure 2. It is initially decreasing and then increasing in both $\phi$ and $\psi$. Both analytical and numerical analyses show that $R_0(2)$ cannot surpass any given positive number under appropriate human and mosquito movements such that the maximum of $R_0(2)$ does not exist. Interestingly, although the limiting processes $\phi \to 0^+$ and $\phi \to +\infty$ both result in the number of humans approaching $H = 1$ in one patch and zero in the other patch, the limits are completely different even if the movement rate matrix for mosquitoes is symmetric ($\psi = 1$) or there is no mosquito movement.

**Example 2 Higher diffusion rates.** By changing the travel rate matrices $C$ and $D$ to $d_HC$ and $d_LD$, respectively, we consider the relation between the basic reproduction number $R_0(2)$ and the diffusion coefficients of humans and mosquitoes, $d_H$ and $d_V$. The travel related parameters are set as $c_{12} = 0.01$, $c_{21} = 0.05$, $d_{12} = 0.01$, $d_{21} = 0.02$, other parameters are fixed at one. Clearly, the ratios of mosquitoes to humans in patches 1 and 2 at the disease-free equilibrium are respectively 2 and 0.8 which are regardless of the diffusion coefficients. The dependence of $R_0(2)$ on $d_H$ and $d_V$ is illustrated in Figure 3. Both numerical and analytical approaches demonstrate that $R_0(2)$ is monotone decreasing in both $d_H$ and $d_V$ if $R_0(2) \neq R_0(1)$. Namely, faster diffusion
leads to lower risk of infection when only two identical patches are considered. Further, this result remains valid for an environment with an arbitrary number of identical or nonidentical patches connected by either human or mosquito movement (Gao 2019; Gao and Dong 2019). In addition, the limits of $R_0(2)$ as $d_H$ and $d_V$ go to zero and infinity are respectively

$$\lim_{d_H \to 0^+} R_0(2) = \max_{1 \leq i \leq 2} \sqrt{\frac{d^2bV^*}{\gamma_i H_i^*}} \quad \text{and} \quad \lim_{d_H \to \infty} R_0(2) = R_0(1)$$

and

$$\lim_{d_V \to \infty} R_0(2) = R_0(1) \sqrt{1 + \frac{\gamma(c_{12}d_{21} - c_{21}d_{12})^2}{c_{12}c_{21}(d_{12} + d_{21})^2(\gamma + (c_{12} + c_{21})d_H)}} \geq R_0(1),$$

which again suggest that the effects of human and mosquito movements on malaria spread are different.

**Fig. 3** The contour plot of the basic reproduction number $R_0(2)$ in terms of $d_H$ and $d_V$.

For the same parameter setting, however, Figure 4a indicates that the model (2) with diffusion may constantly incur a larger number of infected humans than that without diffusion (or $d_H \to 0^+$ and $d_V \to 0^+$). The disease prevalence in humans over two patches could be monotone or nonmonotone in $d_H$ and $d_V$. There are inconsistent consequences between the risk of infection and the disease prevalence as the diffusion coefficients $d_H$ and $d_V$ vary. When we change the travel rates to $c_{12} = 0.01, c_{21} = 0.009, d_{12} = 0.01$ and $d_{21} = 0.04$, there is a dashed curve passing through the origin as shown in Figure 4b above which diffusion causes more infections and below which diffusion causes less infections.

5 Discussion

It is well known that population dispersal can intensify or weaken disease spread like diffusion-driven population persistence or extinction in popula-
Fig. 4 The contour plot of the difference of the overall disease prevalence in humans with and without diffusion in terms of $d_H$ and $d_V$ under two travel patterns.

tion ecology. Wang and Zhao (2004) considered an SIS multipatch model with bilinear incidence and gave two numerical examples: one showed that suitable dispersal rates lead to either disease spread or disease extinction in both patches when a low transmission patch and a high transmission patch are concerned, the other found that population dispersal can result in the spread of disease in both patches even though the disease cannot spread in each isolated patch. Jin and Wang (2005) further studied the model and showed that population dispersal may result in disease extinction even though it cannot be eradicated in each isolated patch. Wang and Mulone (2003) proposed a two-patch SIS model with standard incidence and showed that the disease remains extinct/persistent in both patches when population dispersal presents if it disappears/spreads in each isolated patch. Gao and Ruan (2011) drew the same conclusion for an $n$-patch SIS model incorporating the impact of media coverage. Based on an SIS model with two patches, Salmani and van den Driessche (2006) found that small and large travel rates could aid disease persistence whereas intermediate rates stabilize the disease-free equilibrium. Gao and Ruan (2012) considered a complicated multipatch malaria model and numerically showed that human movement can help malaria become extinct or persistent in two identical patches, even though the disease persists or dies out in each isolated patch. Hsieh et al. (2007) proposed an SEIRP patch model and performed numerical simulations under various travel policies.

In this paper, we considered a Ross–Macdonald type model with $n$ identical patches to address the impact of human and/or mosquito movement on malaria persistence. We first proved a generalized eigenvalue inequality and used it to estimate the spectral radius of the product of a class of nonnegative matrices. Then we showed that the basic reproduction number of the multipatch Ross–Macdonald model is no less than that of the single patch model. Biologically speaking, habitat fragmentation strengthens the persistence of the disease. Ignorance of spatial structure could substantially underestimate...
the basic reproduction number such that more efforts are required to achieve
disease elimination or eradication. A similar result associated with the La-
grangian approach was previously obtained by Dye and Hasibeder (1986) and
Hasibeder and Dye (1988). The findings are in accordance with a recent study
on pathogen dynamics by White et al. (2018) using an individual-based model
integrated with movement ecology approaches. The multipatch basic reproduc-
tion number equals that of the single patch model if and only if all connected
patches have the same ratio of mosquitoes to humans at the disease-free equi-
librium. The human population acts as a blood source for mosquitoes. In other
words, once the distribution of humans is determined, the basic reproduction
number is minimized when the movement of mosquito population follows a
strategy for which the resulting distribution of mosquitoes is proportional to
that of humans. A similar result holds if the distribution of the mosquito pop-
ulation is fixed. This diffusion strategy is somewhat linked to the concept of
the ideal free distribution (IFD) in ecology, which states that the distribution
of organisms should match the distribution of resources (Cantrell et al. 2012a;
Fretwell and Lucas 1969). Malaria persistence is minimized when the distribu-
tion of mosquitoes obeys IFD. However, in reality, mosquitoes are unevenly
distributed due to their limited mobility. For example, an urban area with
dense human population has less mosquitoes while a rural area with sparse
human population has more mosquitoes. To reduce the disease persistence, a
control strategy that makes the geographic distribution of hosts and vectors
nearly uniform may be desirable.

Moreover, we numerically and analytically showed that the basic repro-
duction number goes to infinity when one of the two human movement rates
tends to zero and the remaining one is fixed. The fact was observed by Auger
et al. (2008) in case only hosts migrate between patches. There is some incon-
sistency between the reproduction number and the overall disease prevalence
in response to increasing diffusion. That is, fast host and/or vector diffusion
decreases the disease transmission potential, but may increase the number of
infected humans. Dye and Hasibeder (1986) studied the single patch case and
they showed that the reproduction number is increasing in the human pop-
ulation size \( H \), but the number of infected hosts is initially increasing then
decreasing in \( H \). The main conclusion that the multipatch basic reproduction
number is greater than or equal to the single patch reproduction number is
generally invalid if part of the model assumptions are not satisfied. Some math-
ematical results like Lemma 3 and Theorem 2 are applicable to the proof of
similar arguments for multipatch epidemic models with different model struc-
tures or transmission modes.

Finally, we remark that current work can be extended in at least three
possible ways. The first is to study the malaria model in a temporal vary-
ing environment driven by periodic human migration and seasonal changes
in mosquito population and behavior. The global dynamics for such a peri-
odic multipatch malaria model established by Gao et al. (2014) are a good
first step. The second is to extend the multipatch ODE model to the nonlocal
model with integral kernel \( k(x, y) \) and diffusion-advection model with diffusion
rate \( d(x) \) and advection \( p(x) \) (Cosner 2015) where, for example, the movement term \( \sum_{j=1}^{n} c_{ij} H_j(t) \) is replaced by
\[
\int_{\Omega} k(x,y) H(y, t) \, dy - \left( \int_{\Omega} k(y,x) \, dy \right) H(x, t)
\]
and
\[
\nabla \cdot \left[ d(x) \nabla H - H p(x) \right],
\]
respectively. Here \( \Omega \) is a bounded subset of \( \mathbb{R}^N \), and \( x, y \in \Omega \). The continuous version of Lemma 2 in terms of integrals to nonlocal diffusion established by Cantrell et al. (2012b) should be helpful in comparing the basic reproduction numbers of the model with and without diffusion. The impact of the distribution of humans on malaria risk in a continuous space was partially observed by Lou and Zhao (2011). The third is to consider similar questions for epidemic models with different structures (e.g., SEIR for humans and SEI for mosquitoes) or different transmission modes (e.g., water-borne diseases and sexually transmitted diseases). We leave these challenging problems for future investigation.

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Appendix: Unequal Travel Rates

Let \( S_i, I_i, X_i, \) and \( Y_i \) be the numbers of susceptible and infectious humans, susceptible and infectious mosquitoes, respectively. Denote the total human and mosquito populations in the \( i \)-th patch by \( H_i = S_i + I_i \) and \( V_i = X_i + Y_i \), respectively. Assuming unequal travel rates for susceptible and infectious humans, the model equations are
\[
\begin{align*}
\frac{dS_i}{dt} &= -ab \frac{Y_i}{H_i} S_i + \gamma I_i + \sum_{j=1}^{n} \tilde{c}_{ij} S_j, \quad 1 \leq i \leq n, \\
\frac{dX_i}{dt} &= -ac \frac{I_i}{H_i} X_i + \mu Y_i + \sum_{j=1}^{n} d_{ij} X_j, \quad 1 \leq i \leq n, \\
\frac{dI_i}{dt} &= ab \frac{Y_i}{H_i} S_i - \gamma I_i + \sum_{j=1}^{n} c_{ij} I_j, \quad 1 \leq i \leq n, \\
\frac{dY_i}{dt} &= ac \frac{I_i}{H_i} X_i - \mu Y_i + \sum_{j=1}^{n} d_{ij} Y_j, \quad 1 \leq i \leq n.
\end{align*}
\]

We assume that the travel rate matrices \( \tilde{C} = (\tilde{c}_{ij})_{n \times n}, C = (c_{ij})_{n \times n}, \) and \( D = (d_{ij})_{n \times n} \) are irreducible. For any given nonnegative initial condition, the model (A) has a unique disease-free equilibrium
\[
E_0 = (H_1^*, \ldots, H_n^*, V_1^*, \ldots, V_n^*, 0, \ldots, 0, 0, \ldots, 0),
\]
where \((H^*_1, \ldots, H^*_n)\) and \((V^*_1, \ldots, V^*_n)\) are respectively the unique positive solution to
\[
\sum_{j=1}^{n} \tilde{c}_{ij} H_j = 0, \ i = 1, \ldots, n, \ \sum_{i=1}^{n} H_i = \sum_{i=1}^{n} H_i(0) = H > 0,
\]
and
\[
\sum_{j=1}^{n} d_{ij} V_j = 0, \ i = 1, \ldots, n, \ \sum_{i=1}^{n} V_i = \sum_{i=1}^{n} V_i(0) = V > 0.
\]
Following the next generation matrix method (Diekmann et al. 1990; van den Driessche and Watmough 2002), we define the basic reproduction number of the model (A) as
\[
\hat{R}_0(n) = \sqrt{\rho(ab\tilde{G}^{-1}B\tilde{C}^{-1})},
\]
where \(ab = abI_n\), \(\tilde{B} = ac(\delta_{ij}V^*_i/H^*_j)_{n \times n}\), \(\tilde{C} = \gamma I_n - C\), and \(\tilde{G} = \mu I_n - D\). In particular, the basic reproduction number of a single patch model is
\[
\hat{R}_0(1) = \sqrt{\frac{a^2bVe^{-\gamma\mu H}}{\gamma\mu H}}.
\]
**Claim:** consider \(n\) identical patches connected by human movement (i.e., \(\tilde{C}\) and \(C\) are irreducible, and \(D = 0_{n \times n}\)) and mosquitoes are initially evenly distributed (i.e., \(V_1(0) = \cdots = V_n(0) = V/n\)), then \(\hat{R}_0(n) \geq \hat{R}_0(1)\) may fail.

Under the above assumptions we actually have
\[
\hat{R}_0(n) = \sqrt{\rho(ab\tilde{G})/(n\mu)} \cdot \sqrt{\rho(MN^{-1})}
\]
with \(M = \text{diag}(1/H^*_1, \ldots, 1/H^*_n)\) and \(N = \gamma I_n - C\). Thus,
\[
\hat{R}_0(n) \geq \hat{R}_0(1) \iff \rho(MN^{-1}) \geq n/(\gamma H).
\]
In particular, the above inequality for the two-patch case holds if and only if
\[
e_1 \equiv (\bar{c}_{12} - \bar{c}_{21})(\bar{c}_{12} \gamma - \bar{c}_{21} \gamma + 2\bar{c}_{12}c_{21} - 2\bar{c}_{21}c_{12}) > 0
\]
or
\[
e_2 \equiv \bar{c}_{12}c_{21}(\bar{c}_{12} - 3\bar{c}_{21}) + \bar{c}_{21}c_{12}(\bar{c}_{21} - 3\bar{c}_{12}) + \gamma(\bar{c}_{12} - \bar{c}_{21})^2 > 0.
\]
However, even if a realistic restriction \(\bar{c}_{ij} \geq c_{ij}\) for \(i \neq j\) is introduced, \(\gamma = 0.25, \bar{c}_{12} = 0.5 > \bar{c}_{12} = 0.125\) and \(\bar{c}_{21} = 1 > c_{21} = 0.5\) giving \(e_1 = -0.0625\) and \(e_2 = -0.625\), a counterexample.

Nevertheless, consider model (A) with \(D = 0_{n \times n}\) and \(C = d_j\tilde{C}\) for \(d_j \in (0, 1)\) denoting the relative diffusion rate of infectious humans to susceptible humans, then \(\hat{R}_0(n) \geq \hat{R}_0(1)\) still holds. Moreover, \(\hat{R}_0(n)\) is strictly decreasing and strictly convex in \(d_j\) if \(\hat{R}_0(n) \neq \hat{R}_0(1)\), i.e., \((V_1(0), \ldots, V_n(0)) \gg 0\) is not a right eigenvector of \(\tilde{C}\) associated with the eigenvalue zero (Gao and Dong 2019). In this case, the assumption that susceptible and infectious individuals have identical travel rates can underestimate the risk of infection.
References


Habitat fragmentation promotes malaria persistence


