

# A metapopulation model for the population dynamics of anopheles mosquito

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## Abstract

A more robust assessment of malaria control will come from a better understanding of the distribution and connectivity of breeding and blood feeding sites. Spatial heterogeneity of mosquito resources, such as hosts and breeding sites, affects mosquito dispersal behavior. This paper analyzes and simulates the spreading of anopheles mosquito on a complex metapopulation, that is, networks of populations connected by migratory flows whose configurations are described in terms of connectivity distribution of nodes (patches) and the conditional probabilities of connections between nodes. We examine the impacts of vector dispersal on the persistence and extinction of a mosquito population in both homogeneous and heterogeneous landscapes. For uncorrelated networks in a homogeneous landscape, we derive an explicit formula of the basic offspring number  $\mathcal{R}_0^{(m)}$ . Using the theory of monotone operators, we obtain sufficient conditions for the global asymptotic stability of equilibria. Precisely, the value 1 of the basic offspring number is a forward bifurcation for the dynamics of anopheles mosquito, with the trivial (mosquito-free) equilibrium point being globally asymptotically stable (GAS) when  $\mathcal{R}_0^{(m)} \leq 1$ , and one stable nontrivial (mosquito-persistent) equilibrium point being born with well determined basins of attraction when  $\mathcal{R}_0^{(m)} > 1$ . Theoretical results are numerically supported and the impact of the migration of mosquitoes are discussed through global sensitivity analysis and numerical simulations.

*Keywords:* Anopheles mosquito; dispersal; monotone system; stability analysis; metapopulation; simulation.

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## 1. Introduction

For many centuries, vector-borne diseases among all infectious diseases of human beings, have constituted a major cause of human mortality and morbidity. Even with the recent advances in the biomedical sciences, vector-borne diseases still seriously threaten world health. For example, according to the latest WHO estimates, released in December 2015, there were 214 million cases of malaria in 2015 and 438000 deaths [1]. It is well known that the malaria parasite is transmitted from human-to-human through the anopheles mosquito bites, and that the transmission cycle is essentially driven by the human biting habit of the mosquito [2]. Now, the female anopheles mosquito bites a human being for the sole purpose of harvesting blood that she needs for the development of her eggs. The malaria parasite has exploited the mosquito's life style by adapting its life cycle so that part of it is in the human being and the other part in the mosquito. By so doing, the mosquito can then propagate the parasite from human to human. Transmission of most indirectly transmitted diseases of human being follows the same pattern.

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The vector (in most cases an insect) interacts with a human being, and depending on the disease status of both organisms, will either infect or be infected. Thus, understanding the population dynamics of mosquitoes, and relationship between mosquitoes and the environment is fundamental to the study of the epidemiology of mosquito-borne diseases. Mosquito abundance is a key determining factor that affects the persistence or resurgence of mosquito-borne diseases in a given region [3]. Hence, it is crucial to study the dynamics of mosquitoes, and devise effective and realistic methods for controlling mosquito population in communities.

The spatial distribution of anopheles vectors has shown great potential to affect malaria transmission intensity [3]. Therefore, a better understanding of the distribution, productivity and connectivity of anopheles breeding sites in order to determine their influence on anopheles distribution could be very useful in malaria control. Several theoretical studies of malaria vector dynamics have emphasized the importance of considering individual larval habitats, but few have addressed the effects of interactions between larval habitat connectivity [3, 4].

Mathematical models play an important role in understanding and providing solutions to natural phenomena which are difficult to measure in the field, and some models have incorporated dispersal or heterogeneity when modeling mosquito population [5, 6, 7]. Spatial models usually used the diffusion approach, which considers space as a continuous variable. Although partial differential equations (PDEs) are a good and classical way of modeling such dispersal [6, 8], their analysis is usually limited and do not incorporate the various factors that affect migrations. However, discrete approaches offer a better and simpler way of modeling heterogeneity [5, 9]. Thus, in areas where resources can be located in patches, mosquito dispersal is more suitably modeled by using a metapopulation approach, in which the population is subdivided into discrete patches. Then, in each patch, the population is subdivided into compartments corresponding to different status. This leads to a multi-patch, multi-compartment system.

Talking about the metapopulation setting, a recent approach based on the formalism used in statistical mechanics of complex networks is presented in [10, 11, 12, 13]. Under this approach, the structure of the spatial network of patches is encapsulated by means of the connectivity (degree) distribution  $p(k)$  defined as the probability that a randomly chosen patch has connectivity  $k$ . Note that the degree or connectivity of a patch (node) is the number of links connected to that node (i.e., the number its neighbors). Recent works have shown that it is possible to investigate the dynamics of epidemic spread using statistical mechanics on configuration model networks [14, 15, 16, 17, 18]. Most of above-mentioned investigations [13, 15, 16, 18] mainly considered epidemic models on networks with no degree correlation (i.e., uncorrelated networks). In such networks, a patch which is only constrained by degree distribution (and hence by the number of neighbors it has), can point to any patch from a pool of the network. However, few recent works [14, 17] have taken into account the degree correlation in complex networks and have conducted comparison studies on the prediction of disease evolution on correlated networks.

Many other works have focused on a metapopulation approach to model the mosquito population [4, 5]. In their work in [4], the authors presented a stochastic network model not governed by a dynamical system and did not consider all main stages of the mosquito life cycle to analyze the significance of the productivity of breeding sites. The work in [5] considered a set of discrete hexagonal patches to investigated the effects of mosquito dispersal on its dynamics.

In this work, we intend to fill some of the gaps mentioned above in order to better take into account the heterogeneity in the connectivity of the nodes of network. To fulfill our goal, we make use of an approach based on statistical mechanics which could allow us identifying other breeding site characteristics which could best explain the distribution and abundance of mosquitoes. The methodology and objectives of this paper are to design a complex network extension of the seminal model in [19], analyze and simulate a mathematical model for the spatio-temporal dynamics of anopheles mosquito using the alternative approach based on a statistical mechanics. This extension is inspired by the works [4, 5, 11, 12, 13] and

some references therein. We consider the spread of anopheles mosquitoes on complex metapopulations, i.e., networks of populations connected by migratory flows whose configurations are described in terms of the conditional probabilities of connections between nodes. Note that nodes of the network represent potential breeding and feeding sites of mosquitoes, around which are human hosts habitations.

From the modeling perspective, the model proposed in this manuscript is a substantial extension of the basic model in [19] by incorporating the dispersal of mosquitoes. It also extends and enriches the work in [4, 5] by considering: (i) all the stages of the mosquito life cycle and (ii) heterogeneity in the connectivity of patches. From the theoretical and numerical perspectives, we examine the significance of larval habitat connectivity and mosquito dispersal in a homogeneous and a heterogeneous landscapes on the persistence of mosquitoes populations. More precisely, we construct corresponding metapopulation models and perform their qualitative and quantitative analyzes. Specifically, for the mathematical tractability, uncorrelated networks in a homogeneous landscape are considered and the following investigations are highlighted:

- The bifurcation/threshold parameter (basic offspring number) is explicitly computed.
- The sensitivity analysis of the threshold parameter, the model variables with respect to model parameters is given.
- A simple and digestive proof based on the Hethcote-Thieme fixed point theorem [20], of a unique nontrivial equilibrium point is provided.
- Contrary to the few existing works where, Lyapunov-LaSalle techniques are usually used, the monotone operator theory [21] is the main ingredient here for the establishment of global asymptotic stability of both trivial and nontrivial equilibrium points.

Moreover for both homogeneous and heterogeneous landscapes, the effects of dispersal/migration and patch heterogeneity on the mosquito population are numerically investigated. Finally, the comparison of metapopulation models in homogeneous and heterogeneous landscapes are presented through numerical simulations. The rest of the paper is organized as follows. After the presentation of the basic model without mosquito dispersal in Section 2, we formulate metapopulation models for both homogeneous and heterogeneous landscapes in Section 3. Their qualitative and quantitative analyses are further presented. Theoretical results and the role of dispersal, patch connectivities and migration are investigated through numerical simulations in Section 4. The summary of the main results of our work and its possible extensions conclude the paper in Section 5.

## 2. The basic model in a single patch: mosquito dynamics without dispersal

We consider the classical Anguelov-Dumont-Lubuma model [19]:

$$\begin{cases} \dot{A} &= \Phi F - (\gamma + \mu_1 + \mu_2 A)A, \\ \dot{Y} &= r\gamma A - (\beta + \mu_Y)Y, \\ \dot{M} &= (1-r)\gamma A - \mu_M M, \\ \dot{F} &= \beta Y - \mu_F F. \end{cases} \quad (2.1)$$

This model was developed according to the following biological and entomological facts recalled hereafter. The life cycle of mosquitos consists of two main stages: aquatic (egg, larva, pupa) and adult. After emergence from pupa, a female mosquito needs to mate and get a blood meal before it starts laying eggs. Depending on the condition, this takes about a week. Then, every 4-5 days she will take a blood meal and lay 100-150 eggs at different places (10-15 per place). Mathematically, the population of mosquitoes is then divided into the following compartments: population in aquatic stage  $A$ ; young female not yet

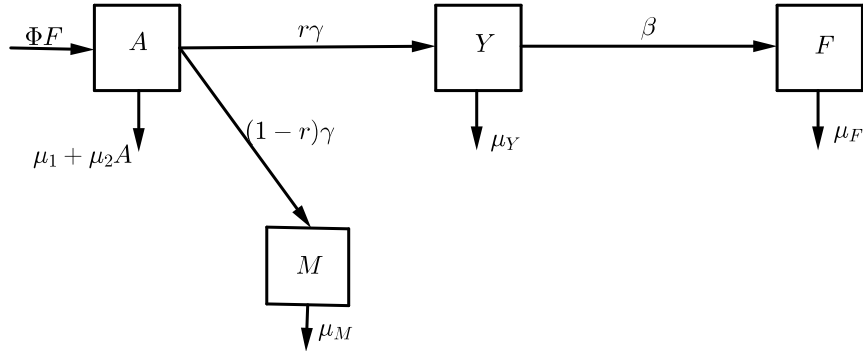


Figure 1: Wild mosquito flow chart.

laying eggs  $Y$ ; fertilized and eggs laying females  $F$  and males  $M$ . This description was depicted in [19] by the flowchart in Fig. 1.

Note that the first equation of system (2.1) can be combined as logistic population with harvesting. A female needs to mate successfully only once. The eggs are laid in the so-called gonotrophic cycle, which consists of taking blood meal, maturation of the eggs and oviposition. Before a female begins to lay eggs, two essential events need to take place, mating and taking a blood meal, occurring in varying order.

A female mosquito is considered to be in the  $Y$ -compartment since its emergence from pupa until her gonotrophic cycle has began, that is the time needed to mate and take the first blood meal, which takes typically 3-4 days. The death rate during that period reflects essentially only death from predators and adverse climatic conditions. Therefore, it is generally lower than the death rate for the  $F$ -compartment. Typically, the male mosquitoes are (depending on the temperature) about half or 40 percent of the total population.

In the model, the fraction of the emerging female mosquitoes is denoted by  $r$ , with  $(1-r)$  being the fraction of emerging male mosquitoes. A male mosquito can mate practically through all its life. Since a female needs one successful mating, there is an overabundance of males. Therefore, in general, it is reasonable to assume that the waiting time for mating does not depend on the number of males ( $M$ ) in the sense that, if  $M$  is increased further this rate remains the same. For the model, this means that the transfer rate  $\beta$  from compartment  $Y$  to compartment  $F$  is independent of  $M$ . Mathematically, this means that the third equation of system (2.1) can be decoupled from the system. Sometimes  $\beta$  is referred to as "mating rate", which, as explained above, can be abetted misleading and does not defined well the boundary between compartments  $Y$  and  $F$ . The model under derivation clearly fixed boundary at the beginning of the first gonotrophic cycle of female, that is immediately after the mating and first blood meal. Then, the rate (per day) of laying eggs in the breeding sites is  $\phi F$ , where  $\phi$  is the average amount of eggs laid per fertilized female per day. In the model, the size of the population is restricted by a density dependent death rate similar to [22, 23]. However, the density dependent death rate is used only for the aquatic stage. The reason is that in a typical environment the size of the mosquito population is also restricted mainly by the available breeding sites. In [24], the size of the population is also restricted only in the aquatic stages but in a different way by an explicit carrying capacity beyond which no egg is laid. In equation (2.1), the parameters  $\mu_1$  and  $\mu_2$  denote the density independent and the density dependent death rates of the aquatic stage, respectively. In all equations of model (2.1),  $\mu$  with respective index refers to the death rate for the specific compartment (which is density independent).

The parameter values of model (2.1) used for simulations are given in Table 1 and the analytical results for this model can be found in [19]. However, for the easier readability of our work, we recall without proof the main results. System (2.1) has two equilibria: the trivial equilibrium  $Q_0 = (0,0,0,0)$  and the

Table 1: Numerical values for the parameters of system (2.1) [19].

Parameter	Description	Value
$r$	Fraction of the emerging female mosquitoes (per day)	0.5
$\gamma$ nontrivial	Maturation rate from larvae to adult (per day)	0.1
$\beta$	Transfer rate from the compartment $Y$ to $F$ (per day)	0.25
$1/\mu_M$	Average lifespan of male mosquitoes (in days)	7
$1/\mu_F$	Average lifespan of female mosquitoes (in days)	10
$1/\mu_Y$	Average lifespan of adult female mosquitoes (in days)	20
$\Phi$	Number of eggs at each deposit per capita (per day)	variable
$\mu_1$	Mortality rate of the aquatic stage (per day)	0.25
$\mu_2$	Density mortality rate of the aquatic stage (per day)	$10^{-5}$

nontrivial equilibrium  $Q^* = (A^*, Y^*, F^*, M^*)^T$  where  $A^*$ ,  $Y^*$ ,  $F^*$  and  $M^*$  are defined as follows:

$$\begin{aligned} A^* &= \frac{(\gamma + \mu_1)(\mathcal{R}_0 - 1)}{\mu_2}, & Y^* &= \frac{r\gamma(\gamma + \mu_1)(\mathcal{R}_0 - 1)}{\mu_2(\beta + \mu_Y)}, \\ F^* &= \frac{\beta r\gamma(\gamma + \mu_1)(\mathcal{R}_0 - 1)}{\mu_F\mu_2(\beta + \mu_Y)} & \text{and} & \quad M^* = \frac{(1-r)\gamma(\gamma + \mu_1)(\mathcal{R}_0 - 1)}{\mu_2\mu_M}, \end{aligned} \quad (2.2)$$

where  $\mathcal{R}_0$  is given by

$$\mathcal{R}_0 = \frac{r\gamma\beta\Phi}{(\gamma + \mu_1)(\beta + \mu_Y)\mu_F}. \quad (2.3)$$

The nontrivial equilibrium  $Q^*$  has a biological meaning if and only if  $\mathcal{R}_0 \geq 1$ . The threshold quantity  $\mathcal{R}_0$  is the basic offspring number for the population of anopheles mosquitoes in a single patch model [19]. It is the average number of the newly anopheles mosquitoes generated by a single fertilized and eggs laying female anopheles mosquito during her life when she is introduced into a population of male anopheles mosquitoes in the absence of any given intervention strategies.

The following result summarizes the asymptotic behavior of model (2.1) as shown in [19].

**Theorem 2.1.** *System (2.1) is a dissipative dynamical system in  $\Omega = \mathbb{R}_+^4 = \{(S, Y, F, M) \in \mathbb{R}^4 / S, Y, F, M \geq 0\}$ . Moreover,*

- (i) *If  $\mathcal{R}_0 \leq 1$ , then the trivial (mosquito-free) equilibrium  $Q_0$  is globally asymptotically stable on  $\Omega$ .*
- (ii) *If  $\mathcal{R}_0 > 1$ , then the system has two equilibria  $Q_0$  and  $Q^*$  on  $\Omega$  where  $Q^*$  (the mosquito-persistent equilibrium) is stable with basin of attraction  $\Omega \setminus \{(A, Y, M, F) \in \mathbb{R}_+^4, A = Y = F = 0\}$  and  $Q_0$  is unstable with the nonnegative  $M$ -axis being a stable manifold.*

### 3. Metapopulation models in complex networks

#### 3.1. A generic reaction-diffusion model in a complex network

Herein, we extend model (2.1) to incorporate the diffusion/migration process. Mosquitoes disperse while searching for hosts or breeding sites [4]. We consider the dynamical evolution of the population of anopheles mosquitoes in heterogeneous metapopulation. The model consists of  $n$  patches. We recall that these patches represent breeding-feeding sites around which are potential human habitats and between which mosquitoes move creating links between these nodes. A given fraction of adult mosquitoes searching for hosts and a fraction of adult mosquitoes searching for breeding sites leave their current patches of residence, while the remaining fraction is motionless. We assume that the architecture of the network of patches (nodes) where local populations live is mathematically encoded by means of the connectivity (degree) distribution  $p(k)$ . Typically,  $p(k)$  is defined as the probability that a randomly chosen path has degree  $k$ . We recall that the degree or connectivity of a patch is the number of links connected

to that patch. At any given time, in each patch, an individual mosquito is in one of the following states: population in aquatic stage ( $\rho_{A,k}$ ), young female not yet laying eggs ( $\rho_{Y,k}$ ), fertilized and eggs laying females ( $\rho_{F,k}$ ), male mosquitoes ( $\rho_{M,k}$ ). The total variable population size in patches of degree  $k$  at time  $t$  is given by  $\rho_k(t) = \rho_{A,k}(t) + \rho_{Y,k}(t) + \rho_{F,k}(t) + \rho_{M,k}(t)$ . Note again that, we focus in this part on the migration of mosquitoes from patch to patch (that is the case of connected patches). A reasonable assumption is that, mosquitoes in aquatic phase can not move out of their residence patch, while those in adult phase can migrate.

In Fig. 2, we give an example of a  $n$ -patches network: each patch here is breeding-feeding site. Without

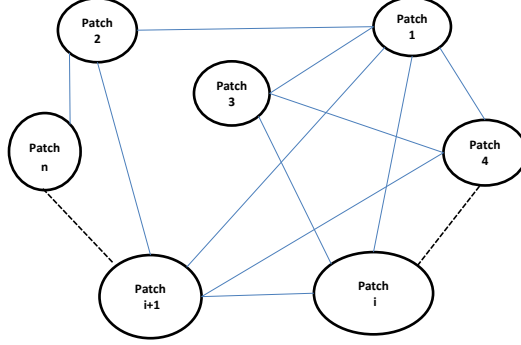


Figure 2: A general  $n$ -patches network for the population dynamics of anopheles mosquito between  $n$  feeding-breeding sites.

loss of generality, we suppose that in each patch, the population dynamics of anopheles mosquitoes is governed by the basic system (2.1). Mosquitoes move from a patch with degree  $k$  to another with degree  $k'$  with a diffusion rate  $D_{kk'}$  that depends on the degrees of the origin and destination patches. The probability  $P_k$  of leaving a patch with degree  $k$  is then given by

$$P_k = k \sum_{k'} P(k'|k) D_{kk'}, \quad (3.1)$$

where  $P(k'|k)$  is the conditional probability that any given edge departing from a node of degree  $k$  is pointing to a node of degree  $k'$  [12].

Under this generic type of diffusion, the equations governing the spatio-temporal evolution of anopheles mosquitoes are giving by the system below :

$$\begin{cases} \dot{\rho}_{A,k} &= \Phi \rho_{F,k} - (\gamma + \mu_1 + \mu_2 \rho_{A,k}) \rho_{A,k}, \\ \dot{\rho}_{Y,k} &= r \gamma \rho_{A,k} - (\beta + \mu_Y) \rho_{Y,k} - P_k \rho_{Y,k} + k \sum_{k'} P(k'|k) D_{k'k} \rho_{Y,k'}, \\ \dot{\rho}_{M,k} &= (1-r) \gamma \rho_{A,k} - \mu_M \rho_{M,k} - P_k \rho_{M,k} + k \sum_{k'} P(k'|k) D_{k'k} \rho_{M,k'}, \\ \dot{\rho}_{F,k} &= \beta \rho_{Y,k} - \mu_F \rho_{F,k} - P_k \rho_{F,k} + k \sum_{k'} P(k'|k) D_{k'k} \rho_{F,k'}. \end{cases} \quad (3.2)$$

As in classical reaction-diffusion processes, system (3.2) expresses the time variation of the subpopulations of mosquitoes in aquatic phase, young female not yet laying eggs, fertilized and eggs laying females and males mosquitoes as the sum of two independent contributions: reaction and diffusion. In particular, the diffusion term includes the outflow of mosquitoes (diffusing particles) from patches of degree  $k$  and the inflow of migratory mosquitoes from the nearest patches of degree  $k'$ . In general, with  $n$  different patches of corresponding degrees  $k_1, k_2, \dots, k_n$  in the network, Eq. (3.2) is a  $4 \times n$  system of differential equations. The solutions of system (3.2) remain nonnegative in  $\mathbb{R}_+^{4n}$  because the out movement always stops when the corresponding patch is emptied. This latter assertion is mathematically established in the following result.

**Theorem 3.1.** *If system (3.2) with initial condition in  $\mathbb{R}_+^{4n}$  has a solution, then the latter solution remains in  $\mathbb{R}_+^{4n}$  (i.e. nonnegative) for all times.*



**Proof:** It suffices to show that system (3.2) can be written in the following form:

$$\dot{X} = \mathcal{M}(X)X, \quad (3.3)$$

where  $\mathcal{M}(X)$  is a  $4n \times 4n$  cooperative (Metzler) matrix, and  $X$  a  $4n$  column matrix to be determined below. To this end, system (3.2) rewrites:

$$\begin{cases} \dot{\rho}_{A,k_i} &= \Phi \rho_{F,k_i} - (\gamma + \mu_1 + \mu_2 \rho_{A,k_i}) \rho_{A,k_i}, \\ \dot{\rho}_{Y,k_i} &= r\gamma \rho_{A,k_i} - (\beta + \mu_Y) \rho_{Y,k_i} - P_{k_i} \rho_{Y,k_i} + k_i \sum_{j=1}^n P(k_j|k_i) D_{k_j,k_i} \rho_{Y,k_j}, \\ \dot{\rho}_{M,k_i} &= (1-r)\gamma \rho_{A,k_i} - \mu_M \rho_{M,k_i} - P_{k_i} \rho_{M,k_i} + k_i \sum_{j=1}^n P(k_j|k_i) D_{k_j,k_i} \rho_{M,k_j} \\ \dot{\rho}_{F,k_i} &= \beta \rho_{Y,k_i} - \mu_F \rho_{F,k_i} - P_{k_i} \rho_{F,k_i} + k_i \sum_{j=1}^n P(k_j|k_i) D_{k_j,k_i} \rho_{F,k_j}. \end{cases} \quad i = \{1, 2, \dots, n\}, \quad (3.4)$$

Now, let

$$X_A = (\rho_{A,k_1}, \rho_{A,k_2}, \dots, \rho_{A,k_n})^T, \quad X_Y = (\rho_{Y,k_1}, \rho_{Y,k_2}, \dots, \rho_{Y,k_n})^T,$$

$$X_M = (\rho_{M,k_1}, \rho_{M,k_2}, \dots, \rho_{M,k_n})^T, \quad X_F = (\rho_{F,k_1}, \rho_{F,k_2}, \dots, \rho_{F,k_n})^T,$$

$$\mathbf{Q}_1 = \text{diag}(P_{k_1}, \dots, P_{k_n}), \quad \mathbf{Q}_2 = (k_i P(k_j|k_i) D_{k_j,k_i})_{(i,j)}, \quad M_A = -(\gamma + \mu_1)I_n - \mu_2 \text{diag}(X_A),$$

$$M_Y = -(\beta + \mu_Y + \mathbf{Q}_1)I_n + \mathbf{Q}_2, \quad M_M = -(\mu_M + \mathbf{Q}_1)I_n + \mathbf{Q}_2, \quad M_F = -(\mu_F + \mathbf{Q}_1)I_n + \mathbf{Q}_2,$$

and

$$\mathcal{M}(X) = \begin{pmatrix} M_A & O_n & O_n & \Phi I_n \\ r\gamma I_n & M_Y & O_n & O_n \\ (1-r)\gamma I_n & O_n & M_M & O_n \\ O_n & \beta I_n & O_n & M_F \end{pmatrix},$$

where  $I_n$  and  $O_n$  denote the  $n \times n$  identity and null matrices, respectively. Since the entries of  $\mathbf{Q}_1$  and  $\mathbf{Q}_2$  are nonnegative, it is straightforward that  $M_A$ ,  $M_Y$ ,  $M_M$ ,  $M_F$  are Metzler matrices, so is  $\mathcal{M}(X)$ . Finally, let

$$X = (X_A, X_Y, X_M, X_F)^T,$$

then model (3.4) becomes

$$\dot{X} = \mathcal{M}(X)X.$$

This achieves the proof.  $\square$

In the following subsections we study special cases of system (3.2) depending on the type of diffusion processes by considering diffusion rates that are inherent to the traffic characteristics of each node. Typically there are two distinguishable landscapes with different features which must retain our attention.

### 3.2. The metapopulation model in a homogeneous landscape

A landscape is homogeneous when all its patches have similar characteristics. Thus, in such landscapes, it is reasonable to assume that the mosquitoes have the same dispersal/diffusion rate between patches. The mosquitoes searching for breeding sites to lay their eggs are attracted by the availability of breeding sites [25]. Therefore they move randomly in any breeding sites to lay their eggs. Mosquitoes can detect host odor, but it is unclear whether they have the learning capacity they would need to enable them to return to particular hosts or breeding sites [5, 26]. In the case where all patches have similar characteristics (i.e. homogeneous landscape), the mosquitoes disperse equally between the patches and the dispersal parameter is the same for all patches. In this case, the diffusion rate along any given link of a node with degree  $k$  is simply equal to

$$D_{kk'} = \frac{D_i}{k}, \quad i = Y, M, F. \quad (3.5)$$

For the sake of brevity, we consider strictly positive diffusion rates  $D_Y, D_F, D_M > 0$ . Thus, assuming that distance has no bearing on the probability of mosquito flying between breeding sites and, using the fact that  $\sum_k P(k|k') = 1$ , the dynamics of free-flying mosquitoes in a patch of degree  $k$  is

$$\begin{cases} \dot{\rho}_{A,k} &= \Phi\rho_{F,k} - (\gamma + \mu_1 + \mu_2\rho_{A,k})\rho_{A,k}, \\ \dot{\rho}_{Y,k} &= r\gamma\rho_{A,k} - (\beta + \mu_Y)\rho_{Y,k} - D_Y\rho_{Y,k} + kD_Y \sum_{k'} P(k'|k) \frac{\rho_{Y,k'}}{k'}, \\ \dot{\rho}_{M,k} &= (1-r)\gamma\rho_{A,k} - \mu_M\rho_{M,k} - D_M\rho_{M,k} + kD_M \sum_{k'} P(k'|k) \frac{\rho_{M,k'}}{k'}, \\ \dot{\rho}_{F,k} &= \beta\rho_{Y,k} - \mu_F\rho_{F,k} - D_F\rho_{F,k} + kD_F \sum_{k'} P(k'|k) \frac{\rho_{F,k'}}{k'}, \end{cases} \quad (3.6)$$

Note that, since the number of links emanating from nodes of degree  $k$  to nodes of degree  $k'$  must be equal to the number of links emanating from nodes of degree  $k'$  to nodes of degree  $k$  in non-directed graphs, we have the following relationship between  $p(k)$  and  $P(k'|k)$  [14]:

$$kP(k'|k)p(k) = k'P(k|k')p(k'). \quad (3.7)$$

For networks with a connectivity pattern defined by a set of conditional probabilities  $P(k'|k)$ , we define the elements of the connectivity matrix  $C$  as

$$C_{kk'} = \frac{k}{k'}P(k'|k). \quad (3.8)$$

Note that these elements are the average number of mosquitoes that patches of degree  $k$  receive from neighboring patches of degree  $k'$  assuming that one mosquito leaves each of these patches by choosing at random one of the  $k'$  connections [13]. On the other hand, for those degrees  $k$  that are not present in the network, one must have  $P(k'|k) = 0, \forall k'$ . Hereafter in this paper, when talking about degrees, we implicitly mean those degrees that are present in the network. Furthermore, the case where all patches have the same connectivity is excluded from our consideration because, under the present approach, the model equations reduce to those of a single patch model.

In order to obtain further analytical results about the metapopulation dynamics of anopheles mosquitoes, we need to be precise about the form of  $P(k'|k)$ . As in most network models, the easiest and usual assumption is to restrict ourselves to uncorrelated networks.

### 3.2.1. Uncorrelated networks

In these networks, the degrees of the nodes at the end of any given link are independent. In other words, there is no degree-degree correlation between the connected nodes. Therefore, we have

$$P(k'|k) = k'p(k')/\langle k \rangle, \quad (3.9)$$

which corresponds to the degree distribution of nodes (patches) that arrive at by following a randomly chosen link [10]. Using Eqs. (3.7), (3.8), (3.9),  $\sum_k P(k|k') = 1$  and change the order of summations in system (3.4), one obtains the following equations for the time evolution of anopheles mosquitoes in metapopulations described by uncorrelated networks:

$$\begin{cases} \dot{\rho}_{A,k} &= \Phi\rho_{F,k} - (\gamma + \mu_1 + \mu_2\rho_{A,k})\rho_{A,k}, \\ \dot{\rho}_{Y,k} &= r\gamma\rho_{A,k} - (\beta + \mu_Y)\rho_{Y,k} - D_Y\left(\rho_{Y,k} - \frac{k}{\langle k \rangle}\rho_Y\right), \\ \dot{\rho}_{M,k} &= (1-r)\gamma\rho_{A,k} - \mu_M\rho_{M,k} - D_M\left(\rho_{M,k} - \frac{k}{\langle k \rangle}\rho_M\right), \\ \dot{\rho}_{F,k} &= \beta\rho_{Y,k} - \mu_F\rho_{F,k} - D_F\left(\rho_{F,k} - \frac{k}{\langle k \rangle}\rho_F\right), \end{cases} \quad (3.10)$$



where

$$\langle k \rangle = \sum_k kp(k) \quad \text{and} \quad \rho_j(t) = \sum_k p(k)\rho_{jk}, \quad j = A, Y, M, F.$$

$\langle k \rangle$  is defined as the average network degree.  $\rho_A, \rho_Y, \rho_F$  and  $\rho_M$ , represent the average number of population in aquatic stage, young females and eggs laying females, and population of males mosquitoes in each patch at time  $t$ , respectively. In this case, the diffusion term is simply given by the difference between the outflow of young females not yet laying eggs ( $D_Y\rho_{Y,k}$ ), fertilized and eggs laying females ( $D_F\rho_{F,k}$ ) and male mosquitoes ( $D_M\rho_{M,k}$ ) in patches of connectivity  $k$  and the total inflow of young females not yet laying eggs ( $D_Y\rho_Y/\langle k \rangle$ ), fertilized and eggs laying females ( $D_F\rho_F/\langle k \rangle$ ) and male mosquitoes ( $D_M\rho_M/\langle k \rangle$ ) in patches of connectivity  $k$ , respectively; across all their  $k$  connections, which is  $k$  times the average flow of mosquitoes across a connection in the network. Note that this average flow across a connection does not depend on the degree  $k$  of the considered patch because we have assumed that the architecture of the metapopulation is described by an uncorrelated network. In these network configurations, the elements of the connectivity matrix  $C$  are simply

$$C_{kk'} = \frac{kp(k')}{\langle k \rangle}. \quad (3.11)$$

Clearly,  $C$  is a rank-one matrix and the vector  $v$ , whose components  $v_k = k$ , is its eigenvector corresponding to its unique non-zero eigenvalue 1. Thus, if there are (as assumed above)  $n$  different patches in the network, then the eigenvalues of the said connectivity matrix are  $\lambda = 0$  (with algebraic multiplicity  $n - 1$ ) and  $\lambda = 1$  (which is a simple eigenvalue). This latter remark will be used to prove the stability of equilibria of the model. For the way forward, we first "vectorialize" system (3.10), using the following set of vectors as formerly defined:

$$\begin{aligned} X_A &= (\rho_{A,k_1}, \rho_{A,k_2}, \dots, \rho_{A,k_n})^T, & X_Y &= (\rho_{Y,k_1}, \rho_{Y,k_2}, \dots, \rho_{Y,k_n})^T, \\ X_M &= (\rho_{M,k_1}, \rho_{M,k_2}, \dots, \rho_{M,k_n})^T, & X_F &= (\rho_{F,k_1}, \rho_{F,k_2}, \dots, \rho_{F,k_n})^T. \end{aligned}$$

Remind that, if  $X \in \mathbb{R}^n$  is a vector,  $\text{diag}(X)$  denotes the  $n \times n$  diagonal matrix whose entries are given by the respective components of  $X$ . With these notations, system (3.10) becomes

$$\begin{cases} \dot{X}_A = f_1(X) &= \Phi X_F - [\gamma + \mu_1 + \mu_2 \text{diag}(X_A)] X_A, \\ \dot{X}_Y = f_2(X) &= r\gamma X_A - [\beta + \mu_Y + D_Y] X_Y + D_Y C X_Y, \\ \dot{X}_M = f_3(X) &= (1-r)\gamma X_A - [\mu_M + D_M] X_M + D_M C X_M, \\ \dot{X}_F = f_4(X) &= \beta X_Y - [\mu_F + D_F] X_F + D_F C X_F, \end{cases} \quad (3.12)$$

where  $C$  is the connectivity matrix defined in Eq. (3.11).

Notice that, in the case where the parameters  $\Phi, \gamma, \beta, \mu_1, \mu_2, \mu_Y, \mu_M$  and  $\mu_F$  are not the same for all patches, they are replaced in system (3.12) by nonnegative diagonal blocs matrices and this does not change the fundamental structure of the system.

#### a) Basic offspring number

System (3.12) has a trivial (mosquito-free) equilibrium  $\mathcal{P}_0 = (\mathbf{0}, \mathbf{0}, \mathbf{0}, \mathbf{0})$  with  $\mathbf{0}$  standing for the zero vector of dimension  $n$  when there is no fertilized and eggs laying females in each patch. We calculate the basic offspring number,  $\mathcal{R}_0^{(m)}$  (where the subscript "m" stands for "metapopulation" and simply differentiate it with the single patch basic offspring number  $\mathcal{R}_0$ ), using the next generation approach developed in [27].

Let

$$\mathcal{F} = \begin{pmatrix} \Phi X_F \\ \mathbf{0} \\ \mathbf{0} \end{pmatrix} \quad \text{and} \quad \mathcal{V} = \begin{pmatrix} \gamma X_A + (\mu_1 + \mu_2 \text{diag}(X_A)) X_A \\ -r\gamma X_A + (\mu_Y + \beta) X_Y + D_Y X_Y - D_Y C X_Y \\ -\beta X_Y + \mu_F X_F + D_F X_F - D_F C X_F \end{pmatrix}.$$

The Jacobian matrices of  $\mathcal{F}$  and  $\mathcal{V}$  at the trivial equilibrium  $\mathcal{P}_0$  are

$$F = \begin{bmatrix} F_{11} & F_{12} \\ F_{21} & F_{22} \end{bmatrix} \quad \text{and} \quad V = \begin{bmatrix} (\gamma + \mu_1)I_n & \mathbf{0} & \mathbf{0} \\ -r\gamma I_n & (\beta + \mu_Y + D_Y - D_Y C)I_n & \mathbf{0} \\ \mathbf{0} & -\beta I_n & (\mu_F + D_F - D_F C)I_n \end{bmatrix},$$

where

$$F_{11} = \mathbf{0}, \quad F_{12} = [\mathbf{0}, \Phi], \quad F_{21} = \begin{bmatrix} \mathbf{0} \\ \mathbf{0} \end{bmatrix} \quad \text{and} \quad F_{22} = \begin{bmatrix} \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{0} \end{bmatrix}.$$

To compute  $V^{-1}$ , denote

$$V = \begin{bmatrix} V_1 & V_2 \\ V_3 & V_4 \end{bmatrix}, \quad \text{where} \quad V_1 = (\gamma + \mu_1)I_n, \quad V_2 = [\mathbf{0} \quad \mathbf{0}], \quad V_3 = \begin{bmatrix} -r\gamma I_n \\ \mathbf{0} \end{bmatrix}$$

and

$$V_4 = \begin{bmatrix} (\beta + \mu_Y + D_Y - D_Y C)I_n & \mathbf{0} \\ -\beta I_n & (\mu_F + D_F)I_n - D_F C \end{bmatrix}.$$

We emphasize that, since  $V$  is a M-matrix and  $-V$  is stable,  $V^{-1} \geq 0$ . Let the inverse matrix of  $V$  be written in the following form:

$$V^{-1} = \begin{bmatrix} W_{11} & W_{12} \\ W_{21} & W_{22} \end{bmatrix},$$

where  $W_{11}$  and  $W_{22}$  are square matrices of dimension  $(2n \times 2n)$  and  $(n \times n)$ , respectively. With this in mind, one has

$$FV^{-1} = \begin{bmatrix} \mathcal{A} & \mathcal{B} \\ \mathbf{0} & \mathbf{0} \end{bmatrix},$$

where  $\mathcal{A} = F_{12} W_{21}$  and  $\mathcal{B} = F_{12} W_{22}$ . Then following [27], the basic offspring number  $\mathcal{R}_0^{(m)}$  is defined as the spectral radius of the next generation matrix,  $FV^{-1}$ . Precisely,

$$\mathcal{R}_0^{(m)} = \rho(FV^{-1}) = \rho(F_{12} W_{21}). \quad (3.13)$$

To obtain an explicit expression of the basic offspring number, we only need to compute  $W_{21}$ . The following lemma demonstrated in Appendix A, is instrumental:

**Lemma 3.2.** *Let  $N$  be a square block matrix of the following form:*

$$N = \begin{bmatrix} N_1 & N_2 \\ N_3 & N_4 \end{bmatrix},$$

where  $N_1$  and  $N_4$  are square matrices.

If  $N_1$  and  $D = N_4 - N_3 N_1^{-1} N_2$  are invertible, then the inverse matrix of  $N$  is given by

$$N^{-1} = \begin{bmatrix} N_1^{-1} + N_1^{-1} N_2 D^{-1} N_3 N_1^{-1} & -N_1^{-1} N_2 D^{-1} \\ -D^{-1} N_3 N_1^{-1} & D^{-1} \end{bmatrix}.$$

Notice that  $V$  defined above has the same form as  $N$  defined in Lemma 3.2 (with:  $N_1 = V_1$ ,  $N_2 = V_2$ ,  $N_3 = V_3$  and  $N_4 = V_4$ ). Moreover, it is easy to check that  $V$  satisfies all the assumptions in Lemma 3.2. Thus, applying Lemma 3.2,  $V^{-1}$  is given by

$$V^{-1} = \begin{bmatrix} V_1^{-1} & \mathbf{0} \\ -V_4^{-1} V_3 V_1^{-1} & V_4^{-1} \end{bmatrix},$$

from which one can extract  $W_{21} = -V_4^{-1} V_3 V_1^{-1}$ . Thus, computing  $W_{21}$  amounts to compute  $V_4^{-1}$  since  $V_3$  is given and  $V_1^{-1}$  is obvious. Notice also that  $V_4$  has the same form as  $N$  in Lemma 3.2 (with  $N_1 = (\beta + \mu_Y + D_Y - D_Y C)I_n$ ,  $N_2 = 0$ ,  $N_3 = -\beta I_n$  and  $N_4 = (\mu_F + D_F)I_n - D_F C$ ). Hence, another application of Lemma 3.2 yields

$$V_4^{-1} = \begin{bmatrix} N_1^{-1} & \mathbf{0} \\ -N_4^{-1} N_3 N_1^{-1} & N_4^{-1} \end{bmatrix}.$$

From the above expressions, it appears that to obtain an explicit expressions of  $V_4^{-1}$ , we need to compute the inverse matrices of  $N_1^{-1}$  and  $N_4^{-1}$ . These shall be done using another instrumental lemma, stated below and proved in Appendix B.

**Lemma 3.3.** Let  $G = U + KWZ$  be an  $n \times n$  invertible matrix. Assume the matrices  $U$ ,  $W$  and  $W^{-1} + ZU^{-1}K$  are invertible. Then the inverse matrix of  $G$  is given by

$$G^{-1} = U^{-1} - U^{-1}K[W^{-1} + ZU^{-1}K]^{-1}ZU^{-1}. \quad (3.14)$$

Now, we can explicitly calculate  $N_1^{-1}$  and  $N_4^{-1}$ . We shall use recursively Lemma 3.3 and the fact that  $C^m = C, \forall m \in \mathbb{N}^*$ .

Note that  $N_4 = (\mu_F + D_F)I_n - D_FC$  has the form of the matrix  $G$  with

$$U = (\mu_F + D_F)I_n, \quad K = (k_1, \dots, k_n)^T, \quad W = I_n \quad \text{and}$$

$$Z = \frac{-D_F}{\langle k \rangle} (P(k_1), \dots, P(k_n)).$$

With this in mind and using Lemma 3.3, it is straightforward that

$$\begin{aligned} N_4^{-1} &= \frac{I_n}{(\mu_F + D_F)} - \frac{I_n}{(\mu_F + D_F)} \begin{pmatrix} k_1 \\ \vdots \\ k_n \end{pmatrix} \left[ I_n - \frac{D_F}{\mu_F + D_F} \right]^{-1} \\ &\times \frac{-D_F}{\langle k \rangle (\mu_F + D_F)} (P(k_1), \dots, P(k_2)), \\ &= \frac{I_n}{(\mu_F + D_F)} + \frac{I_n}{(\mu_F + D_F)} \frac{D_FC}{\mu_F} = \frac{1}{(\mu_F + D_F)} \left[ I_n + \frac{D_F}{\mu_F} C \right]. \end{aligned}$$

Now, let us compute  $N_1 = (\beta + \mu_Y + D_Y - D_Y C)I_n$ . One can also observe that  $N_1$  has the form of  $G$  in Lemma 3.3, with

$$U = (\beta + \mu_Y + D_Y)I_n, \quad K = (k_1, \dots, k_n)^T, \quad W = I_n \quad \text{and}$$

$$Z = \frac{-D_Y}{\langle k \rangle} (P(k_1), \dots, P(k_n)).$$

Thus, another application of Lemma 3.3 yields

$$N_1^{-1} = \frac{1}{(\beta + \mu_Y + D_Y)} \left[ I_n + \frac{D_Y}{\beta + \mu_Y} C \right].$$

Using the expressions of  $N_1^{-1}$  and  $N_4^{-1}$ , one has

$$N_4^{-1} N_3 N_1^{-1} = \frac{-\beta}{(\mu_F + D_F)(\beta + \mu_Y + D_Y)} \left( I_n + \frac{D_Y C}{\beta + \mu_Y} + \frac{D_F C}{\mu_F} + \frac{D_F D_Y C}{\mu_F(\beta + \mu_Y)} \right).$$

Thus,

$$F_{12} W_{21} = \frac{r\beta\gamma\Phi}{(\gamma + \mu_1)(\mu_F + D_F)(\beta + \mu_Y + D_Y)} \left[ I_n + \frac{D_Y C}{\beta + \mu_Y} + \frac{D_F C}{\mu_F} + \frac{D_F D_Y C}{\mu_F(\beta + \mu_Y)} \right].$$

The basic offspring number is therefore

$$\begin{aligned} \mathcal{R}_0^{(m)} &= \rho(F_{12} W_{21}), \\ &= \rho[\Gamma(a_0 I_n + (b_0 + c_0 + d_0)C)], \end{aligned} \quad (3.15)$$

where

$$a_0 = 1, \quad b_0 = \frac{D_Y}{\beta + \mu_Y}, \quad c_0 = \frac{D_F}{\mu_F}, \quad d_0 = \frac{D_F D_Y}{\mu_F(\beta + \mu_Y)} \quad \text{and} \quad \Gamma = \frac{r\beta\gamma\Phi}{(\gamma + \mu_1)(\mu_F + D_F)(\beta + \mu_Y + D_Y)}.$$

Since the rank of  $C$  is one and  $\lambda = 1$  is its unique non-zero and positive eigenvalue, the largest eigenvalue of the matrix  $\Gamma[a_0 I_n + (b_0 + c_0 + d_0)C]$  is  $\Gamma(a_0 + b_0 + c_0 + d_0) > 0$ . Thus,  $\mathcal{R}_0^{(m)}$  for system (3.10) is

$$\mathcal{R}_0^{(m)} = \frac{r\beta\gamma\Phi}{(\gamma + \mu_1)(\mu_F + D_F)(\beta + \mu_Y + D_Y)} \left[ 1 + \frac{D_Y}{\beta + \mu_Y} + \frac{D_F}{\mu_F} + \frac{D_F D_Y}{\mu_F(\beta + \mu_Y)} \right]. \quad (3.16)$$

**Remark 3.4.** The relevance of the above techniques (Lemma 3.2 and Lemma 3.3) used to compute  $\mathcal{R}_0^{(m)}$  lies in that it enables us to obtain an explicit formula of the basic offspring number for a complex metapopulation model. More importantly, it gives an easy interpretable expression of the basic offspring number. In metapopulation settings, this kind of result is quite rare (or does not exist at all). It is worth pointing out that, this achievement have been probably made possible due the "statistical" modeling approach used in this work.

b) Sensitivity analysis

We carried out sensitivity analysis to determine the model robustness to parameter values [28, 29]. This amounts to single out the most influential parameters on  $\mathcal{R}_0^{(m)}$  and mosquito subpopulation dynamics. A Latin Hypercube Sampling (LHS) scheme [29] samples 1000 values for each input parameter using a uniform distribution over the range of biologically realistic values, listed in Table 3 with descriptions and references given in Table 1 and Table 2. Using system (3.12), 1000 model simulations are performed by randomly pairing sampled values for all LHS parameters. Outcome measures are calculated for each run : the basic offspring number ( $\mathcal{R}_0^{(m)}$ ), the average number of population in aquatic stage ( $\rho_A$ ), young females ( $\rho_Y$ ) and fertilized females ( $\rho_F$ ) for a network of five patches. Partial Rank Correlation Coefficients (PRCC) and corresponding  $p$ -values are computed. An output is assumed sensitive to an input if the corresponding PRCC is less than  $-0.50$  or greater than  $+0.50$ , and the corresponding  $p$ -values is less than 5%.

Parameter	Range	Parameter	Range	Parameter	Range
$r$	[0.49 , 0.51]	$\mu_2$	$[10^{-6} , 10^{-4}]$	$\mu_F$	[0.05 , 0.2]
$\gamma$	[0.05 , 0.2]	$\beta$	[0.05 , 0.35]	$D_Y$	$[10^{-2} , 1]$
$\Phi$	[0.5 , 50]	$\mu_Y$	[0.01 , 0.2]	$D_M$	$[10^{-2} , 1]$
$\mu_1$	[0.1 , 0.5]	$\mu_M$	[0.05 , 0.2]	$D_F$	$[10^{-2} , 1]$

Table 2: Parameter value ranges of model (3.12) used as input for the LHS method.

Parameter	$\mathcal{R}_0^{(m)}$	$\rho_A$	$\rho_Y$	$\rho_F$
$r$	0.0831	0.0003	0.0325	0.0593
$\gamma$	**0.6617	0.3648	0.2364	0.4401
$\Phi$	***0.9281	0.4003	*0.5414	*0.5079
$\mu_1$	** - 0.7047	-0.0565	-0.0123	-0.0520
$\mu_2$	--	-0.3327	-0.4112	-0.3789
$\beta$	*0.5329	0.2586	0.2033	0.1317
$\mu_Y$	* - 0.5770	-0.2008	-0.1530	-0.1389
$\mu_M$	--	0.0874	-0.0066	-0.1577
$\mu_F$	** - 0.7959	-0.3169	-0.2749	-0.1873
$D_Y$	0.0136	***0.9103	***0.8641	***0.8411
$D_M$	--	-0.0237	0.0283	0.0231
$D_F$	0.0402	*** - 0.9058	*** - 0.8712	*** - 0.8547

Table 3: PRCCs between  $\mathcal{R}_0^{(m)}$ ,  $\rho_A$ ,  $\rho_Y$ ,  $\rho_F$  and each parameter: The (\*)'s indicate the most influential parameters. Precisely, (\*) indicates a parameter whose sensitivity level (in absolute value) is between 0.5 and 0.65. The (\*\*) indicates a parameter whose sensitivity level (in absolute value) is between 0.66 and 0.8. The (\*\*\*) indicates a parameter whose sensitivity level (in absolute value) is above 0.84.

Table 3 suggests that parameter  $\Phi$  has the highest influence on the offspring number  $\mathcal{R}_0^{(m)}$ , following in decreasing order by the parameters  $\mu_F$ ,  $\mu_1$ ,  $\gamma$ ,  $\mu_Y$  and  $\beta$ . One can also observe that, for the values of  $\rho_A$ ,  $\rho_Y$  and  $\rho_F$ , the parameters with more influence are  $D_Y$ ,  $D_F$  and  $\Phi$ . This suggests that the migration of female mosquitoes between the patches may play a dominant role on the persistence of the mosquito's population.

c) Global stability of the trivial (mosquito-free) equilibrium point.

Using Theorem 2 in [27], the following result is straightforward.

**Lemma 3.5.** *The trivial (mosquito-free) equilibrium point  $\mathcal{P}_0$  of system (3.12) is locally asymptotically stable whenever  $\mathcal{R}_0^{(m)} < 1$ , and unstable if  $\mathcal{R}_0^{(m)} > 1$ .*

Biologically speaking, Lemma 3.5 implies that mosquitoes can be eliminated in all breeding sites (when  $\mathcal{R}_0^{(m)} < 1$ ) if the initial sizes of the population of anopheles mosquitoes are in the basin of attraction of the trivial equilibrium point  $\mathcal{P}_0$ .

System (3.12) can be written in the form  $\dot{X} = f(X)$ , where  $X = (X_A, X_Y, X_M, X_F)^T$  and  $f(X) = (f_1(X), f_2(X), f_3(X), f_4(X))^T$ . It is straightforward that system (3.12) is cooperative on  $\Omega = \mathbb{R}_+^{4n}$  because the jacobian matrix of (3.12) is a Metzler matrix. Furthermore,  $f$  is continuous on  $\Omega$  and the vector field defined by  $f$  is directed inwards on the border  $\partial\Omega$  of  $\Omega$ . Thus, Theorems 2, 5 and 6 in [19] can be applied to extend the local result in Lemma 3.5 to a global one on  $\Omega$  as follows:

**Theorem 3.6.** *System (3.12) defines a dissipative dynamical system on  $\Omega = \mathbb{R}_+^{4n}$ . Moreover, if  $\mathcal{R}_0^{(m)} \leq 1$  then the trivial (mosquito-free) equilibrium point  $\mathcal{P}_0$  is globally asymptotically stable on  $\Omega$ .*

*Proof :* It hinges basically on the monotone properties of model (3.12). The inequalities

$$\frac{4\mathcal{R}_0^{(m)}k_i p(k_i) + 4\Gamma \sum_{j=1, j \neq i}^n k_j p(k_j)}{\langle k \rangle} < \frac{\gamma + \mu_1 + \mu_2 \rho_{A, k_i}}{\gamma + \mu_1}, \quad i = 1, 2, \dots, n, \quad (3.17)$$

hold for all sufficiently large  $X_A$ . Let  $m = (m_1, m_2, \dots, m_n) > 0$  and let  $X_{A_m}$  be so large that in addition to (3.17) the following inequalities also hold :

$$X_{A_m} \geq m, \quad (3.18)$$

$$X_{F_m} := \frac{(\gamma + \mu_1 + \mu_2 \text{diag}(X_{A_m}))X_{A_m}}{2\Phi} \geq m, \quad (3.19)$$

$$X_{Y_m} := \frac{(\mu_F I_n + D_F I_n - D_F C)X_{F_m}}{2\beta} \geq m, \quad (3.20)$$

$$X_{M_m} := \frac{2(1-r)\gamma}{\mu_M + D_M} \left[ I_n + \frac{D_M}{\mu_M} C \right] X_{A_m} \geq m. \quad (3.21)$$

Let  $b_m = (X_{A_m}, X_{Y_m}, X_{F_m}, X_{M_m})^T$ . Then, one has

$$f_1(b_m) = -\Phi X_{F_m} < 0; \quad f_3(b_m) = -(1-r)\gamma X_{A_m} < 0; \quad f_4(b_m) = -\beta X_{Y_m} < 0;$$

$$\begin{aligned} f_2(b_m) &= r\gamma \left[ I_n - \frac{(N_1^{-1})^{-1}(N_4^{-1})^{-1}[\gamma + \mu_1 + \mu_2 \text{diag}(X_{A_m})]}{4\beta\Phi r\gamma} \right] X_{A_m}, \\ &= r\gamma \left[ I_n - \frac{(a_0 I_n + (b_0 + c_0 + d_0)C)^{-1}[\gamma + \mu_1 + \mu_2 \text{diag}(X_{A_m})]}{4\Gamma} \right] X_{A_m}, \\ &< 0 \quad \text{if} \quad 4\Gamma(a_0 I_n + (b_0 + c_0 + d_0)C) < \frac{\gamma + \mu_1 + \mu_2 \text{diag}(X_{A_m})}{\gamma + \mu_1}, \end{aligned}$$

i.e.

$$f_2(b_m) < 0 \quad \text{if} \quad \frac{4\mathcal{R}_0^{(m)}k_i p(k_i) + 4\Gamma \sum_{j=1, j \neq i}^n k_j p(k_j)}{\langle k \rangle} < \frac{\gamma + \mu_1 + \mu_2 \rho_{A, k_i}}{\gamma + \mu_1}, \quad i = 1, 2, \dots, n.$$

So,  $f(b_m) = (f_1(b_m), f_2(b_m), f_3(b_m), f_4(b_m))^T < 0$ . Applying Theorem 6 in [19] with  $a = 0$  and  $b = b_m$ , we obtain that (3.12) defines a dynamical system on  $[0, b_m]$ . However,  $b_m$  can be selected larger than any  $X \in \mathbb{R}_+^{4n}$ . Thus, (3.12) defines a dynamical system on  $\Omega = \mathbb{R}_+^{4n}$ . The only equilibrium point in  $\Omega$  is the trivial equilibrium  $\mathcal{P}_0$ . It follows from Theorem 6 in [19] that  $\mathcal{P}_0$  is globally asymptotically stable on  $[0, b_m]$  for any  $m > 0$ , and therefore is globally asymptotically stable on  $\Omega = \mathbb{R}_+^{4n}$ .  $\square$

d) *Nontrivial (mosquito-persistent) equilibrium point and its stability*

In this paragraph, we begin by showing that system (3.12) has a unique nontrivial equilibrium point when  $\mathcal{R}_0^{(m)} > 1$ . To achieve our goal, we reformulate the problem in terms of fixed point problem and use Theorem 2.1 in [20] for the existence and uniqueness of a positive fixed point of a multi-variable function. To be self contained, Theorem 2.1 in [20] is recalled hereafter.

**Theorem 3.7 ([20], Theorem 2.1).** *Let  $F(x)$  be a continuous, monotone non-decreasing, strictly sublinear, bounded function which maps the non-negative orthant  $\mathbb{R}_+^n$  into itself. Let  $F(0) = 0$  and  $F'(0)$  exists and be irreducible. Then  $F(x)$  does not have a nontrivial fixed point on the boundary of  $\mathbb{R}_+^n$ . Moreover,  $F(x)$  has a positive fixed point iff  $\rho(F'(0)) > 1$ . If there is a positive fixed point, then it is unique.*

An equilibrium point  $\mathcal{P}^* = (X_A^*, X_Y^*, X_M^*, X_F^*)$  for system (3.12) satisfies the following system of equations

$$\begin{cases} \Phi X_F^* - [\gamma + \mu_1 + \mu_2 \text{diag}(X_A^*)] X_A^* = 0, \\ r\gamma X_A^* - [(\beta + \mu_Y) + D_Y] X_Y^* + D_Y C X_Y^* = 0, \\ (1-r)\gamma X_A^* - [\mu_M + D_M] X_M^* + D_M C X_M^* = 0, \\ \beta X_Y^* - [\mu_F + D_F] X_F^* + D_F C X_F^* = 0. \end{cases} \quad (3.22)$$

Solving (3.22) yields

$$\begin{aligned} X_F^* &= \frac{[\gamma + \mu_1 + \mu_2 \text{diag}(X_A^*)] X_A^*}{\Phi}, \\ X_Y^* &= \frac{(\mu_F I_n + D_F I_n - D_F C)[\gamma + \mu_1 + \mu_2 \text{diag}(X_A^*)] X_A^*}{\beta \Phi}, \\ X_M^* &= \frac{(1-r)\gamma}{\mu_M + D_M} \left[ I_n + \frac{D_M}{\mu_M} C \right] X_A^*. \end{aligned} \quad (3.23)$$

Replacing (3.23) in the second equation of system (3.22), one obtain

$$r\gamma \left[ I_n - \frac{N_1 N_4 [\gamma + \mu_1 + \mu_2 \text{diag}(X_A^*)]}{\beta \Phi r \gamma} \right] X_A^* = 0.$$

Hence, the existence of the nontrivial equilibrium point is reformulated as the following fixed point problem: Find a unique positive  $X_A^*$  such that  $X_A^* = F(X_A^*)$ , where

$$F(X_A^*) = r\beta\gamma\Phi \left[ \gamma + \mu_1 + \mu_2 \text{diag}(X_A^*) \right]^{-1} N_4^{-1} N_1^{-1} X_A^*.$$

Notice that  $F$  is a continuous, bounded function that maps  $\mathbb{R}_+^n$  into itself and it is infinitely differentiable.

Let us prove that  $F$  is strictly sublinear in  $\mathbb{R}_+^n$  i.e.  $F(\nu X_A^*) > \nu F(X_A^*)$ , for any  $X_A^* \in \mathbb{R}_+^n$  with  $X_A^* > 0$ , and  $\nu \in (0, 1)$ . Direct, but lengthy calculations give

$$\nu F(X_A^*) [F(\nu X_A^*)]^{-1} = \text{diag} \left( \frac{\gamma + \mu_1 + \nu \mu_2 \rho_{A,k_1}}{\gamma + \mu_1 + \mu_2 \rho_{A,k_1}}, \dots, \frac{\gamma + \mu_1 + \nu \mu_2 \rho_{A,k_n}}{\gamma + \mu_1 + \mu_2 \rho_{A,k_n}} \right).$$

Since  $\nu \in (0, 1)$ , we have

$$\frac{\gamma + \mu_1 + \nu \mu_2 \rho_{A,k_i}}{\gamma + \mu_1 + \mu_2 \rho_{A,k_i}} < 1, \quad i = 1, 2, \dots, n.$$

Thus,  $\nu F(X_A^*) [F(\nu X_A^*)]^{-1} < I_n$  i.e.  $\nu F(X_A^*) < F(\nu X_A^*)$ . Hence,  $F$  is strictly sublinear.

One can easily check that the off-diagonal elements  $a_{i,j}$  ( $i \neq j$ ) of the matrix  $F'(X_A^*)$  are

$$a_{ij} = \frac{\Gamma(b_0 + c_0 + d_0) k_i p(k_j)}{\langle k \rangle (\gamma + \mu_1 + \mu_2 \rho_{A,k_i})} > 0, \quad \forall i \neq j \in \{1, 2, \dots, n\}.$$

Thus,  $F$  is a monotone non-decreasing function. We have also that  $F(0) = 0$  and  $F'(0) = \Gamma(a_0 I_n + (b_0 + c_0 C + d_0) C)$ . Therefore  $\rho(F'(0)) = \mathcal{R}_0^{(m)} > 1$  iff  $\mathcal{R}_0^{(m)} > 1$ . Thanks to the graph theory and the irreducibility of the matrix  $C$ ,  $F'(0)$  is irreducible because its associated graph is strongly connected. Thus, we have established the following theorem :



**Theorem 3.8.** If  $\mathcal{R}_0^{(m)} \leq 1$ , the only equilibrium point of the system is the trivial equilibrium  $\mathcal{P}_0$ . If  $\mathcal{R}_0^{(m)} > 1$  there also exists a unique nontrivial (mosquito-persistent) equilibrium point  $\mathcal{P}^*$  in  $\text{int}(\Omega)$ .

By Lemma 3.5, the trivial equilibrium point  $\mathcal{P}_0$  is unstable whenever  $\mathcal{R}_0^{(m)} > 1$ . We terminate this section by proving the following result which establishes the global stability of the nontrivial equilibrium.

**Theorem 3.9.** If  $\mathcal{R}_0^{(m)} > 1$ , the nontrivial (mosquito-persistent) equilibrium  $\mathcal{P}^*$  of the system (3.12) is GAS on  $\Omega$ .

*Proof:* Since  $\mathcal{R}_0^{(m)} > 1$ , the inequalities

$$\frac{\gamma + \mu_1 + \mu_2 \rho_{A, k_i}}{\gamma + \mu_1} < \frac{\mathcal{R}_0^{(m)} k_i p(k_i) + \Gamma \sum_{j=1, j \neq i}^n k_j p(k_j)}{\sqrt{\mathcal{R}_0^{(m)}} \langle k \rangle}, \quad i = 1, 2, \dots, n, \quad (3.24)$$

hold for all sufficiently small values  $X_A$ . Let  $\varepsilon = (\varepsilon_1, \varepsilon_2, \dots, \varepsilon_n) > 0$  and let  $X_{A_\varepsilon}$  be so small that in addition to (3.24) the following inequalities also hold :

$$X_{A_\varepsilon} \leq \varepsilon, \quad (3.25)$$

$$X_{F_\varepsilon} := \frac{\sqrt[4]{\mathcal{R}_0^{(m)}} (\gamma + \mu_1 + \mu_2 \text{diag}(X_{A_\varepsilon})) X_{A_\varepsilon}}{\Phi} \leq \varepsilon, \quad (3.26)$$

$$X_{Y_\varepsilon} := \frac{\sqrt[4]{\mathcal{R}_0^{(m)}} (\mu_F I_n + D_F I_n - D_F C) X_{F_\varepsilon}}{\beta} \leq \varepsilon, \quad (3.27)$$

$$X_{M_\varepsilon} := \frac{(1-r)\gamma}{\sqrt[4]{\mathcal{R}_0^{(m)}} (\mu_M + D_M)} \left[ I_n + \frac{D_M C}{\mu_M} \right] X_{A_\varepsilon} \leq \varepsilon. \quad (3.28)$$

Let  $a_\varepsilon = (X_{A_\varepsilon}, X_{Y_\varepsilon}, X_{F_\varepsilon}, X_{M_\varepsilon})^T$ . Then, one has

$$f_1(a_\varepsilon) = \left( 1 - \frac{1}{\sqrt[4]{\mathcal{R}_0^{(m)}}} \right) \Phi X_{F_\varepsilon} > 0; \quad f_3(a_\varepsilon) = \frac{(\sqrt{\mathcal{R}_0^{(m)}} - 1)(1-r)\gamma}{\sqrt{\mathcal{R}_0^{(m)}}} X_{A_\varepsilon} > 0;$$

$$f_4(a_\varepsilon) = \left( 1 - \frac{1}{\sqrt[4]{\mathcal{R}_0^{(m)}}} \right) \beta X_{Y_\varepsilon} > 0;$$

$$\begin{aligned} f_2(a_\varepsilon) &= r\gamma \left[ I_n - \frac{\sqrt{\mathcal{R}_0^{(m)}} (N_1^{-1})^{-1} (N_4^{-1})^{-1} [\gamma + \mu_1 + \mu_2 \text{diag}(X_{A_m})]}{\beta \Phi r \gamma} \right] X_{A_m}, \\ &= r\gamma \left[ I_n - \frac{\sqrt{\mathcal{R}_0^{(m)}} (a_0 I_n + b_0 I_n C + c_0 I_n C + d_0 I_n C)^{-1} [\gamma + \mu_1 + \mu_2 \text{diag}(X_{A_m})]}{\Gamma} \frac{\gamma + \mu_1 + \mu_2 \text{diag}(X_{A_m})}{\gamma + \mu_1} \right] X_{A_m} \\ &> 0 \quad \text{if} \quad \frac{\Gamma (a_0 I_n + b_0 I_n C + c_0 I_n C + d_0 I_n C)}{\sqrt{\mathcal{R}_0^{(m)}}} > \frac{\gamma + \mu_1 + \mu_2 \text{diag}(X_{A_m})}{\gamma + \mu_1}, \end{aligned}$$

i.e.

$$f_2(a_\varepsilon) > 0 \quad \text{if} \quad \frac{\gamma + \mu_1 + \mu_2 \rho_{A, k_i}}{\gamma + \mu_1} < \frac{\mathcal{R}_0^{(m)} k_i p(k_i) + \Gamma \sum_{j=1, j \neq i}^n k_j p(k_j)}{\sqrt{\mathcal{R}_0^{(m)}} \langle k \rangle}, \quad i = 1, 2, \dots, n.$$

Thus,  $f(a_\varepsilon) = (f_1(a_\varepsilon), f_2(a_\varepsilon), f_3(a_\varepsilon), f_4(a_\varepsilon))^T > 0$ . Applying once again Theorem 6 in [19] (with  $a = a_\varepsilon$  and  $b = b_m$ ), we obtain that the nontrivial equilibrium point  $\mathcal{P}^*$  is globally asymptotically stable on  $[a_\varepsilon, b_m]$ . Since  $a_\varepsilon$  can be selected to be smaller than any  $X > 0$  and  $b_m$  can be selected to be larger than any  $X > 0$ , we obtain that  $\mathcal{P}^*$  is asymptotically stable on  $\Omega = \mathbb{R}_+^{4n}$  with basin of attraction being at least the interior of  $\Omega$ .  $\square$

### 3.3. The metapopulation model in a heterogeneous landscape

Differences in the distribution of resources create heterogeneity on the network, since patches may have different degrees of attractiveness to mosquitoes. According to [5] we describe how heterogeneity and differences in patch attractiveness to mosquitoes during movement is incorporated. Here, each patch represent a potential breeding-feeding site. The number of hosts is allowed to differ between patches across the local network, introducing heterogeneity. Heterogeneity of breeding sites is incorporated here by taking different values for parameter  $\mu_2$  in each patch. In this case, the carrying capacities of breeding sites would be different.

Let  $H$  be the total population of hosts in the network and  $H_k$  the population of hosts in patches of degree  $k$ . The proportion of hosts in patches of degree  $k$  is

$$\bar{H}_k = \frac{H_k}{H}, \quad \text{with} \quad \sum_k \bar{H}_k = 1. \quad (3.29)$$

Mosquitoes are attracted to odors released by hosts, this leads to mosquitoes being less likely to leave the patch if their current patch is a home to many hosts and more likely to move out of the patch if there are few hosts [26, 30]. As in [5], we mimic this phenomenon by using a decreasing exponential function to model the movement rate. We assume that heterogeneity of hosts also influence the males dispersal because females go to the hosts for blood-meal and males go to meet females [31]. Note that immature females are not subjected to the attraction of hosts, they diffuse randomly in any direction. We also incorporate the spatial proximity of patches by using a decreasing linear function, since mosquitoes have a limited mobility. Hence, we can define the diffusion rate along any given link of a patch of degree  $k$  to a patch of degree  $k'$  as

$$D_{kk'} = \frac{D_Y \psi(d_{kk'})}{k} \quad \text{and} \quad D_{kk'} = \frac{D_i \psi(d_{kk'})}{k} e^{-\lambda(\bar{H}_k - \bar{H}_{k'})}, \quad i = M, F, \quad (3.30)$$

where  $\lambda$  is a constant parameter for the decay function,  $d_{kk'} = \sqrt{(x_k - x_{k'})^2 + (y_k - y_{k'})^2}$  is the cartesian distance between a node of degree  $k$  and a node of degree  $k'$ ;  $\psi$  the distance function defined as

$$\psi(d_{kk'}) = \begin{cases} \frac{d_{max} - d_{kk'}}{d_{max}} & \text{if } d_{kk'} < d_{max}, \\ 0 & \text{else,} \end{cases} \quad (3.31)$$

with  $d_{max}$  the maximal mobility distance.

Thus, the equations governing the spatio-temporal evolution of anopheles mosquitoes in this case for

a  $n$ -patches in an uncorrelated network are giving by the system below:

$$\left\{ \begin{array}{l} \dot{\rho}_{A,k} = \Phi_k \rho_{F,k} - (\gamma_k + \mu_{1k} + \mu_{2k} \rho_{A,k}) \rho_{A,k}, \\ \dot{\rho}_{Y,k} = r \gamma_k \rho_{A,k} - (\beta_k + \mu_{Y,k}) \rho_{Y,k} - \frac{D_Y}{\langle k \rangle} \left( \sum_{k'} k' p(k') \psi(d_{kk'}) \right) \rho_{Y,k} + \frac{k D_Y}{\langle k \rangle} \sum_{k'} p(k') \psi(d_{kk'}) \rho_{Y,k'}, \\ \dot{\rho}_{M,k} = (1-r) \gamma_k \rho_{A,k} - \mu_{M,k} \rho_{M,k} - \frac{D_M}{\langle k \rangle} \left( \sum_{k'} e^{-\lambda(\bar{H}_k - \bar{H}_{k'})} k' p(k') \psi(d_{kk'}) \right) \rho_{M,k} \\ \quad + \frac{k D_M}{\langle k \rangle} \sum_{k'} e^{-\lambda(\bar{H}_{k'} - \bar{H}_k)} p(k') \psi(d_{kk'}) \rho_{M,k'}, \\ \dot{\rho}_{F,k} = \beta_k \rho_{Y,k} - \mu_{F,k} \rho_{F,k} - \frac{D_F}{\langle k \rangle} \left( \sum_{k'} e^{-\lambda(\bar{H}_k - \bar{H}_{k'})} k' p(k') \psi(d_{kk'}) \right) \rho_{F,k} \\ \quad + \frac{k D_F}{\langle k \rangle} \sum_{k'} e^{-\lambda(\bar{H}_{k'} - \bar{H}_k)} p(k') \psi(d_{kk'}) \rho_{F,k'}, \end{array} \right. \quad (3.32)$$

From Theorem 3.1 above, one can easily see that (3.32) is a dynamical system in  $\mathbb{R}_+^{4n}$ . A patch of degree  $k$  is at a mosquito-free equilibrium point if  $\rho_{A,k} = \rho_{Y,k} = \rho_{M,k} = \rho_{F,k} = 0$ . However, given the complexity of the equations, we do not perform further theoretical analysis for model (3.32). We shall rather focus on numerical analysis in the next section.

#### 4. Numerical simulations

To illustrate the various theoretical results of the previous sections, we consider a metapopulation network with five patches and the following connectivities:  $k_1 = 2$ ;  $k_2 = 3$ ;  $k_3 = 4$ ;  $k_4 = 1$  and  $k_5 = 2$  (see Figure 3). Since we do not know what trajectories mosquitoes adopt in reality, we use strategies such

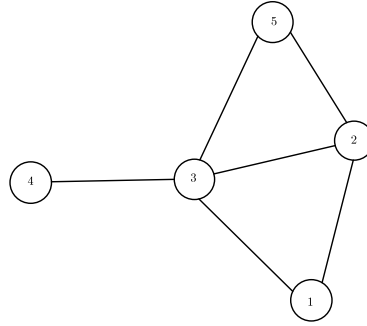


Figure 3: An example of a network with five patches.

as Levy-flight (which are comprised of random sequences of movement-segments with lengths  $l$  drawn from a probability distribution function having a power-law tail  $p(l) \sim l^{-\mu}$  where  $1 < \mu \leq 3$ ) to optimize foraging efficiency [32]. Thus, we consider an architecture network given by the distribution  $p(k) \sim k^{-3}$  [12, 13].

Models (3.12) and (3.32) are both simulated by using data from recent works. These data are summarized in Table 1. As far as mosquito dispersal is concerned, some studies have shown that daily flights range from 200 to 400 m, where the maximum distance recorded is 661 m [33]. We run all simulations with the following initial conditions: the total number mosquitoes in aquatic stages is 1500, 1000 young mosquitoes are females not yet laying eggs, 1000 are males, while 1250 are fertilized and eggs laying females. They are evenly distributed across the network.

##### 4.1. General dynamics

In this subsection, we numerically illustrate the asymptomatic behavior of model (3.12). For that, we consider a network of metapopulation with five patches. The dynamics of all compartments are very

similar to each other. Hence, only the graphs of mosquitoes at the aquatic stage and total flying mosquito population (that is,  $Y + M + F$ ) are presented here.

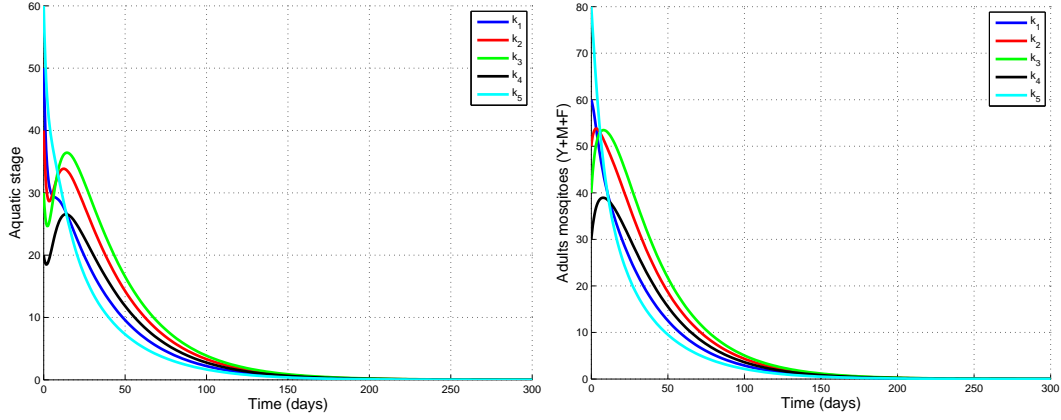


Figure 4: Simulation results showing the GAS of the trivial equilibrium  $\mathcal{P}_0$  for the basic model when  $\Phi = 0.5$ ,  $D_Y = D_M = D_F = 0.1$  and  $\mathcal{R}_0^{(m)} \leq 1$ . All other parameters are as in Table 1.

Figure 4 presents the trajectories of model (3.12) for all patches when  $\Phi = 0.5$ ,  $D_Y = D_M = D_F = 0.1$  and the basic offspring number  $\mathcal{R}_0^{(m)}$  is less than one ( $\mathcal{R}_0^{(m)} = 0.6531$ ). From this figure, we can see that the mosquito populations die out in all patches. Thus, the trajectories converge to the trivial equilibrium as shown in Theorem 3.6.

Figure 5 plots the trajectories of system (3.12) when  $\Phi = 10$ ,  $D_Y = D_M = D_F = 0.1$  and the basic offspring number  $\mathcal{R}_0^{(m)}$  is greater than one ( $\mathcal{R}_0^{(m)} = 13.0612$ ). This illustrates the fact that the mosquitoes are always present in all patches and the trajectories converge to the nontrivial equilibrium as established in Theorem 3.9.

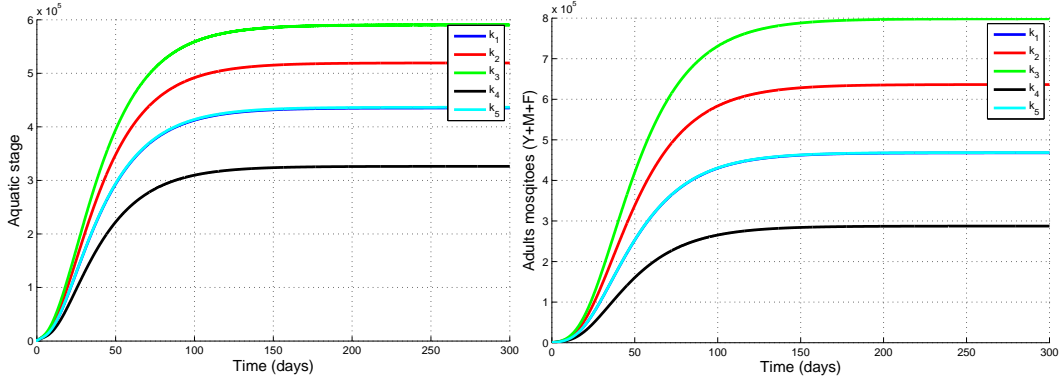


Figure 5: Simulation results showing the GAS of the nontrivial equilibrium  $\mathcal{P}^*$  when  $\Phi = 10$ ,  $D_Y = D_M = D_F = 0.1$  and  $\mathcal{R}_0^{(m)} > 1$ . All other parameters are as in Table 1.

#### 4.2. Impact of dispersal on population dynamics

To evaluate the impact of dispersal on population dynamics, we carry out in Figure 6 numerical simulations (when  $\Phi = 10$ ) on system (3.12) both without and with dispersal. This figure shows that persistence of mosquito population is more important in the presence of dispersal than in the case without dispersal, especially in high-degree patches.

#### 4.3. Impact of the heterogeneous connectivity of patches on population dynamics

To investigate the significance of heterogeneous connectivity of patches on vector population dynamics, system (3.12) is simulated in Figure 7 with variable degree of patches.

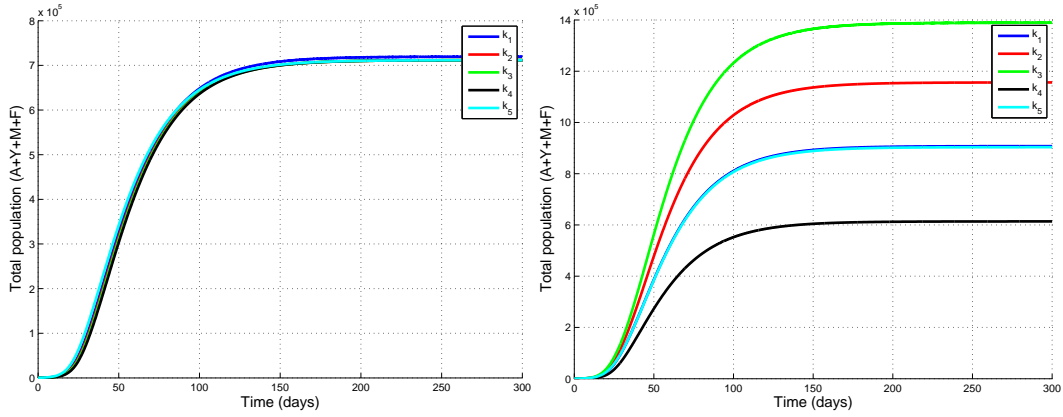


Figure 6: Trajectories plots of model (3.12) without dispersal (left) and with dispersal (right) when  $\Phi = 10$ : the total mosquito population increases as the diffusion coefficients increase.

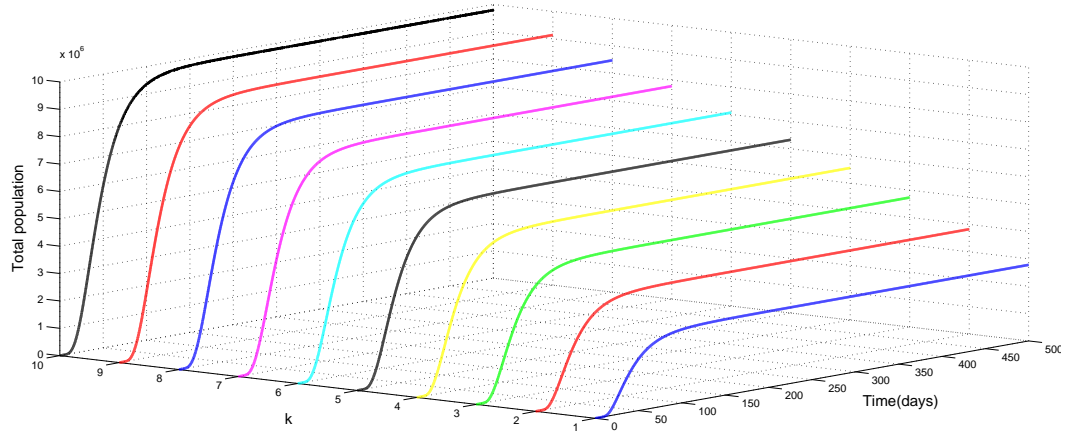


Figure 7: Mosquito population in patches of degree  $k = 1, 2, \dots, 10$ , when  $\Phi = 10$  and  $D_M = D_Y = D_F = 0.1$ : the total mosquito population increases as the patch connectivity increases.

Figure 7 illustrates the fact that, with the same diffusion coefficients ( $D_M = D_Y = D_F$ ), the total mosquito population increases as the connectivity of the patch increases. This suggests that the heterogeneous connectivity of patches play an important role on vector population dynamics. This heterogeneity may come from the daily productivity and destruction of some breeding sites, since small pools of water are continually destroyed and reformed [4].

#### 4.4. Impact of migration and heterogeneity on mosquito spread

In this section, numerical simulations are carried out to investigate the role of dispersal/diffusion and heterogeneity on mosquito spread. Models (3.12) and (3.32) are both simulated with different values of  $\Phi$  in each patch. In order to observe more effects of the migration on the dynamics of model (3.12) and (3.32), we consider the hypothetical scenario where the mosquito-persistent equilibrium is GAS in the patch of minimal degree (patch 4) and unstable in the other patches (patch 1, 2, 3, 5). Model (3.32) is simulated with  $\bar{H}_{k_1} = 0.6, \bar{H}_{k_2} = 0.07, \bar{H}_{k_3} = 0.06, \bar{H}_{k_4} = 0.03, \bar{H}_{k_5} = 0.24, d_{\max} = 661$  m and  $\lambda = 0.5$ . Let  $\mathcal{R}_0^{(i)}$ ,  $i = 1, 2, 3, 4, 5$ , denotes the basic offspring number for the local population of anopheles mosquito in patch  $i$  as defined in (2.3). Choose  $\Phi_1 = \Phi_2 = \Phi_3 = \Phi_5 = 0.5, \Phi_4 = 10$  so that  $\mathcal{R}_0^{(1)} = \mathcal{R}_0^{(2)} = \mathcal{R}_0^{(3)} = \mathcal{R}_0^{(5)} = 0.5714 < 1$  and  $\mathcal{R}_0^{(4)} = 11.4286 > 1$ . It is observed from Figure 8 that, in the absence of migration/diffusion (i.e.  $D_M = D_Y = D_F = 0$ ), the mosquito-persistent equilibrium point is unstable in patches 1, 2, 3, 5 and stable in the fourth patch, as expected.

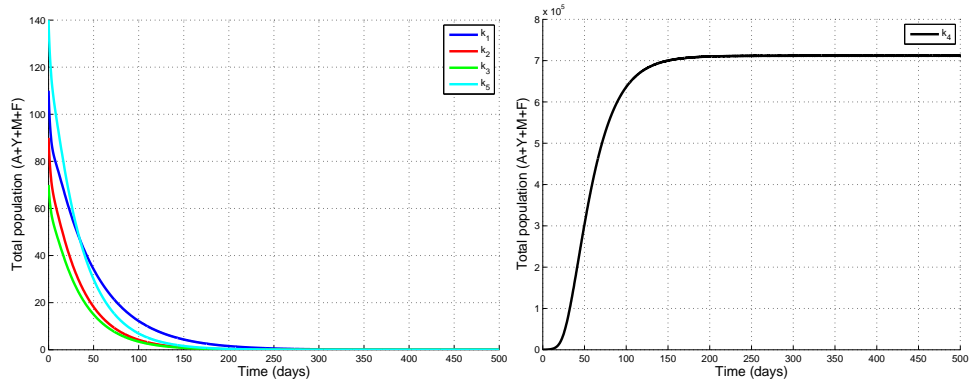


Figure 8: Simulation results of systems (3.12) and (3.32) showing the mosquito population in mosquito-free patches (left) and mosquito-persistent patch (right) in absence of migration.  $\mathcal{R}_0^{(i)} < 1$ ,  $i = 1, 2, 3, 5$  and  $\mathcal{R}_0^{(4)} > 1$ . All other parameters are as in Table 1.

Figures 9-12 present the mosquito spread from an mosquito-persistent patch (patch 4) to mosquito-free patches (patches 1, 2, 3, 5) under different scenario when  $D_M = D_Y = D_F = 0.1$ .

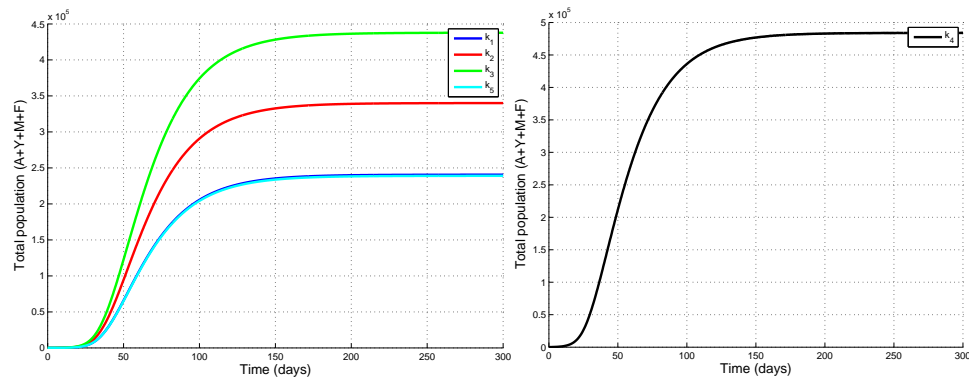


Figure 9: Simulation result showing the mosquito spread from mosquito-persistent patch (right) to mosquito-free patches (left) in a homogeneous landscape (Eq. 3.12) with  $D_M = D_Y = D_F = 0.1$  and all other parameters are as in Table 1.  $\mathcal{R}_0^{(i)} < 1$ ,  $i = 1, 2, 3, 5$  and  $\mathcal{R}_0^{(4)} > 1$ .

Observing these latter figures, one can see that in the presence of dispersal, mosquitoes moving out of an mosquito-persistent patch (patch 4) migrate into the mosquito-free patches (patches 1, 2, 3, 5). This illustrates the fact that mosquito dispersal could lead to a larger presence of mosquitoes in all patches and, shows the important effects of dispersal and connectivity of patches on population spread. However, this diffusion varies according to the type of landscape.

#### 4.4.1. Dispersal in a homogeneous landscape

Figure 9 presents the trajectories of the mosquito spread from mosquito-persistent patch (right) to mosquito-free patches (left) in a homogeneous landscape (Eq. (3.12)). We observe in this case that mosquitoes coming from mosquito-persistent patch (patch 4) migrate more to the high-degree patches (see patches 3 and 2) and equitably to the patches with equal degree (see patches 1 and 5).

#### 4.4.2. Dispersal in a heterogeneous landscape

Figure 10 gives numerical solutions of model (3.32), depicting the mosquito spread from mosquito-persistent patch (right) to non mosquito-persistent patches (left) in a heterogeneous landscape (heterogeneity of hosts and homogeneity of breeding sites), when distance has no effect on mosquito flights (i.e.  $\psi(d_{kk'}) = 1, \forall k, k'$ ). Even though a great number of mosquitoes moves into the patches of high degree, the dispersal becomes more important in the patches with more hosts.



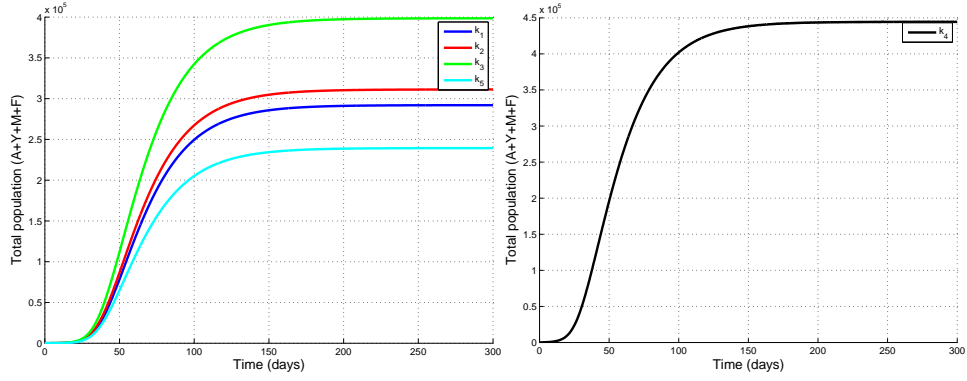


Figure 10: Simulation results showing the mosquito spread from mosquito-persistent patch (right) to mosquito-free patches (left) in a heterogeneous landscape (heterogeneity of hosts and homogeneity of breeding sites) with  $\psi(d_{kk'}) = 1, \forall k, k', D_M = D_Y = D_F = 0.1$  and all other parameters are as in Table 1.  $\mathcal{R}_0^{(i)} < 1, i = 1, 2, 3, 5$  and  $\mathcal{R}_0^{(4)} > 1$ .

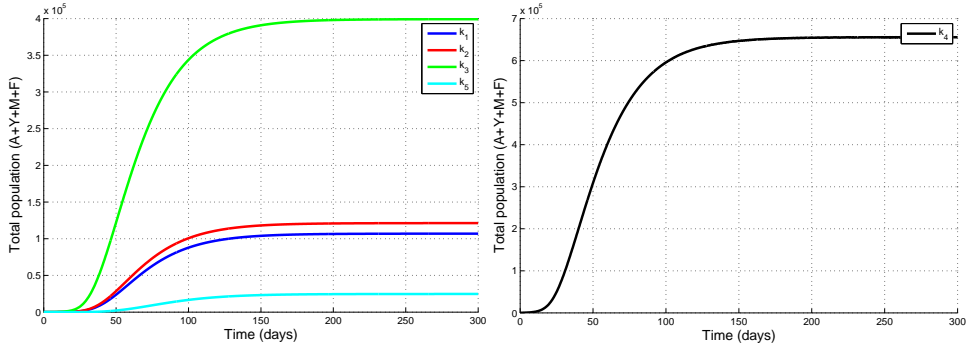


Figure 11: Simulation results showing the mosquito spread from mosquito-persistent patch (right) to non mosquito-persistent patches (left) in a heterogeneous landscape (heterogeneity of hosts and homogeneity of breeding sites) with  $\psi(d_{kk'})$  as in (3.31),  $D_M = D_Y = D_F = 0.1$  and all other parameters are as in Table 1.  $\mathcal{R}_0^{(i)} < 1, i = 1, 2, 3, 5$  and  $\mathcal{R}_0^{(4)} > 1$ .

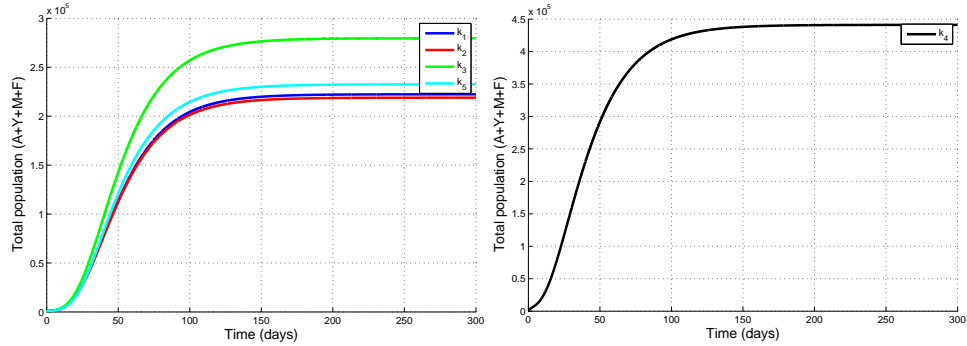


Figure 12: Simulation result showing the mosquito spread from mosquito-persistent patch (right) to non mosquito-persistent patches (left) in a heterogeneous landscape (heterogeneous hosts and breeding sites) with  $\psi(d_{kk'}) = 1, \forall k, k', \mu_{21} = 10^{-4}, \mu_{22} = 10^{-3}, \mu_{23} = 10^{-2}, \mu_{24} = 10^{-5}, \mu_{25} = 10^{-5}$  and  $D_M = D_Y = D_F = 0.1 D_M = D_Y = D_F = 0.1$ .  $\mathcal{R}_0^{(i)} < 1, i = 1, 2, 3, 5$  and  $\mathcal{R}_0^{(4)} > 1$ .

Figure 11 simulates the solutions of model (3.32) and displays the mosquito spread from mosquito-persistent patch (right) to non mosquito-persistent patches (left) in a heterogeneous landscape (heterogeneity of hosts and homogeneity of breeding sites), when distance affects mosquito dispersal (i.e.  $\psi(d_{kk'})$  as in (3.31), with  $d_{k_3k_4} = 300$  m,  $d_{k_5k_1} = 370$  m,  $d_{k_3k_1} = 361$  m,  $d_{k_3k_2} = 361$  m,  $d_{k_3k_5} = 400$  m,  $d_{k_2k_5} = 380$  m). As in the latter Figure 10, similar result is observed, with the difference in that the mosquito dispersal from mosquito-persistent patch (patch 4) to mosquito-free patches (patches 1, 2, 3 and 5) is less important in this case.

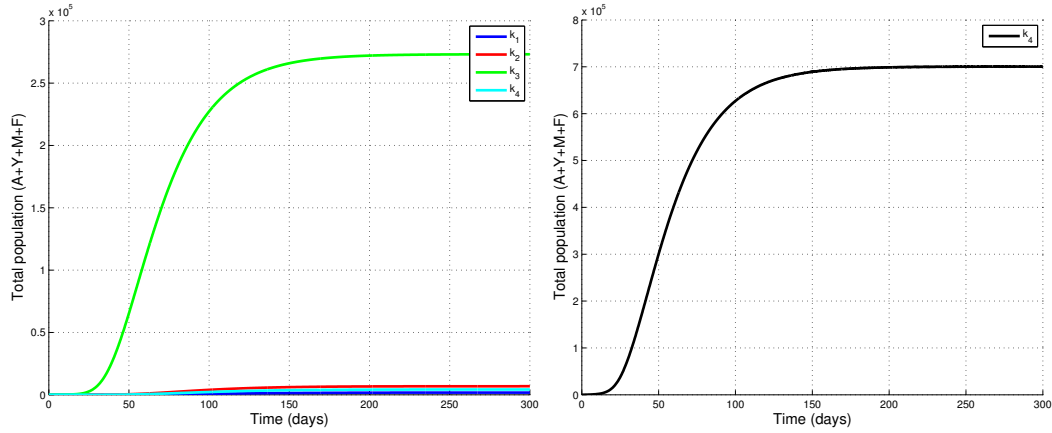


Figure 13: Simulation result showing the mosquito spread from mosquito-persistent patch (right) to non mosquito-persistent patches (left) (heterogeneity of hosts and homogeneity of breeding sites) with  $\psi(d_{kk'})$  as in (3.31), when distances between patches 1, 2, 3, 5 are large.

Figure 12 presents the simulation results of model (3.32), showing the mosquito spread from mosquito-persistent patch (right) to mosquito-free patches (left) in a heterogeneous landscape (heterogeneity of hosts and breeding sites), with  $\mu_{21} = 10^{-4}$ ,  $\mu_{22} = 10^{-3}$ ,  $\mu_{23} = 10^{-2}$ ,  $\mu_{24} = 10^{-5}$ ,  $\mu_{25} = 10^{-5}$  and  $\psi(d_{kk'}) = 1, \forall k, k'$ . From this figure, it is noticeable that heterogeneity of hosts and breeding sites greatly influences the mosquito dispersal and their spatial distribution. This suggests that the heterogeneous connectivity of patches and heterogeneous distribution of hosts and breeding sites may play an important role on the spatial distribution of mosquitoes.

Figure 13 simulates model (3.32) and shows that the mosquito spread from mosquito-persistent patch (right) to mosquito-free patches (left) in a heterogeneous landscape (heterogeneity of hosts and homogeneity of breeding sites), with  $\psi(d_{kk'})$  as in (3.31) when patches are highly distanced from each other and close to the maximal distance  $d_{max}$  between nodes ( $d_{k_3k_4} = 500$  m,  $d_{k_5k_1} = 510$  m,  $d_{k_3k_1} = 589$  m,  $d_{k_3k_2} = 539$  m,  $d_{k_3k_5} = 400$  m,  $d_{k_2k_5} = 539$  m). From this figure, one observe that mosquito migration rate to distant patches is very low. This is coherent with the known preference of the mosquito dispersal: indeed, according to [34] the dispersal of adult mosquitoes can be classified into long-range and short-range dispersals. Long-range dispersal is often unintentional and aided by wind or human transport while short-range dispersal is often intentional. Furthermore, Figure 13 shows that the availability and abundance of sites have a strong influence on the distance that individual adult female mosquitoes need to fly in order to lay their eggs, since spatial distance between patches is large when breeding sites are eliminated from neighborhoods of hosts or are not available in most patches. Similar findings were obtained in [23]. Thus, more efforts to reduce breeding sites in close proximity to houses (mechanical control) is needed and can be very efficient as a vector control strategy.

Our simulations results in homogeneous landscape (Eq. 3.12) and heterogeneous landscape (Eq. 3.32) reveal that the heterogeneous connectivity of patches plays an important role on the spatial distribution of mosquito population. Simulations in a homogeneous landscape indicate that there is a linear relationship between connectivity of patches and mosquitoes distribution (see Figures 6 and 9). However, when there are heterogeneities in the network (hosts, distances), this linear relationship is perturbed and induces a strong influence on spatial distribution and population dynamics of mosquitoes (see Figures 10-13).

## 5. Conclusion and perspectives

In this paper, we have developed a reaction-diffusion type model to describe the spatial evolution of anopheles mosquito in heterogeneous complex metapopulations and assess the influences of larvae

habitats (breeding-feeding sites) connectivity and vector on the spatial distribution and populations dynamics of mosquitoes. We have focused on the migration of mosquitoes from one patch to another in both homogeneous and heterogeneous landscapes. The spatial configuration was given by the degree  $p(k)$  and the conditional probabilities  $P(k'/k)$ .

For uncorrelated networks in a homogeneous landscape, we have derived an explicit formula for the basic offspring number,  $\mathcal{R}_0^{(m)}$ , which has been proven to be a sharp threshold parameter for our model. The most influential parameter on the expression for  $\mathcal{R}_0^{(m)}$  is the number of eggs at each deposit  $\Phi$ . Using the theory of monotone operators, we have established the global stability of equilibrium points. Precisely, we have shown that the mosquito-free equilibrium is GAS whenever  $\mathcal{R}_0^{(m)} \leq 1$  and unstable otherwise. In the case where  $\mathcal{R}_0^{(m)} > 1$ , we have shown that there exists a unique mosquito-persistent equilibrium, which is GAS.

For uncorrelated networks in a heterogeneous landscape, we have only carried out numerical studies. Comparing our simulation results in Figures 6-12, we have concluded that numerous factors considered in our models play important roles in spatial distribution of mosquitoes and could lead to a larger amount of mosquitoes. Further, our sensitivity analysis results have revealed that an efficient strategy to reduce the amount of mosquitoes in all patches could be to control the production of eggs (by mechanical control for example) and minimize the migration of female mosquitoes.

To summarize our contributions in few words, the methodology and results we have obtained are as follows:

- From the modeling perspective, we have extended to a complex network of patches the single patch models in [4, 19] by incorporating the dispersal of mosquitoes and patch connectivity.
- From the theoretical and numerical perspectives, we have examined the impacts of larval habitat connectivity and mosquito dispersal in a homogeneous and a heterogeneous landscapes on the persistence of mosquitoes populations.
- From the qualitative and quantitative aspects for uncorrelated networks we have obtained the following analytical results:
  1. The bifurcation/threshold parameter (basic offspring number) has been explicitly computed.
  2. The sensitivity analysis of the threshold parameter has been performed.
  3. A simple and digestive proof based on Hethcote-Thieme fixed point theorem [20], of a unique mosquito-persistent equilibrium has been provided.
  4. Contrary to the few existing works where, Lyapunov-LaSalle techniques are usually used, the monotone operator approach [21] has been the main ingredient here, for the establishment of the global asymptotic stability of both mosquito-free and mosquito-persistent equilibria.

An immediate possible extension of this work we are already working on is to consider correlated networks with precise configuration/distribution of patches (i.e., some assortative or disassortative networks) and investigate if the techniques used here could be applied to obtain similar theoretical/analytical results. Moreover, since we take into account the male dispersal, another extension of this work could be to consider the Sterile Insect Technique (SIT) in our model by releasing sterilized male mosquitoes near of high-degree patches. We hope our model could be used to develop other possible and efficient vector control strategies, which can optimize the allocation of scarce resources.

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## Appendixes

### Appendix A: Proof of Lemma 3.2

Note that the matrix  $N$  can be written as

$$N = \begin{bmatrix} N_1 & N_2 \\ N_3 & N_4 \end{bmatrix} = \begin{bmatrix} N_1 & \mathbf{0} \\ N_3 & I \end{bmatrix} \begin{bmatrix} I & N_1^{-1}N_2 \\ \mathbf{0} & D \end{bmatrix}.$$

Then, one can deduce that

$$\begin{aligned} N^{-1} &= \begin{bmatrix} I & N_1^{-1}N_2 \\ \mathbf{0} & D \end{bmatrix}^{-1} \begin{bmatrix} N_1 & \mathbf{0} \\ N_3 & I \end{bmatrix}^{-1} = \begin{bmatrix} I & -N_1^{-1}N_2D^{-1} \\ \mathbf{0} & D^{-1} \end{bmatrix} \begin{bmatrix} N_1^{-1} & \mathbf{0} \\ -N_3N_1^{-1} & I \end{bmatrix}, \\ &= \begin{bmatrix} N_1^{-1} + N_1^{-1}N_2D^{-1}N_3N_1^{-1} & -N_1^{-1}N_2D^{-1} \\ -D^{-1}N_3N_1^{-1} & D^{-1} \end{bmatrix}. \end{aligned}$$

This ends the proof. □

### Appendix B: Proof of Lemma 3.3

It suffices to verified that  $GG^{-1} = I_n$ . Indeed, one has

$$\begin{aligned} GG^{-1} &= UU^{-1} - K[W^{-1} + ZU^{-1}X]^{-1}ZU^{-1} + KWZU^{-1} \\ &\quad - KWZU^{-1}K[W^{-1} + ZU^{-1}K]^{-1}ZU^{-1}, \\ &= I_n - K\left[[W^{-1} + ZU^{-1}K]^{-1} + W - WZU^{-1}K[W^{-1} + ZU^{-1}K]^{-1}\right]ZU^{-1}, \\ &= I_n - KW\left[W^{-1}[W^{-1} + ZU^{-1}K]^{-1} - I_n + ZU^{-1}K[W^{-1} + ZU^{-1}K]^{-1}\right]ZU^{-1}, \\ &= I_n - KW\left[[W^{-1} + ZU^{-1}K][W^{-1} + ZU^{-1}K]^{-1} - I_n\right]ZU^{-1}, \\ &= I_n - KW(I_n - I_n)ZU^{-1}, \\ &= I_n. \end{aligned}$$

This concludes the proof. □