Mathematical Study of Two-Patches of Predator-Prey System with Unidirectional Migration of Prey

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Abstract In this chapter we consider a model describing the dynamics of predator-prey populations living in two patches. The two patches follow the Lotka-Volterra type and are coupled through prey migration. Our purpose is to study the effect of migration rate on the behavior of the coupled systems. We prove the positivity of solutions and find the upper and lower bounds with respect to the migration rate of prey. Also, we show the stability/instability of the possible steady states and we establish the global stability of the positive steady state by giving a candidate lyapunov function. Some numerical simulations are provided to graphically demonstrate the population dynamics of the system.

1 Introduction

One of the oldest and well known mathematical model which describes the interaction between two species predator and prey was introduced by Lotka [1] and Volterra [2], known as Lotka-Volterra mathematical model. The model was given by a system of two differential equations as follows:

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$$\begin{cases} \frac{dx}{dt} = ax - byx \\ \\ \frac{dy}{dt} = -cy + dxy \end{cases} \tag{1}$$

where $x(t)$ and $y(t)$ are the total numbers of prey and predator at time t, respectively, the constants a, b, c and d are nonnegative and the rate $\frac{c}{d}$ is related to the conversion of prey biomass into predator biomass. One weakness of the above model is the exponential growth of the prey in the absence of predator. This is not the case as while the prey continues to grow, space and resources will run out eventually, thereby limiting the growth of the prey population. To handle this case, the predator-prey system (1) can be modified to:

$$\begin{cases} \frac{dx}{dt} = ax - fx^2 - byx \\ \\ \frac{dy}{dt} = -cy + dxy \end{cases} \tag{2}$$

In the last years, this model have been studied in various forms by many authors (see, [3–5]) by changing the functional response, by taking into account the effect of diffusion terms or including the time delay in order to better understanding the dynamics of population interaction or studying the model with different form of functional response (see, [6–10]. Other authors consider some models which describe the interaction between two patches or more by taking into account the effect of the migration of one or two species from one patch to another (see, [11–16] and references therein). The analysis of these models focuses on the existence of possible steady states and their qualitative behavior: local and global stability/instability, bifurcation and when the dynamics of the two interacting patches are synchronous and asynchronous.

In [17], Kuang et al. introduce a model in which a single specie disperses between two patches of a heterogenous environment with barriers between patches and a predator for which the dispersal between patches involve a barrier. The model is given by a system of three ordinary differential equations, and the authors studied the existence of steady states with local and global stability. Also, the uniform persistence is proved and an example of Lotka-Volterra is given in order to prove that the dispersion stabilizes the system when the dispersal rate is small and destabilizes the system when this rate is increased.

In [18], the author introduced a two diffusively coupled predator prey populations. The coupled system is composed of four differential equations that is modelling the interaction of two identical patches in which dynamics are coupled through the migration of individuals of predator population only. This interaction between the predator and prey populations takes the form given by Rosenzweig and MacArthur [19] in which the prey population grows logistically and the predator has a Holling type II functional response. It was shown by numerical simulations that oscillations synchronize for very small migration rate and instability of synchronous oscillations for intermediate migration rate and periodicity, quasi-periodicity, and chaotic attractors with asynchronous dynamics. The existence of attractors in the form of equilibria or limit cycles in which one of the patches contains no prey for large predator migration rates was also proved. The qualitative behavior (stability/instability, numerical simulations) of the possible steady state of this model are studied by Feng et al. [20]. In [21], Feng et al. consider the same model by taking into account the migration of both prey and predator population and studied the stability/instability of the possible steady states.

Recently, Quaglia et al. [22] considered a model of two patches coupled by the migration of both species. The model given by two identical patch with the same reproduction rate and different carrying capacities in each patch. The authors studied the existence and stability of the possible equilibrium points.

At now all the presented coupled patches of predator prey models take into account the migration of one species in one direction (from one patch to another patch only) or in the two directions (mutual migration) and the migration of both species in one direction or in two directions without considering the effect of the migrated (refuged) population on the refuge patch.

In the current chapter we consider two symmetric (identical) patch given by Lotka-Volterra system as follows (before migration):

$$\begin{cases} \frac{dx_i}{dt} = ax_i(1-x_i) - bx_i y_i \\ \frac{dy_i}{dt} = cx_i y_i - dy_i \\ \quad i \in \{1,2\} \end{cases} \tag{3}$$

In the next, we take into account the migration of the prey population from the first patch to the second patch only (in one direction only) with a migration rate k and we consider the contribution of the migrated (refuged) prey population in the growth of the predator population of the refuge patch (second patch). The model is given by a system of four ordinary differential equations as follows:

$$\begin{cases} \frac{dx_1}{dt} = ax_1(1-x_1) - bx_1 y_1 - kx_1 \\ \frac{dy_1}{dt} = cx_1 y_1 - dy_1 \\ \frac{dx_2}{dt} = ax_2(1-x_2) - bx_2 y_2 + kx_1 \\ \frac{dy_2}{dt} = c(x_2 + kx_1)y_2 - dy_2 \end{cases} \tag{4}$$

The chapter is organized as follows. In Sects. 2 and 3 we prove the positivity and boundedness of solutions. In Sects. 4 and 5 we show the existence of possible steady states and their local and global stability, while in Sect. 6, we present some numerical simulations to illustrate the theoretical results.

2 Positivity

Consider now the uncoupled systems (3) which correspond to the case when $k = 0$. By integrating from 0 to t, from the $(3)_1$ and for any initial data $x_{i0} > 0, i = 1, 2$ and $y_{i0} > 0, i = 1, 2$, we have

$$x_i(t) = x_{i0}e^{\int_0^t (a(1-x_i(s))-by_i(s))ds} > 0, i = 1, 2 \tag{5}$$

From the $(3)_2$, we have

$$y_i(t) = y_{i0}e^{\int_0^t (cx_i(s)-d)ds} > 0, i = 1, 2 \tag{6}$$

Then we deduce that for $k = 0$ the uncoupled systems has a positive solution for any positive initial data.

Let us now consider the case when the migration rate is positive ($k > 0$) which corresponds to the coupled system (4). From $(4)_1$ and $(4)_2$, we have

$$x_1(t) = x_{10}e^{\int_0^t (a(1-x_1(s))-by_1(s)-k)ds} > 0 \tag{7}$$

and

$$y_1(t) = y_{10}e^{\int_0^t (cx_1(s)-d)ds} > 0$$

From $(4)_3$,

$$x_2(t) = x_{20}e^{\int_0^t (a(1-x_2(s))-by_2(s))ds} + k\int_0^t e^{\int_s^t (a(1-x_2(u))-by_2(u))du}x_1(s)ds \tag{8}$$

and from (7), we have $x_1(t) > 0, \forall t > 0$. Then, we deduce that $x_2(t) > 0, \forall t > 0$.

3 Boundedness

In this section we focus on the finding of the upper and lower bounds of the predator and prey populations, These bounds will give us information about the extinction, co-existence and exponential behavior of both species. The following comparison argument will be employed in the proofs associated to the upper and lower bounds of species.

Consider the following differential equations

$$\begin{cases} \frac{dx_i}{dt}(t) = f_i(t, x_i(t)), i = 1, 2 \\ x_i(0) = x_{i0}, i = 1, 2 \end{cases} \tag{9}$$

where $f_i, i = 1, 2$ are continuous functions on $[0, T] \times \mathbb{R}$.

Proposition 1 *Let x_1 and x_2 the solution of equations (9) with initial conditions $x_1(0) = x_{10}$ and $x_2(0) = x_{20}$, respectively. Assume that $\frac{\partial f_1}{dx}$ and $\frac{\partial f_2}{dx}$ are continuous on $[0, T] \times \mathbb{R}$.*

If $f_1(t, x) \leq f_2(t, x)$ on $[0, T] \times \mathbb{R}$ and the initial conditions verify $x_{10} \leq x_{20}$, then the solutions x_1 and x_2 satisfy $x_1(t) \leq x_2(t)$ on $[0, T]$.

Theorem 1 *Let $X(t) = x_1(t) + x_2(t)$ the total number of the prey population of the two patches and $X_0 = x_{10} + x_{20}$, $X(t)$ satisfies the following inequality*

$$0 \leq X(t) \leq \left(\left(\frac{1}{X_0} - \frac{1}{2}\right) e^{-at} + \frac{1}{2}\right)^{-1}$$

and

$$\limsup_{t \longrightarrow +\infty} X(t) \leq 2, \forall t \in]0, +\infty[$$

for $X_0 < 2$.

Proof Let $X(t) = x_1(t) + x_2(t)$ the total number of the prey population of the two patches. From $(4)_1$ and $(4)_3$ we have,

$$\begin{aligned} \frac{dX}{dt} &\leq a(x_1 + x_2) - a(x_1^2 + x_2^2) \\ &\leq a(x_1 + x_2) - \frac{a}{2}(x_1 + x_2)^2 \\ &\leq aX(1 - \frac{X}{2}) \end{aligned}$$

As the following logistic equation

$$\begin{cases} \frac{du}{dt} = au(1 - \frac{u}{2}) \\ u(0) = u_0 \end{cases} \tag{10}$$

with solution

$$u(t) = \left(\left(\frac{1}{u_0} - \frac{1}{2}\right) e^{-at} + \frac{1}{2}\right)^{-1}$$

From Proposition 1 and from the positivity of $x_1(t)$ and $x_2(t)$, we have

$$0 \leq X(t) \leq \left(\left(\frac{1}{X_0} - \frac{1}{2}\right) e^{-at} + \frac{1}{2}\right)^{-1}$$

Then, for any initial conditions x_{10} and x_{20} satisfy $X(0) = X_0 = x_{10} + x_{20} < 2$, we get

$$\limsup_{t \longrightarrow +\infty} X(t) \leq 2, \forall t \in]0, +\infty[$$

The following result gives us the boundedness of the predator population.

Theorem 2 *Let $Y(t) = y_1(t) + y_2(t)$ the total population of the predator specie of the two patches. Then, we have*

$$Y_0 e^{-dt} \leq Y(t) \leq \left(Y_0 - \frac{2ck}{2c-d}\right) e^{-(2c-d)t} + \frac{2ck}{2c-d}$$

and for $2c > d$ and for $Y_0 \geq \frac{2ck}{2c-d}$ we obtain

$$\limsup_{t \longrightarrow +\infty} Y(t) \leq \frac{2ck}{2c-d}$$

where $Y_0 = y_{10} + y_{20}$.

Proof From the $(4)_2$ and $(4)_4$, we have

$$\begin{aligned} \frac{dY}{dt}(t) &= \frac{y_1}{dt}(t) + \frac{y_2}{dt}(t) \\ &= c(x_1 y_1 + x_2 y_2) - d(y_1 + y_2) + ckx_1 \\ &\geq -dY(t) \end{aligned}$$

leading to

$$Y(t) \geq Y_0 e^{-dt}$$

As $x_1 \leq X \leq 2$ and $x_2 \leq X \leq 2$, we have

$$\frac{dY}{dt}(t) \leq (2c-d)\, Y(t) + 2ck$$

Let us consider the following equation

$$\begin{cases} \frac{du}{dt}(t) = (2c-d)\, u(t) + 2ck \\ \qquad u(0) = u_0 \end{cases} \tag{11}$$

By applying the variation of constant formula, we obtain

$$u(t) = \left(u_0 - \frac{2ck}{2c-d}\right) e^{-(2c-d)t} + \frac{2ck}{2c-d}$$

From Proposition 1, we have

$$Y(t) \leq \left(Y_0 - \frac{2ck}{2c-d}\right) e^{-(2c-d)t} + \frac{2ck}{2c-d}$$

As $2c > d$ and for $Y_0 \geq \frac{2ck}{2c-d}$, we deduce that

$$\limsup_{t \longrightarrow +\infty} Y(t) \leq \frac{2ck}{2c-d}$$

If $k = 0$, we have

$$\limsup_{t \longrightarrow +\infty} Y(t) = 0$$

4 Steady States and Stability

4.1 Steady States

In this section we will determine the possible equilibrium points and we will study their stability/instability with respect to the migration rate k (Table 1).

The possible steady states are given by resolving the following equations

$$\begin{cases} \frac{dx_1}{dt} = ax_1(1-x_1) - bx_1y_1 - kx_1 = 0 \\ \frac{dy_1}{dt} = cx_1y_1 - dy_1 = 0 \\ \frac{dx_2}{dt} = ax_2(1-x_2) - bx_2y_2 + kx_1 = 0 \\ \frac{dy_2}{dt} = c(x_2 + kx_1)y_2 - dy_2 = 0 \end{cases} \tag{12}$$

Proposition 2 *Under some conditions, system (4) has seven equilibrium points.*
The following table summarize the existence of the steady states:
where $D = a^2 + am$, $D_1 = a^2 + 4ak\frac{d}{c}$ *and* $m = k(1 - \frac{k}{a})$.

Proof The first steady state is trivial $E_0 = (x_{10}, y_{10}, x_{20}, y_{20}) = (0, 0, 0, 0)$.

Table 1 Existence of possible steady states of system (4)

Equilibrium point	Conditions of existence
$E_0 = (x_{10}, y_{10}, x_{20}, y_{20}) = (0, 0, 0, 0)$	No conditions
$E_1 = (x_{11}, y_{11}, x_{21}, y_{21}) = (0, 0, 1, 0)$	No conditions
$E_2 = (x_{12}, y_{12}, x_{22}, y_{22}) = \left(0, 0, \frac{d}{c}, \frac{a\left(1-\frac{d}{c}\right)}{b}\right)$	$c > d$
$E_3 = (x_{13}, y_{13}, x_{23}, y_{23}) = \left(1 - \frac{k}{a}, 0, \frac{a+\sqrt{a^2+am}}{2a}, 0\right)$	$a > k$
$E_4 = (x_{14}, y_{14}, x_{24}, y_{24}) = \left(1 - \frac{k}{a}, 0, \frac{d-cm}{c}, \frac{ax_{24}(1-x_{24})+m}{bx_{24}}\right)$	$cm < d <$ $cm + \frac{c}{2a}\left(a + \sqrt{D}\right)$ and $a > k$ where $m = k(1 - \frac{k}{a}) > 0$ and $D = a^2 + am > 0$
$E_5 = (x_{15}, y_{15}, x_{25}, y_{25}) = \left(\frac{d}{c}, \frac{a}{b}\left(1 - \frac{k}{a} - \frac{d}{c}\right), \frac{a+\sqrt{D_1}}{2a}, 0\right)$	$1 > \frac{k}{a} - \frac{d}{c}$
$E_6 = (x_{16}, y_{16}, x_{26}, y_{26}) =$ $\left(\frac{d}{c}, \frac{a}{b}\left(1 - \frac{k}{a} - \frac{d}{c}\right), \frac{d}{c}(1-k), \frac{ax_{26}(1-x_{26})+k\frac{d}{c}}{bx_{26}}\right)$	$k < 1 < \frac{c}{d}\left(a + \frac{\sqrt{D_1}}{2a}\right) + k$ and $1 > \frac{k}{a} - \frac{d}{c}$ where $D_1 = a^2 + 4ak\frac{d}{c} > 0$

If $c > d$, from $(4)_2$ we obtain

$$y_1 = 0 \Longrightarrow \begin{cases} x_1 = 0 \\ \text{or} \\ x_1 = 1 - \frac{k}{a} \end{cases}$$

In the case when $x_1 = 0$, system (4) have two steady states

$$E_1 = (x_{11}, y_{11}, x_{21}, y_{21}) = (0, 0, 1, 0)$$

and

$$E_2 = (x_{12}, y_{12}, x_{22}, y_{22}) = \left(0, 0, \frac{d}{c}, \frac{a\left(1 - \frac{d}{c}\right)}{b}\right).$$

In the case when $x_1 = 1 - \frac{k}{a}$ and if $c > d$ and $a > k$, we have

$$\begin{cases} ax_2(1 - x_2) - bx_2y_2 + m = 0 \\ c(x_2 + m)y_2 - dy_2 = 0 \end{cases} \tag{13}$$

where $m = k(1 - \frac{k}{a}) > 0$.

From (13)$_2$, if $y_2 = 0$ the forth component of the equilibrium point is given by resolving the second order equation in x_2

$$ax_2 - ax_2^2 + m = 0$$

If $D = a^2 + am > 0$ then $x_2 = \frac{-a+\sqrt{D}}{-2a} < 0$ or $x_2 = \frac{a+\sqrt{D}}{2a} > 0$.

Therefore, the third equilibrium point is as follows

$$E_3 = (x_{13}, y_{13}, x_{23}, y_{23}) = \left(1 - \frac{k}{a}, 0, \frac{a+\sqrt{D}}{2a}, 0\right).$$

From (13)$_2$, if $x_{24} = \frac{d-cm}{c}$ and $d > cm$, from the (13)$_1$ the forth component of the equilibrium point is given by

$$y_{24} = \frac{ax_{24}(1 - x_{24}) + m}{bx_{24}}$$

To determine the region of nonnegativity of y_{24}, let us consider the following second order polynomial for $x > 0$:

$$-ax^2 + ax + m = 0 \tag{14}$$

which is nonnegative if $0 < x < \frac{a+\sqrt{D}}{2a}$. Then, if $0 < x_{24} < \frac{a+\sqrt{D}}{2a}$ which is satisfied if

$$cm < d < cm + \frac{c}{2a}\left(a + \sqrt{D}\right).$$

Then the steady state is given by

$$E_4 = (x_{14}, y_{14}, x_{24}, y_{24}) = \left(1 - \frac{k}{a}, 0, \frac{d-cm}{c}, \frac{ax_{24}(1 - x_{24}) + m}{bx_{24}}\right)$$

From (3)$_2$, we have $x_{15} = \frac{d}{c}$ and from (3)$_1$ we have $y_{15} = \frac{a}{b}\left(1 - \frac{k}{a} - \frac{d}{c}\right)$ which is positive if $1 > \frac{k}{a} - \frac{d}{c}$.

From (3)$_3$ and (3)$_4$, we get

$$\begin{cases} ax_2(1 - x_2) - bx_2y_2 + k\frac{d}{c} = 0 \\ c(x_2 + k\frac{d}{c})y_2 - dy_2 = 0 \end{cases} \tag{15}$$

from (15)$_2$, we have $y_{25} = 0$ and from (15)$_1$ and solving the following polynomial for $x > 0$

$$-ax^2 + ax + k\frac{d}{c} = 0 \tag{16}$$

we find

$$x_{25} = \frac{a + \sqrt{D_1}}{2A}$$

where $D_1 = a^2 + 4ak\frac{d}{c} > 0$.

Then, the sixth steady state is given as follows

$$E_5 = (x_{15}, y_{15}, x_{25}, y_{25}) = \left(\frac{d}{c}, \frac{a}{b}\left(1 - \frac{k}{a} - \frac{d}{c}\right), \frac{a + \sqrt{D_1}}{2a}, 0\right)$$

From (15)$_2$, we have:

$$x_{26} = \frac{d}{c}(1 - k)$$

which is positive if $1 > k$ and from (15)$_1$ we have

$$y_{26} = \frac{ax_{26}(1 - x_{26}) + k\frac{d}{c}}{bx_{26}}$$

As the last equilibrium point y_{26} is nonnegative if $0 < x_{26} < x_{25}$ which is equivalent to

$$k < 1 < \frac{c}{d}\left(a + \frac{\sqrt{D_1}}{2a}\right) + k$$

then the sixth steady state is:

$$E_6 = (x_{16}, y_{16}, x_{26}, y_{26}) = \left(\frac{d}{c}, \frac{a}{b}\left(1 - \frac{k}{a} - \frac{d}{c}\right), \frac{d}{c}(1 - k), \frac{ax_{26}(1 - x_{26}) + k\frac{d}{c}}{bx_{26}}\right)$$

Remark 1 $\underline{E_0 = (0, 0, 0, 0)}$: Extinction of both the predator and prey in each of the two patches (i.e. if there is no prey there is no predator, in this case there is no migration $k = 0$).

$\underline{E_1 = (0, 0, 1, 0)}$: Extinction of both the predator and the prey in the first patch and persistence of the prey and extinction of the predator in the second patch (i.e. if there is no predation there is a persistence in prey and the prey will grow in the absence of the predator population. As there is extinction of the prey in the first patch there is no migration of prey population from the first patch to the second patch $k = 0$).

$\underline{E_2 = \left(0, 0, \frac{d}{c}, \frac{a\left(1-\frac{d}{c}\right)}{b}\right)}$: Extinction of both the predator and prey in the first patch and there is no migration to the second patch and persistence of both the predator and prey in the second patch for the value rate of numerical response bigger than the mortality rate of the predator in the second patch.

$E_3 = \left(1-\frac{k}{a}, 0, \frac{a+\sqrt{a^2+am}}{2a}, 0\right)$: Extinction of the predator and persistence of the prey of both the patches. In this case there is a migration of the prey population from the first patch to the second patch when the migration rate is smaller than the production rate of the prey a.

$E_4 = \left(1-\frac{k}{a}, 0, \frac{d-cm}{c}, \frac{ax_{24}(1-x_{24})+m}{bx_{24}}\right)$: Persistence of the prey and extinction of the predator in the first patch and persistence of both the predator and prey in the second patch and there is a migration of the prey population from the first patch to the second patch.

$E_5 = \left(\frac{d}{c}, \frac{a}{b}\left(1-\frac{k}{a}-\frac{d}{c}\right), \frac{a+\sqrt{D_1}}{2a}, 0\right)$: Persistence of both the predator and prey in the first patch and persistence of the prey and extinction of the predator in the second patch and there is a migration of the prey population from the first patch to the second patch.

$E_6 = \left(\frac{d}{c}, \frac{a}{b}\left(1-\frac{k}{a}-\frac{d}{c}\right), \frac{d}{c}(1-k), \frac{ax_{26}(1-x_{26})+k\frac{d}{c}}{bx_{26}}\right)$: Persistence of both the predator and prey in each of the two patches and there is a migration of the prey population from the first patch to the second patch.

4.2 Local Stability

Definition 1 Let $Pr_1(x_1, y_1, x_2, y_2) = (x_1, y_1)$ the projection of the point (x_1, y_1, x_2, y_2) on the $(4)_1$-$(4)_2$ describing the first patch (x_1, y_1) and $Pr_2(x_1, y_1, x_2, y_2) = (x_2, y_2)$ the projection of the point (x_1, y_1, x_2, y_2) on the $(4)_3$-$(4)_4$ describing the second patch (x_2, y_2).

To study the local stability of the possible equilibrium points, one needs to linearize system (3) around the concerned steady state.

Theorem 3 *Consider that $E_* = \left(x_1^*, y_1^*, x_2^*, y_2^*\right)$ is a steady state of system (4). The stability of E_* is deduced from the stability of $Pr_1 E_* = \left(x_1^*, y_1^*\right)$ and $Pr_2 E_* = \left(x_2^*, y_2^*\right)$.*

(1) If $Pr_1 E_*$ and $Pr_2 E_*$ are asymptotically stable, then E_* is also asymptotically stable.

(2) If $Pr_1 E_*$ or $Pr_2 E_*$ is unstable, then E_* is also unstable

Proof By linearizing around the steady state $E_* = \left(x_1^*, y_1^*, x_2^*, y_2^*\right)$ we obtain the following linearized system:

$$\begin{cases} \frac{dx_1}{dt} = \left(a(1-x_1^*) - by_1^* - ax_1^* - k\right) x_1 - bx_1^* y_1 \\ \frac{dy_1}{dt} = cy_1^* x_1 + \left(cx_1^* - d\right) y_1 \\ \frac{dx_2}{dt} = \left(a(1-x_2^*) - by_2^* - ax_2^*\right) x_2 - bx_2^* y_2 + kx_1 \\ \frac{dy_2}{dt} = cky_2^* x_1 + cky_2^* x_2 + \left(c(kx_1^* + x_2^*) - d\right) y_2 \end{cases} \tag{17}$$

and the jacobian matrix is given by

$$J(E_*) = \begin{pmatrix} A_1 - k & -bx_1^* & 0 & 0 \\ cy_1^* & cx_1^* - d & 0 & 0 \\ k & 0 & A_2 & -bx_2^* \\ cky_2^* & 0 & cy_2^* & c(kx_1^* + x_2^*) - d \end{pmatrix}$$

where

$$A_i = a(1 - x_i^*) - by_i^* - ax_i^* = a(1 - 2x_i^*) - by_i^*, \; i = 1, 2$$

Then

$$\det(\lambda I_4 - J(E_*)) = \det \begin{pmatrix} \lambda I_2 - M_1 & 0_2 \\ M & \lambda I_2 - M_2 \end{pmatrix}$$

where

$$M_1 = \begin{pmatrix} A_1 - k & -bx_1^* \\ cy_1^* & cx_1^* - d \end{pmatrix}, M_2 = \begin{pmatrix} A_2 & -bx_2^* \\ cy_2^* & c(kx_1^* + x_2^*) - d \end{pmatrix}, M = \begin{pmatrix} k & 0 \\ cky_2^* & 0 \end{pmatrix}$$

and I_2 is the 2×2 unit matrix and 0_2 is the 2×2 vanishing matrix.

From the determinant property, we have

$$\det(\lambda I_4 - J(E_*)) = \det(\lambda I_2 - M_1) \times (\lambda I_2 - M_2) \tag{18}$$

Then, $\det(\lambda I_2 - M_1) = 0$ is the characteristic equation associated to $Pr_1 E_*$ and $\det(\lambda I_2 - M_2) = 0$ is the characteristic equation associated to $Pr_2 E_*$.

Therefore, we deduce the result.

Theorem 4 (Stability of E_0)

The equilibrium point $E_0 = (0, 0, 0, 0)$ *is unstable.*

Proof The value of A_2 at E_0 is $A_2 = 0$ and $Pr_2(E_0) = (0, 0)$. From Theorem 3, the stability of $Pr_2(E_0)$ is determined from the following associated characteristic equations

$$\det(\lambda I_2 - M_2) = \begin{vmatrix} \lambda - a & 0 \\ 0 & \lambda + d \end{vmatrix} = (\lambda - a)(\lambda + d) = 0$$

As $\lambda_1 = a > 0$ and $\lambda_2 = -d < 0$, then $Pr_1(E_0)$ is unstable. Therefore, from Theorem 3 E_0 is unstable.

Remark 2 If we consider system (4) with vanishing migration (i.e. there is no migration of the prey population from the first patch to the second patch: $k = 0$), we obtain system (3). Then $Pr_1(E_0) = Pr_2(E_0) = (0, 0)$ is a equilibrium point of system (3) and the stability of E_0 can be deduced from the stability of the trivial equilibrium solution $(0, 0)$ of (3). Therefore, the migration rate does not have any effect on the stability of the equilibrium solution E_0.

Theorem 5 (Stability of E_1)

The equilibrium point $E_1 = (0, 0, 1, 0)$ is asymptotically stable if $a < k$ and unstable if $a > k$.

Proof From the expression of A_1 and A_2 at E_1, we have $A_1 = 0$ and $A_2 = -a$.

As $\det(\lambda I_2 - M_1) = (\lambda - a + k)(\lambda + d) = 0$. Therefore, $\lambda_1 = a - k$ and $\lambda_2 = -d < 0$ and we deduce that $Pr_1(E_1) = (0, 0)$ is asymptotically stable if $a < k$ and unstable if $a > k$.

From $\det(\lambda I_2 - M_2) = (\lambda + a)(\lambda + d) = 0$, we get that $Pr_2(E_1) = (1, 0)$ is asymptotically stable.

From Theorem 3, we deduce that E_1 is asymptotically stable if $a < k$ and unstable if $a > k$.

Remark 3 $Pr_1(E_1) = (0, 0)$ is a trivial equilibrium solution of the first patch when $k = 0$ and $Pr_2(E_1) = (1, 0)$ is an equilibrium solution of the second patch and the stability of E_1 depends on the migration rate k

Theorem 6 (Stability of E_2)

Suppose $c > d$, the equilibrium point $E_2 = \left(0, 0, \frac{d}{c}, \frac{a\left(1-\frac{d}{c}\right)}{b}\right)$ is asymptotically stable if $a < k$ and unstable if $a > k$.

Proof As $Pr_1(E_2) = Pr_1(E_1) = (0, 0)$, $A_1 = 0$ and from the proof of Theorem 5, we have $Pr_1(E_1) = (0, 0)$ is asymptotically stable if $a < k$ and unstable if $a > k$.

From the expression of A_2 at E_2, we have $A_2 = -\frac{ad}{c} < 0$ and the characteristic equation associated to $Pr_1(E_2) = \left(\frac{d}{c}, \frac{a\left(1-\frac{d}{c}\right)}{b}\right)$ is given by

$$\det(\lambda I_2 - M_1) = \lambda^2 + \lambda\frac{ad}{c} + ad\left(1 - \frac{d}{c}\right) = 0$$

As $\Delta = \left(\frac{ad}{c}\right)^2 - 4ad\left(1 - \frac{d}{c}\right)$, if $\Delta > 0$ we get:

$$\lambda_1 = \frac{-\frac{ad}{c} + \sqrt{\Delta}}{2} \text{ and } \lambda_2 = \frac{-\frac{ad}{c} - \sqrt{\Delta}}{2} < 0$$

From the expression of λ_1 and as $c > d$ (condition of the existence of E_2), we have $\lambda_1 < 0$. Then, $Pr_2(E_2)$ is stable asymptotically.

If $\Delta \leq 0$ we get:

$$\lambda_1 = \frac{-\frac{ad}{c} + i\sqrt{-\Delta}}{2} \text{ and } \lambda_2 = \frac{-\frac{ad}{c} - i\sqrt{-\Delta}}{2} < 0$$

and $Re(\lambda_1) = Re(\lambda_2) = -\frac{ad}{c} < 0$. Then, $Pr_2(E_2)$ is stable asymptotically.

From Theorem 3, we deduce that $E_2 = \left(0, 0, \frac{d}{c}, \frac{a\left(1-\frac{d}{c}\right)}{b}\right)$ is asymptotically stable if $a < k$ and unstable if $a > k$.

Remark 4 $Pr_1(E_2) = (0, 0)$ is a trivial equilibrium solution of the first patch when $k = 0$ and $Pr_2(E_2) = \left(\frac{d}{c}, \frac{a\left(1-\frac{d}{c}\right)}{b}\right)$ is not an equilibrium solution of system (3). Then, the stability of E_2 depends on the migration rate k and can be deduced from the stability of $Pr_1(E_2)$.

Let

(H_1): $a(\frac{d}{c} - 1) < k$

(H_2): $c(m + x_{23}) < d$, where $m = k\left(1 - \frac{k}{a}\right) > 0$

Theorem 7 (Stability of E_3)

Suppose $a > k$.

If (H_1) and (H_2) are satisfied, then the equilibrium solution $E_3 = \left(1 - \frac{k}{a}, 0, \frac{a+\sqrt{a^2+am}}{2a}, 0\right)$ *is asymptotically stable.*

If (H_1) or (H_2) are not satisfied, then the equilibrium solution $E_3 = \left(1 - \frac{k}{a}, 0, \frac{a+\sqrt{a^2+am}}{2a}, 0\right)$ *is unstable.*

Proof From the expression of A_1 at E_3, the characteristic equation associated to $Pr_1E_3 = \left(1 - \frac{k}{a}, 0\right)$ is as follows:

$$\det(\lambda I_2 - M_1) = (\lambda - k + a)\left(\lambda - c\left(1 - \frac{k}{a}\right) + d\right) = 0$$

and the corresponding eigenvalues are given by $\lambda_1 = k - a$ and $\lambda_2 = c\left(1 - \frac{k}{a}\right) - d$. As $a > k$, we have $\lambda_1 < 0$ and if (H_1) is satisfied, then $Pr_1 E_3$ is asymptotically stable and if not satisfied, $Pr_1 E_3$ is unstable.

From the expression of x_{23} and by computation at E_3, we have

$$A_2 = -\frac{k}{x23}\left(1 - \frac{k}{a}\right) - ax_{23} < 0$$

and the associated characteristic equation to $Pr_2 E_3 = \left(\frac{a+\sqrt{a^2+am}}{2a}, 0\right)$ is:

$$\det(\lambda I_2 - M_2) = (\lambda - A_2)(\lambda - c(m + x_{23}) + d) = 0$$

The corresponding eigenvalues are

$$\lambda_1 = A_2 < 0 \text{ and } \lambda_2 = c(m + x_{23}) - d$$

If (H_2) is satisfied, we obtain that $\lambda_2 < 0$. Then, $Pr_2 E_3$ is asymptotically stable and if (H_2) is not satisfied, $Pr_2 E_3$ is unstable.

From Theorem 3, we deduce that, the equilibrium solution E_3 is asymptotically stable if (H_1) and (H_2) are satisfied and unstable if (H_1) or (H_2) is not satisfied.

Theorem 8 (Stability of E_4)

Suppose $a > k$ and $cm < d < cm + \frac{c}{2a}\left(a + \sqrt{D}\right)$, where $D = a^2 + am > 0$.

If (H_1) is satisfied, then the equilibrium solution $E_4 = \left(1 - \frac{k}{a}, 0, \frac{d-cm}{c}, \frac{ax_{24}(1-x_{24})+m}{bx_{24}}\right)$ is asymptotically stable.

If (H_1) is not satisfied, then the equilibrium solution $E_4 = \left(1 - \frac{k}{a}, 0, \frac{d-cm}{c}, \frac{ax_{24}(1-x_{24})+m}{bx_{24}}\right)$ is unstable.

Proof As $Pr_1(E_4) = Pr_1(E_3) = \left(1 - \frac{k}{a}, 0\right)$ and from the proof of Theorem 7, we have, if (H_1) is satisfied. Then $Pr_1 E_4$ is asymptotically stable and if not satisfied, $Pr_1 E_4$ is unstable.

As $Pr_2(E_4) = \left(\frac{d-cm}{c}, \frac{ax_{24}(1-x_{24})+m}{bx_{24}}\right)$, then the associated characteristic equation is given by:

$$\det(\lambda I_2 - M_2) = \lambda^2 - \lambda A_2 + cbx_{24}y_{24} = 0$$

By calculations, we obtain the value of A_2 at E_4, that is

$$A_2 = \frac{-m - ax_{24}^2}{x_{24}} < 0$$

If $\Delta_1 = A_2^2 - 4cbx_{24}y_{24} > 0$, the corresponding eigenvalues are

$$\lambda_1 = \frac{A_2 + \sqrt{\Delta_1}}{2} < 0 \text{ and } \lambda_2 = \frac{A_2 - \sqrt{\Delta_1}}{2} < 0.$$

Then, $Pr_2(E_4)$ is asymptotically stable.

If $\Delta \leq 0$, the corresponding eigenvalues are

$$\lambda_1 = \frac{A_2 + i\sqrt{-\Delta_1}}{2} < 0 \text{ and } \lambda_2 = \frac{A_2 - i\sqrt{-\Delta_1}}{2} < 0.$$

and $Re(\lambda_1) = Re(\lambda_2) = \frac{A_2}{2} < 0$.

Then, $Pr_2(E_4)$ is asymptotically stable.

From Theorem 3, we deduce that the equilibrium solution E_4 is asymptotically stable if (H_1) is satisfied and unstable if (H_1) is not satisfied.

Let:
(H_3): $k < \frac{c}{2a}(a + \sqrt{D_1}) + d$, where $D_1 = a^2 + 4ak\frac{d}{c} > 0$.

Theorem 9 (Stability of E_5)
Suppose that $1 > \frac{k}{a} - \frac{d}{c}$.
$E_5 = \left(\frac{d}{c}, \frac{a}{b}\left(1 - \frac{k}{a} - \frac{d}{c}\right), \frac{a+\sqrt{D_1}}{2a}, 0\right)$ *is asymptotically stable if* (H_3) *is satisfied and unstable if* (H_3) *is not satisfied.*

Proof From the expression of E_5, we have $Pr_1(E_5) = \left(\frac{d}{c}, \frac{a}{b}\left(1 - \frac{k}{a} - \frac{d}{c}\right)\right)$ and the value of A_1 at E_5 is $A_1 = k - ax_{15}$ and the associated characteristic equation is given by:

$$\det(\lambda I_2 - M_1) = \lambda^2 + \lambda a x_{15} + cbx_{15}y_{15}$$

By the same method as in the proof of Theorem 8, we find that the real part of the corresponding eigenvalues is negative and $Pr_1(E_5)$ is asymptotically stable.

From the expressions of E_5 and A_2 at E_5, we have $Pr_2(E_5) = \left(\frac{a+\sqrt{D_1}}{2a}, 0\right)$ and $A_2 = -\frac{kd}{cx_{26}} - ax_{26} < 0$.

The associated characteristic equation is

$$\det(\lambda I_2 - M_2) = (\lambda - A_2)\left(\lambda - c\left(\frac{kd}{c} - x_{25}\right) + d\right) = 0$$

and the corresponding eigenvalues are:

$$\lambda_1 = A_2 < 0 \text{ and } \lambda_2 = c\left(\frac{kd}{c} - x_{25}\right) - d.$$

Then, $\lambda_2 < 0$ if (H_3) is satisfied and $Pr_2(E_5)$ is asymptotically stable and unstable if (H_3) is not satisfied.

Therefore, from Theorem 3 we deduce the result.

Theorem 10 (Stability of E_6)
Suppose $k < 1 < \frac{c}{d}\left(a + \frac{\sqrt{D_1}}{2a}\right) + k$ *and* $1 > \frac{k}{a} - \frac{d}{c}$.

Then, the equilibrium solution $E_6 = \left(\frac{d}{c}, \frac{a}{b}\left(1 - \frac{k}{a} - \frac{d}{c}\right), \frac{d}{c}(1-k), \frac{ax_{26}(1-x_{26})+k\frac{d}{c}}{bx_{26}}\right)$ *is asymptotically stable.*

Proof As $Pr_1E_6 = Pr_1E_5 = \left(\frac{d}{c}, \frac{a}{b}\left(1 - \frac{k}{a} - \frac{d}{c}\right)\right)$, from the proof of Theorem 9, we get Pr_1E_6 is asymptotically stable.

From the expression of E_6, we have $Pr_2E_6 = \left(\frac{d}{c}(1-k), \frac{ax_{26}(1-x_{26})+k\frac{d}{c}}{bx_{26}}\right)$ and A_2 at E_6 is

$$A_2 = \frac{kd}{cx_{26}} - ax_{26} < 0$$

$$\det(\lambda I_2 - M_2) = \lambda^2 - \lambda A_2 + cbx_{26}y_{26}$$

By the same method as in the proof of Theorem 8, we find that the real part of the corresponding eigenvalues is negative and $Pr_2(E_6)$ is asymptotically stable.

From Theorem 3, we find that E_6 is asymptotically stable.

5 Global Stability

In this section we try to study the global stability of the a possible steady state $E_* = \left(x_1^*, y_1^*, x_2^*, y_2^*\right)$ of system (4).

Let V_i the Lyapunov function associated to the patch i with $i = 1, 2$ defined by:

$$V_i(x_i, y_i) = \left(x_i - x_i^*\right) - \frac{d}{c}\ln\left(\frac{x_i}{x_i^*}\right) + \frac{b}{c}\left\{\left(y_i - y_i^*\right) - y_i^*\ln\left(\frac{y_i}{y_i^*}\right)\right\}, i = 1, 2$$

This functions are defined and continuous on $Int(\mathbb{R}_+^2)$.

We are interested in constructing Lyapunov function for the coupled system (4).

Theorem 11 *Let*

$$V(x_1, y_1, x_2, y_2) = \sum_{i=1}^{2} V_i(x_i, y_i)$$

For $a > 0$ *and* k *sufficientlly small, the steady state* $E_* = \left(x_1^*, y_1^*, x_2^*, y_2^*\right)$ *is globally asymptotically stable.*

Proof The proof is based on a positive definite Lyapunov function. It can be easily verified that the function is zero at the equilibrium point $E_* = \left(x_1^*, y_1^*, x_2^*, y_2^*\right)$ and is positive for all other positive values x_1, y_1, x_2 and y_2 and thus, $E_* = \left(x_1^*, y_1^*, x_2^*, y_2^*\right)$ is the global minimum of V.

Differentiating $V_i, i = 1, 2$ along (4) gives:

$$\begin{aligned}\dot{V}_1(x_1, y_1) &= \frac{\dot{x}_1}{x_1^*}(x_1 - x_1^*) + \frac{b}{c}\frac{\dot{y}_1}{y_1^*}(y_1 - y_1^*)\\ &= -a(x_1 - x_1^*)^2\end{aligned}$$

and

$$\begin{aligned}\dot{V}_2(x_2, y_2) &= \frac{\dot{x}_2}{x_2^*}(x_2 - x_2^*) + \frac{b}{c}\frac{\dot{y}_2}{y_2^*}(y_2 - y_2^*)\\ &= -a(x_2 - x_2^*)^2 + k\left(\frac{x_1}{x_2} - \frac{x_1^*}{x_2^*}\right)(x_2 - x_2^*) + bk(x_1 - x_1^*)(y_2 - y_2^*)\\ &= -a(x_2 - x_2^*)^2 + kx_1^*\left(\frac{x_1}{x_1^*} - \frac{x_2}{x_2^*} + 1 - \frac{x_1x_2^*}{x_1^*x_2}\right) + bk(x_1 - x_1^*)(y_2 - y_2^*)\end{aligned}$$

Let $G(x_i) = -\frac{x_i}{x_i^*} + \ln\left(\frac{x_i}{x_i^*}\right), i = 1, 2$. By using $1 - x + \ln(x) \leq 0$ for $x > 0$ and equality holding if $x = 1$ we have

$$G(x_2) - G(x_1) + 1 - \frac{x_1x_2^*}{x_1^*x_2} + \ln\left(\frac{x_1x_2^*}{x_1^*x_2}\right) \leq G(x_2) - G(x_1)$$

and

$$\begin{aligned}\dot{V}(x_1, y_1, x_2, y_2) &= -a(x_1 - x_1^*)^2 - a(x_2 - x_2^*)^2 + kx_1^*\left(\frac{x_1}{x_1^*} - \frac{x_2}{x_2^*} + 1 - \frac{x_1x_2^*}{x_1^*x_2}\right)\\ &\quad + bk(x_1 - x_1^*)(y_2 - y_2^*)\\ &= -a(x_1 - x_1^*)^2 - a(x_2 - x_2^*)^2 + kx_1^*\left(G(x_2) - G(x_1) + 1 - \frac{x_1x_2^*}{x_1^*x_2} + \ln\left(\frac{x_1x_2^*}{x_1^*x_2}\right)\right)\\ &\quad + bk(x_1 - x_1^*)(y_2 - y_2^*)\\ &\leq -a(x_1 - x_1^*)^2 - a(x_2 - x_2^*)^2 + kx_1^*\left(G(x_2) - G(x_1)\right) + bk(x_1 - x_1^*)(y_2 - y_2^*)\end{aligned}$$

As the solutions of system (4) are bounded and $a > 0$ and $k > 0$ is sufficiently small, we deduce that $\dot{V} \leq 0$ and $\dot{V} = 0$ if and only if $x_i = x_i^*$ and $y_i = y_i^*$, $i = 1, 2$. By the classical Lyapunov theory, E^* is globally asymptotically stable.

6 Numerical Simulations

In this section, via Matlab software and by using ode45 discretization we give some numerical simulations in order to illustrate the theoretical results presented in the previous sections (Figs. 1, 2, 3, 4, 5, 6, 7, 8).

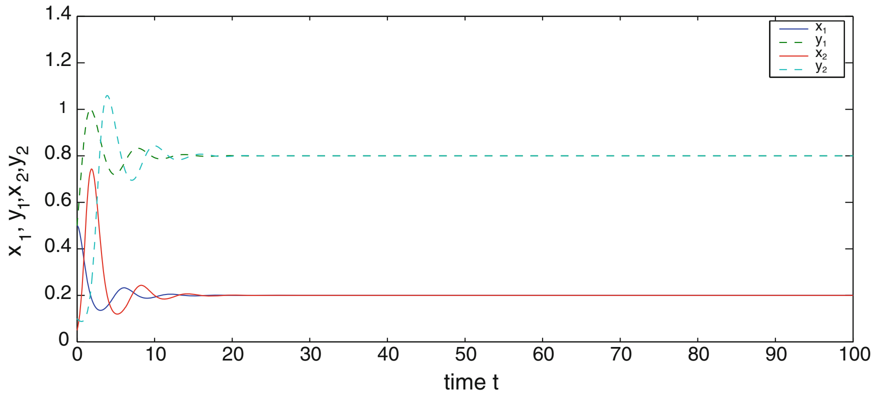

Fig. 1 Identification of solutions of the two patches with a vanishing migration rate $k = 0$

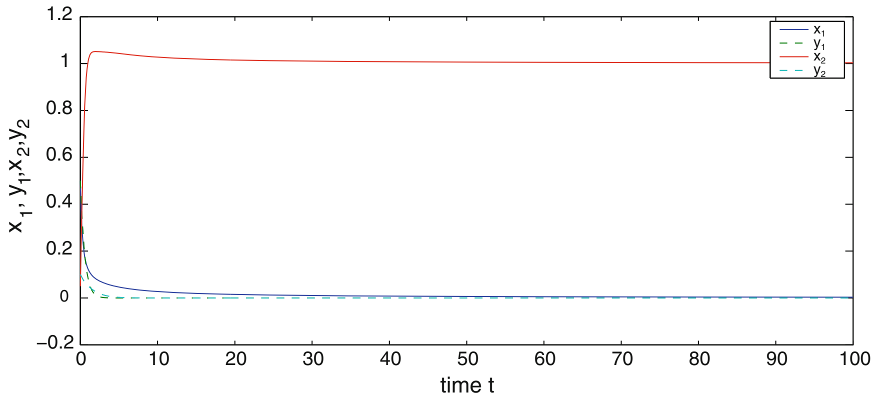

Fig. 2 Stability of E_1 with the following parameters values $a = 2$, $b = 3$, $c = 2$, $d = 0.5$ and $k = 0.5$

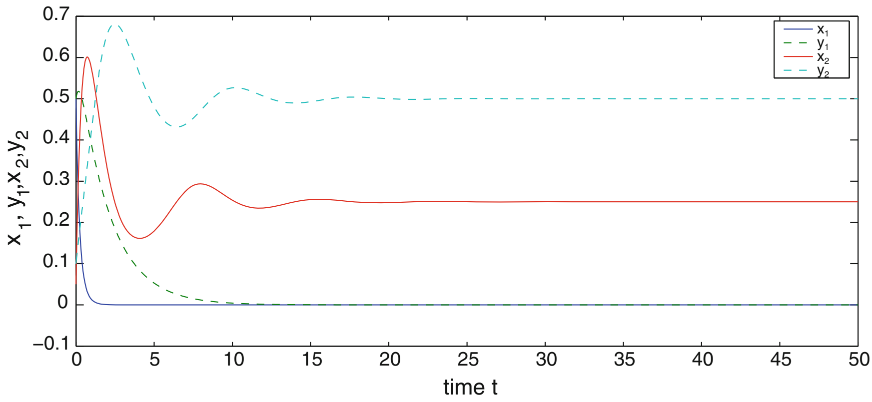

Fig. 3 Stability of E_2 with the following parameters values $a = 2$, $b = 3$, $c = 2$, $d = 0.5$ and $k = 4$

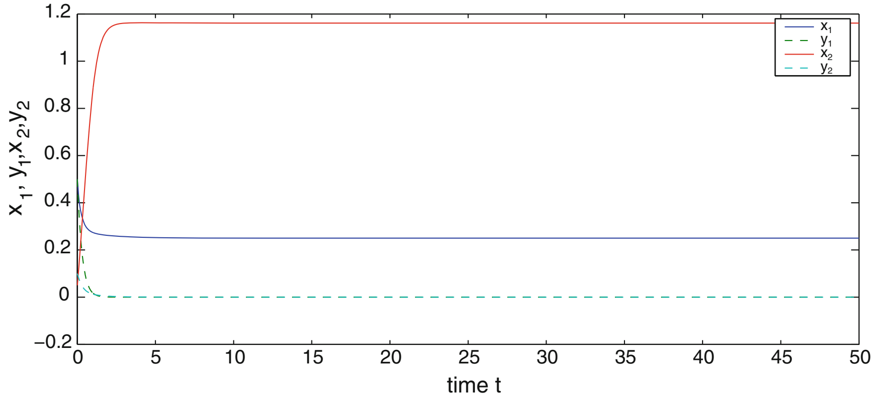

Fig. 4 Stability of E_3 with the following parameters values $a = 2$, $b = 3$, $c = 2$, $d = 4$ and $k = 1.5$

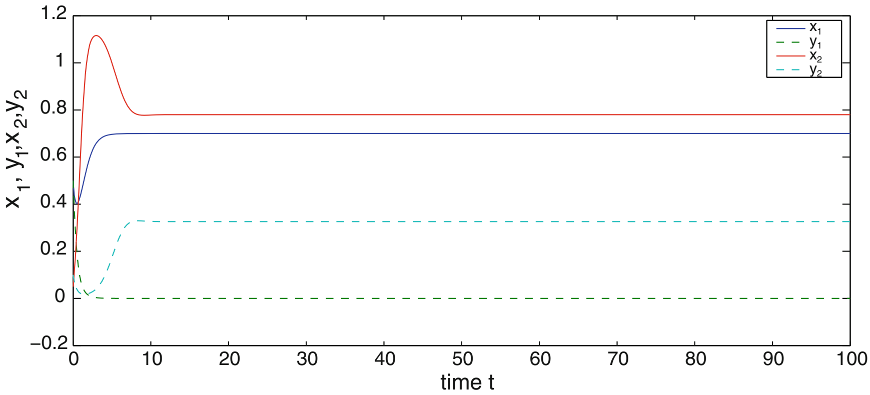

Fig. 5 Stability of E_4 with the following parameters values $a = 2$, $b = 3$, $c = 2$, $d = 4$ and $k = 5$

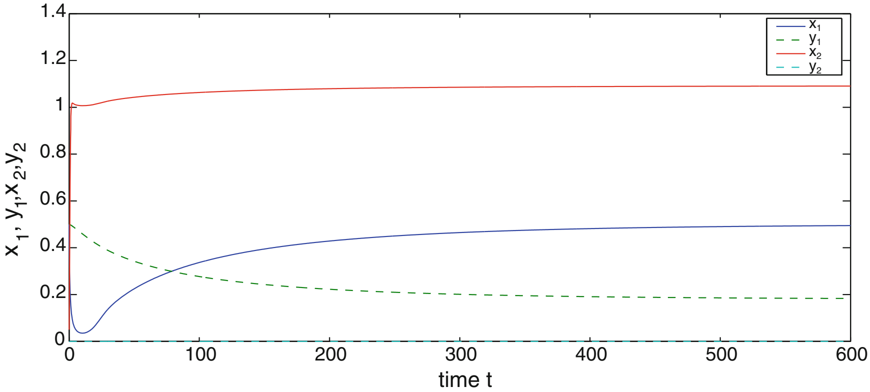

Fig. 6 Stability of E_5 with the following parameters values $a = 3$, $b = 5$, $c = 0.02$, $d = 0.01$ and $k = 0.6$

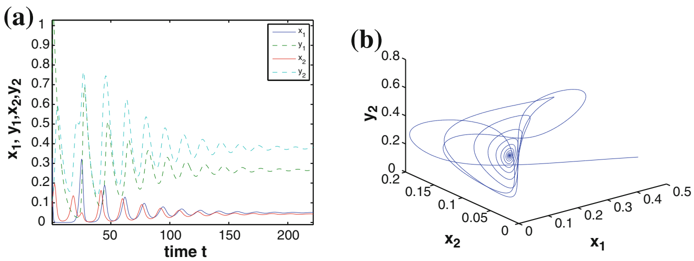

Fig. 7 Stability of E_5 in $(t, x_1y_1x_2y_2)$ plane and in (x_1, x_2, y_2) space with the following parameters values $a = 2$, $b = 3$, $c = 2$, $d = 0.5$ and $k = 0.25$

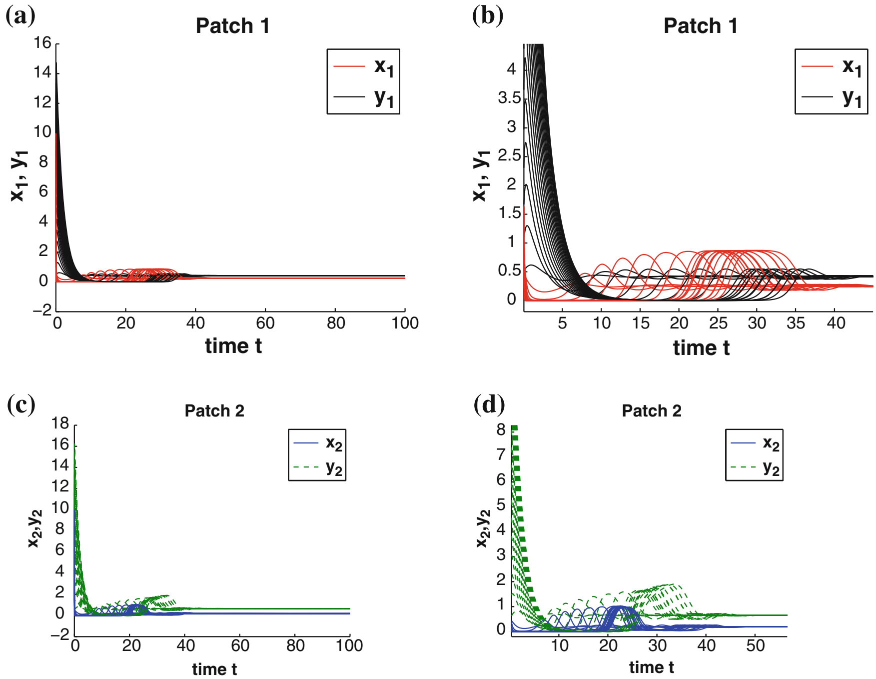

Fig. 8 Global stability of the positive steady state E_6 with different initial conditions values which vary from 0.5 to 20 where $a = 2$, $b = 3$, $c = 2$, $d = 0.5$ and $k = 0.25$; the figure in the right is the zoom of one in the left

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