Stability analysis in competition population model

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Abstract—We consider a competition model with two species for a limited resource in which the habitat is divided into two patches. By using aggregation methods, the reduced model has the form of classical Lotka-Volterra competition model. We represent the stability of equilibria of the model in various parameter spaces. It is found that the transcritical bifurcation takes an important role in explaining the dynamics of model. Numerical investigation shows that the long term behaviour of the complete model and the reduced model is very similar.

Keywords— Competition, equilibrium, species, patch, transcritical bifurcation

I. Introduction

Understanding species coexistence in the face of competition for limited resources has been a center goal in theoretical and conversation ecology (for examples see, [8], [11], [12]). Previous studies have mainly considered models where they omit disparity of temporal scales between migration and competition; and assume symmetric migrations and heterogeneous environment (see [1], [4], [8], [12], [13]).

In this paper, we study an interspecific competition model of two species between two patches that are connected through density independent migrations at a fast time scales, as mentioned in [5]. The model is given by a system of four dimensional ordinary differential equations with two time scales. Using aggregation methods, the system is reduced into a two dimensional system for the total densities of the two species. The reduced system has the form of a classical Lotka-Volterrra competition model. This gives a complete analytical description of the competition outcome by general migration rates and competition intensities. We assume that the competition is asymmetric and the environment is homogeneous.

Our emphasis lies on obtaining a mathematical understanding of the dynamics and bifurcation of the model. We analyze the stability of equilibria and exhibit phase portraits for competition dynamics. Transcritical bifurcation is useful to explain the exchange of competitive effects. We find subspaces of parameters in which one can identify dynamics of competition. Numerical method is used to investigate behaviour of the complete model. It is found that dynamics of the complete model and reduced model is very similar. This proposed model reflects many stability properties of more complicated models.

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II. The stucture of the model

We consider a model with two species for a resource on a habitat divided in two patches. Let $n_{ij}(t)$ be the density of species i in patch j at time t with $i, j \in \{1;2\}$. We assume that both patches are connected and a Lotka-Volterra competitive dynamics locally occurs in each patch. Moreover, the competition is asymmetric.

Species 1 migrates from patch 1 to patch 2 at a rate $\bar{k}$ and from patch 2 to patch 1 at a rate k. Similarly, the migration rate of species 2 from patch 1 to patch 2 is $\bar{m}$ and from patch 2 to patch 1 is m. The parameters $\bar{k}, k, \bar{m}$ and m are positive constants. Migration rates are asymmetric and different for each species.

We suppose the species and patches have similar properties: the same carrying capacity K for both species in both patches, the same growth rates for each species, r_1 for species 1 and r_2 for species 2, and the same pair-wise competition coefficients, a and b, in both patches, measuring the competitive effect of species 2 on species 1 and species 1 on species 2, respectively.

In accordance with the previous assumptions, the complete model has the following form:

$$\begin{cases} \dfrac{dn_{11}}{d\tau} &= (-\bar{k}n_{11} + kn_{12}) + \varepsilon r_1 n_{11}\left(1 - \dfrac{n_{11}}{K} - a\dfrac{n_{21}}{K}\right) \\ \dfrac{dn_{12}}{d\tau} &= (\bar{k}n_{11} - kn_{12}) + \varepsilon r_1 n_{12}\left(1 - \dfrac{n_{12}}{K} - a\dfrac{n_{22}}{K}\right) \\ \dfrac{dn_{21}}{d\tau} &= (-\bar{m}n_{21} + mn_{22}) + \varepsilon r_2 n_{21}\left(1 - \dfrac{n_{21}}{K} - b\dfrac{n_{11}}{K}\right) \\ \dfrac{dn_{22}}{d\tau} &= (\bar{m}n_{21} - mn_{22}) + \varepsilon r_2 n_{21}\left(1 - \dfrac{n_{22}}{K} - b\dfrac{n_{12}}{K}\right). \end{cases} \quad (1)$$

The parameter ε is the ratio between two time scales $t = \varepsilon\tau$ in which t is the slow time scale and τ is the fast time scale. Results in [5] show that there exists a large enough ratio of time scales for which the long term behaviour of both cases is very similar.

For study this system we apply aggregation methods [3] to transform it into a reduced system with two ordinary differential equations governing the dynamics of the global variables: the total density of species 1, $n_1(t) = n_{11}(t) + n_{12}(t)$, and the total density of species 2, $n_2 = n_{21}(t) + n_{22}(t)$. When we ignore the competitive interaction, the distribution of each species between two patches will tend to certain equilibrium proportions. Let us fix values n_1 and n_2 and find the equilibria of the fast part of the system (1). We obtain for species 1

$$n_{11}^* = \frac{k}{k+\bar{k}} n_1 = \nu_1^* n_1 \text{ and } n_{12}^* = \frac{\bar{k}}{k+\bar{k}} n_1 = \nu_2^* n_1 \tag{2}$$

and for species 2

$$n_{21}^* = \frac{m}{m+\bar{m}} n_2 = \mu_1^* n_2 \text{ and } n_{22}^* = \frac{\bar{m}}{m+\bar{m}} n_2 = \nu_2^* n_2, \tag{3}$$

where ν_1^* and ν_2^* represent the fast equilibrium proportions of species 1 on each patch while the constants μ_1^* and μ_2^* represent the fast equilibrium proportion of species 2 on each path. These equilibria are stable for fast dynamics.

From the system (1), we can obtain a system for the two global variables by adding the corresponding equations and substituting the former state variables by the fast equilibria as follow:

$$n_{11} = \nu_1^* n_1,\ n_{12} = \nu_2^* n_1,\ n_{21} = \mu_1^* n_2 \text{ and } n_{22} = \mu_2^* n_2.$$

We obtain the following aggregated system at the slow time scale:

$$\begin{cases} \dfrac{dn_1}{dt} = r_1 n_1 \left(1 - \dfrac{(\nu_1^*)^2 + (\nu_2^*)^2}{K} n_1 - a \dfrac{\nu_1^* \mu_1^* + \nu_2^* \mu_2^*}{K} n_2 \right) \\ \dfrac{dn_2}{dt} = r_2 n_2 \left(1 - b \dfrac{\nu_1^* \mu_1^* + \nu_2^* \mu_2^*}{K} n_1 - \dfrac{(\mu_1^*)^2 + (\mu_2^*)^2}{K} n_2 \right) \end{cases} \tag{4}$$

Using the aggregation methods in [2] and [3], one can study the dynamics of the complete system (1) by studying the aggregated model (4).

The model (4) is a classical Lotka-Volterra competition model [12]. It is convenient to describe asymptotic behaviour of this model by the following change of variables:

$$u_1 = \frac{(\nu_1^*)^2 + (\nu_2^*)^2}{K} n_1,\quad u_2 = \frac{(\mu_1^*)^2 + (\mu_2^*)^2}{K} n_2.$$

This yields

$$\begin{cases} \dfrac{du_1}{dt} = r_1 u_1 (1 - u_1 - \alpha u_2) \\ \dfrac{du_2}{dt} = r_2 u_2 (1 - \beta u_1 - u_2) \end{cases} \tag{5}$$

where $\alpha = \dfrac{\nu_1^* \mu_1^* + \nu_2^* \mu_2^*}{(\mu_1^*)^2 + (\mu_2^*)^2} a$ and $\beta = \dfrac{\nu_1^* \mu_1^* + \nu_2^* \mu_2^*}{(\nu_1^*)^2 + (\nu_2^*)^2} b$.

III. Analysis of Reduced Model

In this section, we study the reduced system (5) with four parameters α, β, r_1 and r_2. We found that r_1 and r_2 do not effect much more the behaviour of the model. The parameters α and β measure the competitive effect of species 1 on species 2 and species 2 on species 1 respectively.

A. Invariant set

We establish the invariance set of the system (5) that is the first quadrant:

$$D = \{(u_1(t), u_2(t)) : (u_1(t) \ge 0, u_2(t) \ge 0 \quad \forall t \ge 0\}.$$

Theorem. *Assuming that the initial conditions lie in D, the system of equations for the model* (5) *has a unique solution that exists and remains in D for all time* $t \ge 0$.

Proof. The right-hand side of (5) is continuous with continuous partial derivatives in *D*, so (5) has a unique solution.

Now we show that *D* is forward-invariant. Consider the first equation in (5). This equation can be rewritten in the form

$$\frac{du_1}{dt} - r_1(1 - \alpha u_2(t)) u_1(t) = -r_1 u_1^2(t).$$

Solve this equation we get $u_1(t) = 0$ or

$$\frac{1}{u_1(t)} = \frac{1}{u_1(0)} e^{-r_1 \int_0^t (1-\alpha u_2(t))dt} + r_1 \int_0^t e^{r_1 \int_0^t (1-\alpha u_2(t))dt} dt.$$

Because $r_1 > 0$, we imply that $u_1(t) \ge 0$ for $t \ge 0$. Similarly, we found that $u_2(t) \ge 0$ for $t \ge 0$. Furthermore, we have

$$\frac{du_1}{dt} = r_1 u_1 (1 - u_1 - \alpha u_2) \le r_1 u_1 (1 - u_1) < 0 \text{ if } u_1 > 1,$$

so that all values u_1 are bounded. Similarly, all values u_2 are also bounded.

B. Equilibria

To find equilibria, we set the right-hand side of the system (5) equal to zero. Then we get the four following equilibria in the (u_1, u_2) plane:

$$O(0, 0),\ S_1(1, 0),\ S_2(0, 1) \text{ and } N\left(\tfrac{\alpha-1}{\alpha\beta-1}, \tfrac{\beta-1}{\alpha\beta-1} \right).$$

The equiliria O, S_1 and S_2 always exist. The equilibrium N exists in the first quadrant *D* if (α - 1)/(αβ - 1) ≥ 0 and (β - 1)(αβ - 1) ≥ 0. This condition only holds for the region in which α < 1, β < 1 or α > 1, β > 1 (region III, IV in Fig 1).

S_1 and S_2 relate to competitive abilities of species 1 and species 2, respectively. N represents a neutral competitive ability of species. This point corresponds to positive solution of the system. Note that N coincides S_1 for β = 1 and N coincides S_2 for α = 1.

The local stability for equilibria is determined by the Jacobian matrix of the system (5), which is

$$A = \begin{pmatrix} r_1(1 - 2u_1 - \alpha u_2) & -\alpha r_1 u_1 \\ -\beta r_2 u_2 & r_2(1 - 2u_2 - \beta u_1) \end{pmatrix}.$$

Eigenvalues for each equilibrium is obtained by solving the characteristic equation

$$\det(J-\lambda I)=0\,.$$

The equilibrium O(0,0) has two positive eigenvalues $\lambda_1 = r_1$ and $\lambda_2 = r_2$. This implies O is always unstable.

The equilibrium S_1 has two eigenvalues $\lambda_1 = -r_2$ and $\lambda_2 = (1-\beta)r_2$ in which λ_1 is negative. So, S_1 is stable for $\beta > 1$ and unstable for $\beta < 1$.

The equilibrium S_2 has two eigenvalues $\lambda_1 = (1-\alpha)r_1$ and $\lambda_2 = -r_2$ in which λ_2 is negative. Therefore, S_2 is stable for $\alpha > 1$ and unstable for $\alpha < 1$.

For the equilibrium N, we have two eigenvalues

$$\lambda_1 = \frac{1}{2(1-\alpha\beta)}\Big[(\alpha-1)r_1 + (\beta-1)r_2 + \sqrt{((\alpha-1)r_1+(\beta-1)r_2)^2 + 4(\alpha-1)(\beta-1)(\alpha\beta-1)r_1r_2}\;\Big] \quad (6)$$

$$\lambda_2 = \frac{1}{2(1-\alpha\beta)}\Big[(\alpha-1)r_1 + (\beta-1)r_2 - \sqrt{((\alpha-1)r_1+(\beta-1)r_2)^2 + 4(\alpha-1)(\beta-1)(\alpha\beta-1)r_1r_2}\;\Big]. \quad (7)$$

N is stable for $\alpha < 1$, $\beta < 1$ and unstable for $\alpha > 1$, $\beta > 1$.

The invading ability of species 1 depends on parameter α which is proportional to parameter *a*. Similarly, the invading of species 2 depends on β which is proportional to *b*.

C. Analysis of the model

In this section, we analyze the stability of equilibria in various regions in the parameter plane (α, β) (see the Fig 1 for regions) and give ecological explanations for the competition of species.

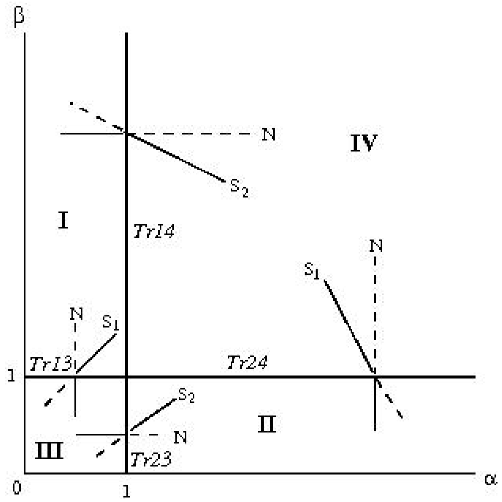

Fig. 1 Bifurcation diagram for the model of the system (5) in (α, β) plane with Region I ($\alpha < 1$, $\beta > 1$), Region II ($\alpha > 1$, $\beta < 1$), Region III ($\alpha < 1$, $\beta < 1$), Region IV ($\alpha > 1$, $\beta > 1$). The solid line is for stable equilibria and the dash line is for unstable equilibria

In Fig. 2, 3, 4 and 5, a circle corresponds to the equilibrium O, a square to the equilibrium S_1, a triangle to the equilibrium S_2 and a solid circle corresponds to the equilibrium N.

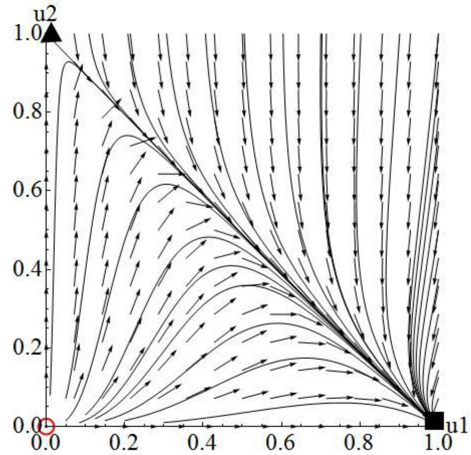

Fig. 2 Phase trajectories near equilibria for the dynamics behavious of the model in the region I for $r_1 = 0.25$, $r_2 = 0.75$, $\alpha = 0.35$ and $\beta = 1.25$. Species 1 invades species 2

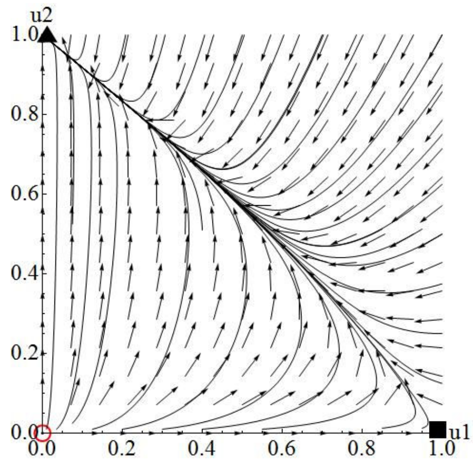

Fig. 3 Phase trajectories near equilibria for the dynamics behavious of the model in the region II for $r_1 = 0.25$, $r_2 = 0.75$, $\alpha = 1.25$, $\beta = 0.75$. Species 2 invades species 1

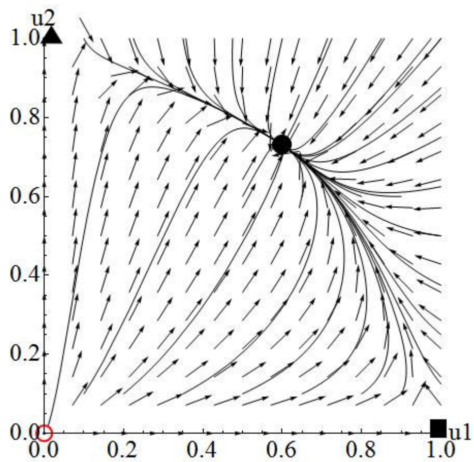

Fig. 4 Phase trajectories near equilibria for the dynamics behavious of the model in the region III for $r_1 = 0.5$, $r_2 = 0.75$, $\alpha = 0.55$, $\beta = 0.45$. Both species coexist with low population

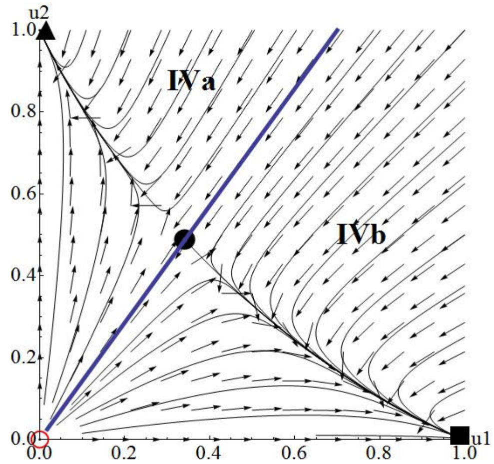

Fig. 5 Phase trajectories near equilibria for the dynamics behavious of the model in the region IV for $r_1 = 0.95$, $r_2 = 0.95$, α = 1.35, β = 1.5. Both species coexist with a separatrix

Region I (α < 1, β > 1):

This region corresponds to Fig 2. For parameters belong to region I, the invariant set *D* contains the equilibria O, S_1 and S_2. There is no interior equilibrium N. The equilibria O and S_2 are unstable, but S_1 is stable. The whole positive quadrant *D* is the domain of attraction of S_1. That means interior trajectories go to the point S_1.

In this case the interspecific competition of species 1 is much stronger than species 2, and species 2 becomes extinct.

Region II (α > 1, β < 1):

Fig 3 is a case for this region. As the same form of region I, for (α, β) in region II then *D* consists of the equilibrium O, S_1 and S_2. The equilibrium N is absent. O and S_1 are unstable. S_2 is a unique stable equilibrium. The domain of attractor of S_2 is the positive quadrant *D*.

For this region, effective ability of species 2 is much stronger than species 1, and species 1 will die out.

Region III (α < 1, β < 1):

This region is illustrated by Fig 4. With conditions of parameters in this region, four equilibria exist in the invariant set *D*. The equilibrium N is a unique stable equilibrium. The whole positive quadrant *D* is the domain of attraction of N. Three remaining equilibria are unstable. O is an unstable node, and both S_1 and S_2 are saddles.

If the interspecific competition is not too strong, the two populations can coexist stably, but at lower populations than their respective carrying capacities. In other word, the competition is not aggressive.

Region IV (α > 1, β > 1):

This region is related to Fig 5. In region IV, four equilibria lie in the positive quadrant *D*. The equilibrium O(0,0) is unstable. N is unstable and from (6) and (7) its eigenvalues are such that $\lambda_1 < 0 < \lambda_2$; so it is a saddle point. Both S_1(1,0) and S_2(0, 1) are stable nodes. Each equilibrium S_1 or S_2 has a domain of attraction. There is a line, a separatrix, which splits *D* into two nonoverlapping regions IVa or IVb as in Fig 5. The separatrix passes through the saddle equilibrium N.

Both species coexist in this region. Interspecific competition is aggressive and ultimately one population wins, while the other is driven to extinction. Competitive ability depends on the starting point of each species. If the initial conditions lie in domain IVa then $u_1 \to 0$ and $u_2 \to 1$, so the species 1 will die out. Therefore, the competition here has eliminated S_1. Otherwise, if the initial condition is in domain IVb then $u_1 \to 1$ and $u_2 \to 0$. In this case, species 2 becomes extinct.

D. Transcritical bifurcation

In this part, transcritical bifurcation is used to analyze the change of competition of one species to other species in the model. A bifurcation diagram for the reduced system (5) is given by Fig 1.

The change of stability of the equilibria S_1, S_2 and N in various regions of bifurcation diagram can be explained by transcritical bifurcation. In bifurcation theory, trancritical bifurcation is a special type of local bifurcation in which an equilibrium has an eigenvalue whose real part passes through zero. In transcritical bifurcation, an equilibrium exists for all values of a parameter and is never destroyed. Moreover, such an equilibrium interchanges its stability with another equilibrium as the parameter is varied. In other words, both before and after the bifurcation, there is one unstable and one stable equilibrium. However, their stability is exchanged when they collide. Then the unstable equilibrium becomes stable and vice versa.

In the model we found the transcritical bifurcation occurs on the lines α = 1 and β = 1.

Tr13 (β =1, 0 ≤ α < 1) and *Tr24* (β =1, α > 1) are lines of transcritical bifurcation of the equilibria N and S_1 where these equilibria coincide and exchange their stability. When β passes through value 1, the equilibrium N from unstable becomes stable while S_1 is from stable to unstable. We remark that from region IV the equilibrium N undergoes the transcritical bifurcation at a point in the line *Tr24 and* moves out the invariant set *D* . Therefore, in the real bifurcation diagram, the line for N in region II does not exist.

Tr23 (α = 1, 0 ≤ β < 1) and *Tr14* (α = 1, β > 1) are lines of transcritical bifurcation of the equilibria N and S_2 where they collide and interchange their stability. When α passes through value 1 then N from stable to unstable while S_2 from unstable to stable. Note that from region IV, the equilibrium N goes to transcritical bifurcation at a point in line *Tr14* and moves out the invariant set D. Therefore, the line for N in region I in the bifurcation diagram is not true.

By using the software package AUTO [7], one can detect the transcritical bifurcation of the equilibria N and S_1 (or S_2).

Fig 6 shows the transcritical bifurcation for the equilibria N and S_1. Fixing $\alpha = 0.5$ and varying β, we found the transcritical bifurcation occurs at value $\beta = 1$. The line for solutions 1, 2, and 3 is the line of N; and line for solutions 2 , 4, 5, 6 and 7 is the line of S_1. The solid line is for stable equilibria and the dash line is for unstable equilibria.

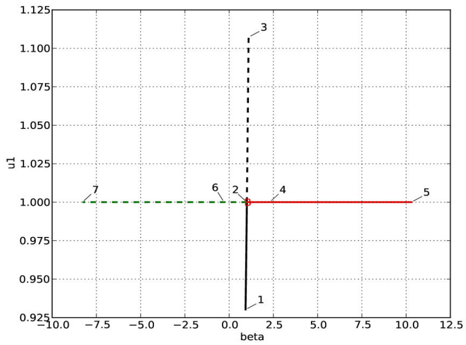

Fig. 6. Transcitical bifurcation of N and S_2 when β varies

Fig 7 represents the the transcritical bifurcation for the equilibria N and S_2. Fixing $\beta = 0.75$ and varying α, we found the transcritical bifurcation occurs at value $\alpha = 1$. The line for solutions 1, 2, 3 and 4 is the line of N; and line for solutions 3, 5, 6, 7 and 8 is the line of S_1. The solid line is for stable equilibria and the dash line is for unstable equilibria.

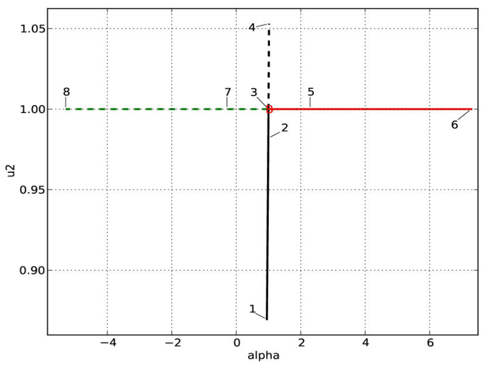

Fig. 7 Transcitical bifurcation of N and S_2 when α varies

E. pace of parameters

In this section, we extend the investigation of species competition to parameters a, b, ν_1^*, ν_2^*, μ_1^* and μ_2^*. Specially, we consider the competition of species 1 and species 2 on patch 1. A similar result is obtained for patch 2. We show a parameter space for which one can define the stability of each equilibrium. So the competition can be identified.

Let us make a change of notations $x = \mu_1^*$ and $y = \nu_1^*$, then $\nu_2^* = 1 - y$, $\mu_2^* = 1 - x$. This implies

$$\alpha = \frac{\nu_1^*\mu_1^* + \nu_2^*\mu_2^*}{(\mu_1^*)^2 + (\mu_2^*)^2} a = \frac{xy + (1-x)(1-y)}{x^2 + (1-x)^2} a$$

and

$$\beta = \frac{\nu_1^*\mu_1^* + \nu_2^*\mu_2^*}{(\nu_1^*)^2 + (\nu_2^*)^2} b = \frac{xy + (1-x)(1-y)}{y^2 + (1-y)^2} b.$$

The condition for transcritical bifurcation $\alpha = 1$ corresponds to

$$a = \frac{x^2 + (1-x)^2}{xy + (1-x)(1-y)} \equiv a(x, y)$$

and $\beta = 1$ corresponds to

$$b = \frac{y^2 + (1-y)^2}{xy + (1-x)(1-y)} \equiv b(x, y).$$

The functions $a(x, y)$ and $b(x, y)$ are defined on the domain $I = [0, 1]\times[0, 1] \setminus \{(0, 1), (1, 0)\}$. As (x, y) is close to the point (0, 1) or (1, 0), the values of $a(x, y)$ and $b(x, y)$ become very large. Then we can get the condition $\alpha > 1$ and $\beta > 1$.

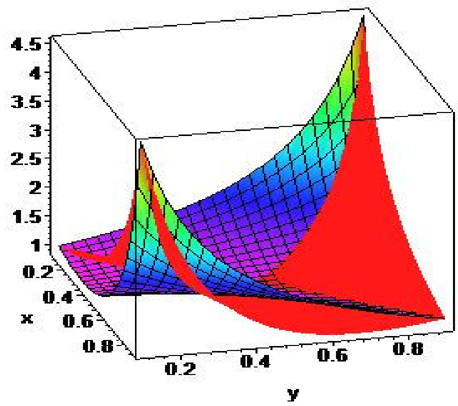

Fig. 8 The graphs of the function $a(x, y)$ (grid) and $b(x, y)$ (solid)

Each of the graphs of $a(x, y)$ and $b(x, y)$ is a surface that divides the space $I \times [0, +\infty)$ into two overlapping spaces. In order to consider the intersection of two surfaces we set $a(x, y) = b(x, y)$ then we get $(x - y)(x + y - 1) = 0$. It yields $y = x$ or $y = 1 - x$. This means that the graphs of the functions $a(x, y)$ and $b(x, y)$ intersect in lines $y = x$ and $y = 1 - x$. Now the domain I is separated into four subdomains:

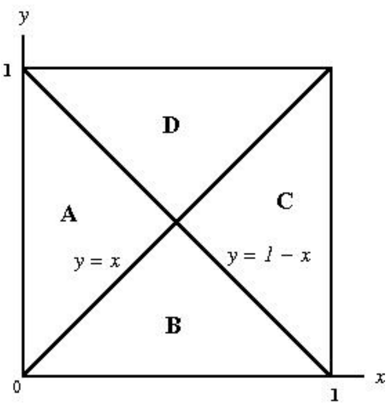

Fig. 9 Subdomains of the domain I

$$A = \{(x, y): y > x, y < 1 - x\},$$
$$B = \{(x, y): y < x, y < 1 - x\},$$
$$C = \{(x, y): y < x, y > 1 - x\},$$
$$D = \{(x, y): y > x, y > 1 - x\}.$$

Let X be one of domains A, B, C, D. Surfaces $a = a(x, y)$ and $b = b(x, y)$ divide the space $X\times[0, +\infty)$ into three overlapping spaces. Therefore, two surfaces separate the space $I \times [0, +\infty)$ into twelve overlapping subspaces. We obtain parameter value regions corresponding to the different competition outcomes.

For $(x, y) \in X$ and $a, b \in [0, +\infty)$ we can obtain values of α and β in comparison with 1, so we know dynamics of the model.

Region A: In this region we have $y > x$ and $y < 1 - x$, so $(x - y)(x + y - 1) > 0$. This implies $b(x, y) < a(x, y)$. We denote a by a_u if $a > a(x, y)$, a_m if $b(x, y) < a < a(x, y)$ and a_l if $a < b(x, y)$. Similarly, we denote b by b_u if $b > a(x, y)$, b_m if $b(x, y) < b < a(x, y)$ and b_l if $b < b(x, y)$. With this definition we have

$$a_l,\ b_l < b(x,y) < a_m,\ b_m < a(x,y) < a_u,\ b_u$$

For various values of a and b, we obtain the following table:

Table I: List of values for parameters a, b, α, β corresponding to region A

a	b	α, β
a_u	b_u	$\alpha > 1,\ \beta > 1$
a_u	b_m	
a_u	b_l	$\alpha > 1, \beta < 1$
a_m	b_u	$\alpha < 1, \beta > 1$
a_m	b_m	
a_l	b_u	
a_l	b_m	
a_m	b_l	$\alpha < 1, \beta < 1$
a_l	b_l	

Region B: For (x, y) belongs to this region, we have $y < x$ and $y < 1 - x$. This implies $a(x, y) < b(x, y)$. Let a be one of values a_l, a_m, a_u, and b be one of values b_l, b_m, b_u where

$$a_l,\ b_l < a(x,y) < a_m,\ b_m < b(x,y) < a_u,\ b_u.$$

We have the following table:

Table II: List of values for parameters a, b, α, β corresponding to region B

a	b	α, β
a_u	b_u	$\alpha > 1,\ \beta > 1$
a_m	b_u	
a_u	b_m	$\alpha > 1, \beta < 1$
a_u	b_l	
a_m	b_m	
a_m	b_l	
a_l	b_u	$\alpha < 1, \beta > 1$
a_l	b_m	$\alpha < 1, \beta < 1$
a_l	b_l	

Region C: We have $y < x$ and $y > 1 - x$. This yields the condition $a(x, y) > b(x, y)$. The table of parameters for this region is the same as Table 1.

Region D: We have $y > x$ and $y > 1 - x$. This leads to $a(x, y) < b(x, y)$. The table for parameters for this region is the same as Table 2.

IV. Numerical analysis for the complete model

In this section, we carry out a numerical investigation for the fast model given by the system (1). Applying results from the reduced model, we explain some dynamical behaviour of the fast model. The results of numerical analysis show that the long term behaviour of the fast time model and slow time model is very similar (see Fig 11, 13 and 15). We found that in the case in which one species wins another species the equilibrium N can exist.

Now, we consider the system (1) of fast model in the coordinates $(n_{11}, n_{12},\ n_{21}, n_{22})$. The invariant set of the system is

$$\bar{D} = \{(n_{11}(t), n_{12}(t), n_{21}(t), n_{22}(t)): \\ n_{11}(t) \geq 0, n_{12}(t) \geq 0, n_{21}(t) \geq 0, n_{22}(t) \geq 0 \quad \forall t \geq 0\}$$

The system has equilibria O(0, 0, 0, 0), $S_1(n_{11}^{s_1}, n_{12}^{s_1}, 0, 0)$, $S_2(0, 0, n_{21}^{s_2}, n_{22}^{s_2})$ and $N(n_{11}^N, n_{12}^N, n_{21}^N, n_{22}^N)$ in $\bar{D}$.

* Case I: Species I wins.

Different from the slow time model (4), the equilibrium N can exist the domain $\bar{D}$. We consider in two cases as follow:

+ *The equilibrium N exists*:

We choose values for parameters: $k = 0.5$, $\bar{k} = 0.6$, $m = 0.75$, $\bar{m} = 0.5$, $K = 10$, $e = 0.2$, $r_1 = 0.75$, $r_2 = 0.5$, $a = 0.5$, $b = 1$. This implies $\alpha = 0.762 < 1$ and $\beta = 2.674 > 1$.

The system has four equilibria:

O($n_{11} = n_{12} = n_{21} = n_{22} = 0$) with eigenvalues -1.15, -0.95, 0.15, 0.1;

$S_1(n_{11} = 9.14,\ n_{12} = 10.7323,\ n_{21} = n_{22} = 0)$ with eigenvalues -1.251, -1.246, -0.1497, 0.00227;

$S_2(n_{11} = n_{12} = 0,\ n_{21} = 11.4640,\ n_{22} = 7.8664)$ with eigenvalues -1.26, -1.0238, 0.0348, 0.0789, -0.0348;

$N(n_{11} = 8.9484,\ n_{12} = 10.522,\ n_{21} = 0.493,\ n_{22} = 0.325)$ with eigenvalues -1.265, -1.23, -0.1487, 0.00004.

All equilibria are unstalble. Although S_1 is unstable, but its strong stable direction is much more stronger than that of S_2 and N. Fig. 10 shows that the values n_{21} and n_{22} tend to 0. This implies species 2 dies out and species 1 wins. Time series of n_1 and u_1 in Fig. 11 indicate the long term behaviour of the fast time and slow time models is very similar.

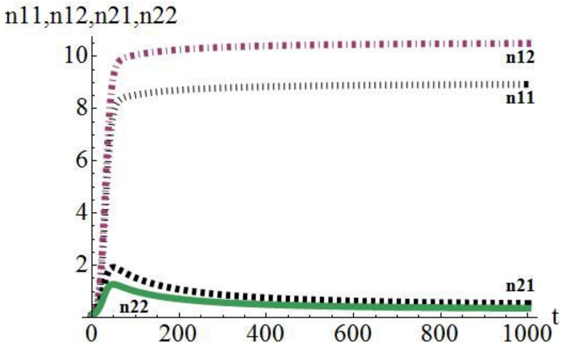

Fig. 10 Time series of n_{11}, n_{12}, n_{21} and n_{22} for case I with the existence of the equilibrium N

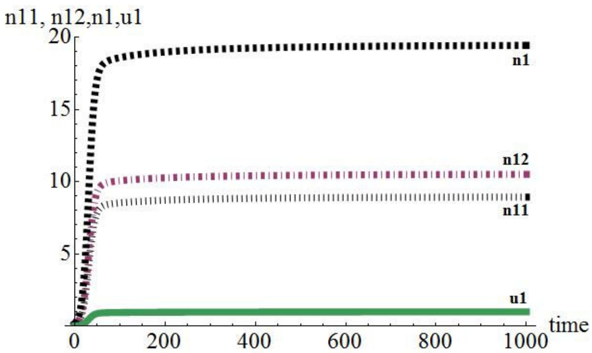

Fig. 11 Time series of n_{11}, n_{12}, n_1 and u_1 for case I with the existence of the equilibrium N. The long term behaviour of n_1 and u_1 is very similar

+ *The equilibrium N does not exist*:

Values for parameters in this case are $k = 0.75$, $\bar{k} = 0.5$, m = 0.85, $\bar{m}$ = 0.2, K = 10, e = 0.2, $r_1 = 0.5$, $r_2 = 0.75$, a = 0.55, b = 1. This implies α = 0.491 < 1 and β = 1.72 > 1.

In the domain $\bar{D}$, the system (1) has three equilibria:

$O(n_{11} = n_{12} = n_{21} = n_{22} = 0)$ with eigenvalues 0.15, -1.1, 0.1, -0.94;

$S_1(n_{11} = 11.4284,\ n_{12} = 7.9454,\ n_{21} = n_{22} = 0)$ with eigenvalues -0.1489, -1.3822, -0.007, -1.0362.

$S_2(n_{11} = n_{12} = 0,\ n_{21} = 11.7887,\ n_{22} = 3.0219)$ with eigenvalues 0.0826, -0.0831, -1.1548, -1.0086.

The equilibria O and S_2 are unstable, but S_1 is a stable equilibrium. We can see $n_{11} \to 11.4284 \equiv n_{11}(S_1)$, $n_{12} \to 7.9454 \equiv n_{12}(S_1)$ and $n_{21} = n_{22} \to 0$. Therefore, species 1 invades.

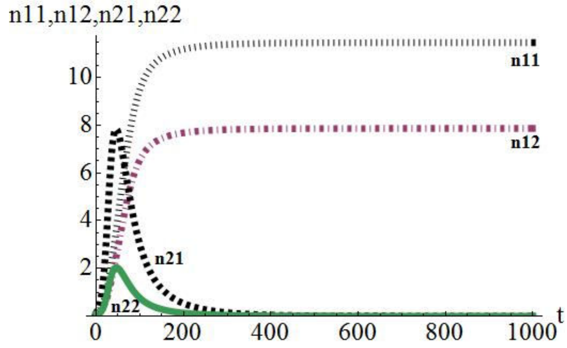

Fig. 12 Time series of n_{11}, n_{12}, n_1 and u_1 for case I without the existence of the equilibrium N

* Case II: Species 2 wins.

This case is similar to case I. Here, we only consider a case in which the equilibrium N is absent in $\bar{D}$.

We choose parameters: $k = 0.85$, $\bar{k} = 0.1$, m = 0.75, $\bar{m} = 0.5$, K = 10, e = 0.2, $r_1 = 0.5$, $r_2 = 0.75$, a = 1, b = 0.5. This leads to α = 1.768 > 1 and β = 0.367 > 1. There are three equilibria in $\bar{D}$:

$O(n_{11} = n_{12} = n_{21} = n_{22} = 0)$ with eigenvalues 0.1, -0.85, 0.15, -1.1.

$S_1(n_{11} = 11.1177,\ n_{12} = 1.4541,\ n_{21} = n_{22} = 0)$ with eigenvalues -0.097, -0.903, 0.096, -1.14;

$S_2(n_{11} = n_{12} = 0,\ n_{21} = 11.4284,\ n_{22} = 7.9454)$ with eigenvalues -0.01, -0.051, -0.933, -1.277.

S_2 is stable while O and S_1 are unstable. Thus, species 1 wins and species 2 extincts.

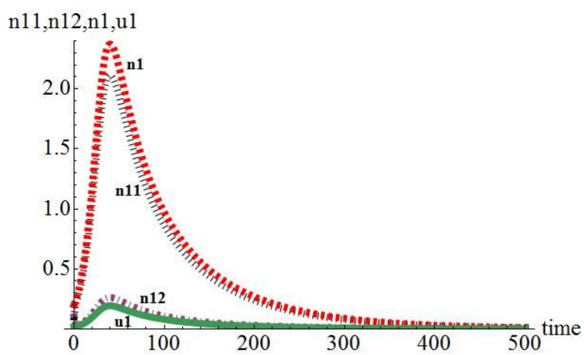

Fig. 13 Time series of n_{11}, n_{12}, n_1 and u_1 for case II

* Case III: Two species coexist with low population.

Chosen parameters are $k = 0.75$, $\bar{k} = 0.25$, m = 0.75, $\bar{m} = 0.5$, K = 10, e = 0.2, $r_1 = 0.75$, $r_2 = 0.5$, a = 0.45,

$b = 0.5$. This implies $\alpha = 0.76 > 1$ and $\beta = 0.52 > 1$.

There are four equilibria in the domain $\bar{D}$:

O($n_{11} = n_{12} = n_{21} = n_{22} = 0$) with eigenvalues -1.15, -0.85, 0.15, 0.1;

S_1($n_{11} = 12.0543$, $n_{12} = 4.5134$, $n_{21} = n_{22} = 0$) with eigenvalues -1.18792, -1.05265, -0.144381, 0.0550849;

S_2($n_{11} = n_{12} = 0$, $n_{21} = 1.1464$, $n_{22} = 0.7866$) with eigenvalues -1.26015, -0.909281, 0.0788007, -0.034863;

N($n_{11} = 6.7003$, $n_{12} = 2.4337$, $n_{21} = 10.6535$, $n_{22} = 7.6711$) with eigenvalues -1.25658, -1.01998, -0.112958, -0.00909511.

The equilibria O, S_1 and S_2 are unstable while N is a unique stable equilibrium. Both species 1 and 2 coexist with low population.

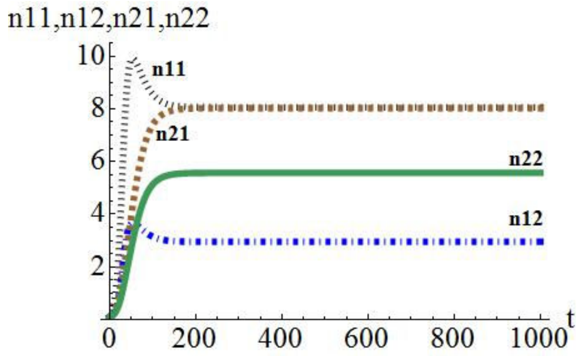

Fig. 14 Time series of n_{11}, n_{12}, n_{21} and n_{22} for case III

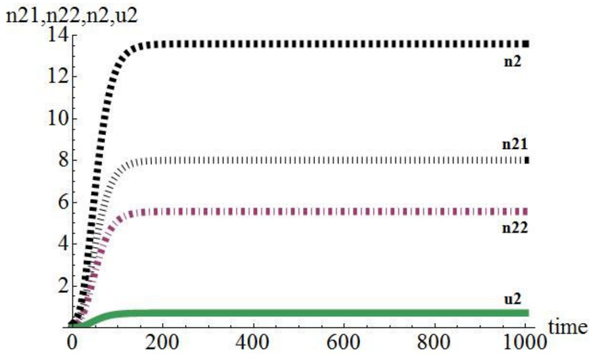

Fig. 15 Time series of n_{11}, n_{12}, n_1 and u_1 for case III. The long term behaviour of n_2 and u_2 is very similar

* Case IV: Two species coexist with their attracting domains.

Values for parameters are $k = 0.5$, $\bar{k} = 0.6$, $m = 0.75$, $\bar{m} = 0.5$, $K = 10$, $e = 0.2$, $r_1 = 0.75$, $r_2 = 0.5$, $a = 2.5$, $b = 1.5$. This implies $\alpha = 3.809 > 1$ and $\beta = 4.01 > 1$.

We have four equilibria in $\bar{D}$:

O($n_{11} = n_{12} = n_{21} = n_{22} = 0$) with eigenvalues -1.15, -0.95, 0.15, 0.1;

S_1($n_{11} = 9.140$, $n_{12} = 10.7323$, $n_{21} = n_{22} = 0$) with eigenvalues -1.30154, -1.24643, -0.149742, -0.0465458;

S_2($n_{11} = n_{12} = 0$, $n_{21} = 11.464$, $n_{22} = 7.8664$) with eigenvalues -1.32262, -1.26015, -0.202272, -0.034863 and

N($n_{11} = 4.9895$, $n_{12} = 6.0509$, $n_{21} = 2.1741$, $n_{22} = 1.4395$) with eigenvalues -1.29969, -1.13731, -0.128501, 0.0368108.

The equilibria S_1 and S_2 are stable while O and N are unstable. Each of equilibria S_1 and S_2 has a domain of atraction. Depending on the initial condition, a solution tends to S_1 or S_2. In Fig. 16, $n_{21} \to 0$, $n_{22} \to 0$, $n_{11} \to 9.14$, $n_{12} \to 10.7323$. So, species 1 invades. Otherwise, in Fig. 17, $n_{11} \to 0$, $n_{12} \to 0$, $n_{21} \to 11.464$, $n_{22} \to 7.8664$. Hence, species 2 wins.

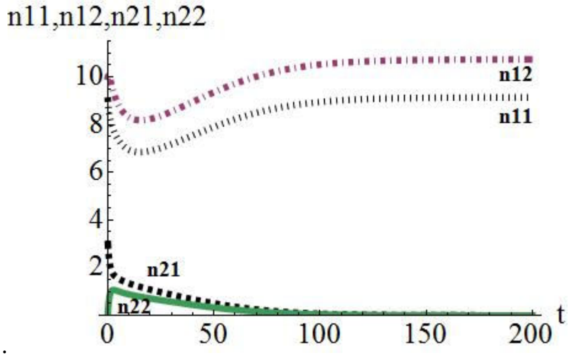

Fig. 16 Time series of n_{11}, n_{12}, n_{21} and n_{22} for case IV (species 1 wins)

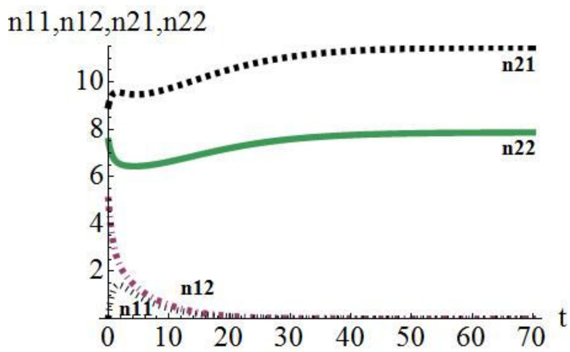

Fig. 17 Time series of n_{11}, n_{12}, n_{21} and n_{22} for case IV (species 2 wins)

V. CONCLUSIONS

In this paper, a interspecific competition model with two species and two patches is studied. Dynamical behaviour of this system is investigated at equilibrium points. It has been shown that the positive solutions possess transcritical bifurcations, as one parameter is varied, the dynamics of the system near to this solution changes the stability. Both analytically and numerically, simulation shows that in the parameter space, the model sensitively depends on the parameter values and initial conditions. It would be interesting if we study more species and more competition patches connected by migrations.

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