Notas de Matemática, No. 239
Mérida, 2005.

Pattern formation in a reaction diffusion ratio-dependent predator-prey model

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Abstract

In this paper we study the effect of the diffusion on the stability of the equilibria in a reaction diffusion ratio-dependent predator-prey model and we explore under which parameter values Turing instability can occur giving rise to non-uniform stationary solutions. Moreover, their stability is studied.

key words. Turing instability, pattern formation, ratio-dependent predator-prey, Reaction-diffusion system.

AMS(MOS) subject classifications. 35K57 ; 92D25

1 Introduction

In this paper we are going to study the following reaction diffusion ratio dependent predator prey model

$$\frac{\partial N}{\partial t} = D_1 \Delta N + aN(1 - \frac{N}{K}) - \frac{cNP}{mP+N}, \quad x \in \Omega, \ t > 0,$$
$$\frac{\partial P}{\partial t} = D_2 \Delta P + P\left(-d + \frac{fN}{mP+N}\right), \qquad x \in \Omega, \ t > 0, \tag{1.1}$$

subject to the Neumann boundary conditions

$$\frac{\partial N}{\partial \eta} = \frac{\partial P}{\partial \eta} = 0, \qquad x \in \partial\Omega, \quad t > 0,$$

and initial conditions

$$N(x,0) = \varphi_1(x) \geq 0, \quad P(x,0) = \varphi_2(x) \geq 0, \quad x \in \Omega.$$

where a, K, c, m, f, d are positive constants and $N(x,t)$, $P(x,t)$ represent the population density of prey and predator at $x \in \Omega$ and at time t respectively. The prey grows with intrinsic growth rate a and carrying capacity K in the absence of predation. The predator consumes the prey with functional response of Michaelis-Menten type $cuy/(m+u)$, $u = x/y$ and contributes to its growth with rate $fuy/(m+u)$. The constant d is the death rate of predator, and $D_i > 0$ are constants, $i = 1, 2$; while Δ denotes the Laplace operator in $\Omega \subset \mathbb{R}^n$, Ω bounded and connected.

The motivation to consider the above described model comes from growing evidence ([1,2,4,7]) that in some situations, specially when predator have to search for food and therefore have to share or compete for food, a more suitable general predator prey theory should be based on the so-called ratio-dependent theory, which can be roughly stated as that the per capita predator growth rate should be a function of the ratio of prey to predator abundance. This is supported by numerous field and laboratory experiments and observations ([2–4]).

Hsu et al. in [11] perform a global analysis of the Michaelis-Menten-type ratio-dependent predator-prey system without diffusion. Moreover, they discuss the main differences between the classical predator-prey models and the ratio dependent predator-prey system. In particular they brought into discussion the well-known “paradox of enrichment" or equivalently “the biological control paradox".

In this paper we will study the effect of the diffusion on the stability of the equilibria in a reaction diffusion ratio-dependent predator-prey model and we explore under which parameter values Turing instability can occur giving rise to non-uniform stationary solutions. Their stability is studied. Moreover, we give a comprehensive description under which parameter values this pattern formation arises. In the concluding remark we will discuss the differences between the dynamics of this model and the classical one.

2 Preliminaries

For simplicity, we nondimensionalizes the system (1.1) with the following scaling

$$t \longrightarrow at, \quad N \longrightarrow \frac{N}{K}, \quad P \longrightarrow \frac{mP}{K}$$

then the system (1.1) takes the form

$$\begin{aligned} \frac{\partial N}{\partial t} &= d_1 \Delta N + N(1-N) - \frac{sNP}{P+N}, \quad x \in \Omega,\ t>0, \\ \frac{\partial P}{\partial t} &= d_2 \Delta P + \delta P \left(-r + \frac{N}{P+N} \right), \quad x \in \Omega,\ t>0, \end{aligned} \tag{2.1}$$

where

$$s = \frac{c}{ma}\ ,\ \delta = \frac{f}{a}\ ,\ r = \frac{d}{f}\ ,\ d_1 = \frac{D_1}{a}\ ,\ d_2 = \frac{D_2}{a}$$

We will show that the reaction-diffusion system (2.1) generates a dynamical system and it is biologically well possed on suitable Banach space.

Let us set $F = (F_1, F_2)$, $U = (N, P)$ and $D = \text{diag}[d_1, d_2]$, where

$$F_1(N,P) = N(1-N) - \frac{sNP}{N+P}, \qquad F_2(N,P) = \delta P(-r + \frac{N}{P+N}).$$

Henceforth, considering also an initial condition, system (2.1) can be rewritten as

$$\frac{\partial U(x,t)}{\partial t} = D\Delta U(x,t) + F(U), \quad x \in \Omega, \quad t > 0 \tag{2.2}$$

$$\frac{\partial U}{\partial \eta}(x,t) = 0, \qquad x \in \partial\Omega, \quad t > 0 \tag{2.3}$$

$$U(x,0) = \varphi(x), \qquad x \in \Omega. \tag{2.4}$$

Let X be the Banach space $X_1 \times X_2$, where $X_i = C(\overline{\Omega}), i = 1,2$. The norm on X is defined by $\mid \varphi \mid = \mid \varphi_1 \mid + \mid \varphi_2 \mid$. Let A_N^0 and A_P^0 be the differential operators $A_N^0 N = d_1 \Delta N$ and $A_P^0 P = d_2 \Delta P$, defined on the domains $D(A_N^0)$ and $D(A_P^0)$, respectively; where

$$D(A_N^0) = \{N \in C^2(\Omega) \cap C^1(\overline{\Omega}) : A_N^0 N \in C(\overline{\Omega}), \frac{\partial N}{\partial \eta}(x) = 0, x \in \partial\Omega\},$$

$$D(A_P^0) = \{P \in C^2(\Omega) \cap C^1(\overline{\Omega}) : A_P^0 P \in C(\overline{\Omega}), \frac{\partial P}{\partial \eta}(x) = 0, x \in \partial\Omega\}.$$

The closures A_N of A_N^0, and A_P of A_P^0 in X_i generate analytic semigroups of bounded linear operators $T_N(t)$ and $T_P(t)$ for $t \geq 0$ such that $N(t) = T_N(t)\varphi_1$ and $P(t) = T_P(t)\varphi_2$ are solutions of the abstract linear differential equations in X_i given by

$$N'(t) = A_N N(t), \; P'(t) = A_P P(t).$$

An additional property of the semigroup is that for each $t > 0$, $T_N(t)$ and $T_P(t)$ are compact operators. In the language of partial differential equations $N(x,t) = [T_N(t)\varphi_1](x)$ and $P(x,t) = [T_P(t)\varphi_2](x)$ are classical solutions of the initial boundary value problem (2.2) with $F_1 = F_2 = 0$.

Let $\mathsf{T}(t) : X \longrightarrow X$ be defined by $\mathsf{T}(t) = T_N(t) \times T_P(t)$. Then $\mathsf{T}(t)$ is a semigroup of operators on X generated by the operator $\mathsf{A} = A_N \times A_P$ defined on $D(\mathsf{A}) = D(A_N) \times D(A_P)$ and $U(x,t) = [\mathsf{T}(t)\varphi](x)$ is the solution of the linear system

$$\frac{\partial U}{\partial t}(x,t) = D\Delta U(x,t), \quad x \in \Omega, \quad t > 0$$

$$\frac{\partial U}{\partial \eta}(x,t) = 0, \quad x \in \partial\Omega, \quad t > 0, \quad U(x,0) = \varphi(x), \quad x \in \Omega.$$

Observe that the nonlinear term F is twice continuously differentiable in U. Therefore, we can define the map $[F^*(\varphi)](x) = F(\varphi(x))$ which maps X into itself and equation (2.2) can be viewed as the abstract O.D.E. in X given by

$$u'(t) = \mathsf{A}u(t) + F^*(u(t)), \; u(0) = \varphi. \tag{2.5}$$

While a solution $u(t)$ de (2.5) can be obtained under the restriction that $\varphi \in D(\mathsf{A})$, a mild solution can be obtained for every $\varphi \in X$ by requiring only that $u(t)$ is a continuous solution of the following integral equation

$$u(t) = \mathsf{T}(t)\varphi + \int_0^t \mathsf{T}(t-s)F^*(u(s))ds, \quad t \in [0,\beta), \tag{2.6}$$

where $\beta = \beta(\varphi) \leq \infty$. Restricting our attention to functions φ in the set

$$X_\Lambda = \left\{\varphi \in X : \varphi(x) \in \Lambda,\ x \in \overline{\Omega}\right\},$$

where $\Lambda = \left\{U = (N,P) \in R^2 : N \geq 0, P \geq 0\right\}$, and taking into account the definition of the functions F_i, we obtain that $F_1(0,P) = 0$ and $F_2(N,0) = 0$ for $U \in \Lambda$. Thus, Corollary 3.2, p. 129 in [16] implies that the Nagumo condition for the positive invariance of Λ is satisfied, i.e.,

$$\lim_{h \to 0^+} h^{-1} dist(\Lambda, U + hF(U)) = 0,\ U \in \Lambda. \tag{2.7}$$

On the other hand, a direct applications of the strong parabolic maximum principle can be used to show that the linear semigroup $\mathsf{T}(t)$ leaves X_Λ positively invariant, i.e.

$$\mathsf{T}(t) X_\Lambda \subset X_\Lambda,\ \ t \geq 0. \tag{2.8}$$

Finally, conditions (2.7) and (2.8) together allow us apply Theorem 3.1, p. 127 in [16], giving us

Lemma 1 *For each $\varphi \in X_\Lambda$, (2.1) has a unique mild solution $u(t) = u(\varphi,t) \in X_\Lambda$ and a classical solution $U(x,t) = [u(t)](x)$. Moreover, the set X_Λ is positively invariant under flow $\Psi_t(\varphi) = u(\varphi,t)$ induced by (2.1).*

So, the model (2.1) is biologically well possed and its relevant dynamic is concentrated in X_Λ.

Finally, we are going to prove that all solutions of system (2.1) are bounded and therefore defined for all $t \geq 0$. Actually, from the following result by using the general theory of infinite dynamical system it follows that the relevant dynamic of the system (2.1) is concentrated in compact set of the space X_Λ.

Theorem 1 *Let (N,P) be any solution of (2.1). Then*

$$\limsup_{t \to \infty} \max_{x \in \Omega} N(x,t) \leq 1 \quad , \quad \limsup_{t \to \infty} \max_{x \in \Omega} P(x,t) \leq \frac{1}{r}\ .$$

Proof 1 *From the first equation of the system (2.1), it follows that*

$$\frac{\partial N}{\partial t} \leq d_1 \Delta N + N(1-N),$$

as long N is defined as a function of t.

Let z be the solution of the equation

$$z'(t) = z(t)(1 - z(t)) \quad , \quad z(0) = \max_{x \in \Omega} N(x,0).$$

From the comparison principle, we obtain $N(x,t) \leq z(t)$. Now, taking into account that for any $\epsilon > 0$ there exists a $T_\epsilon > 0$ such that $z(t) < 1 + \epsilon$ for any $t \geq T_\epsilon$, which in turn implies that $N(x,t)$ is defined for all $t \geq 0$, and $\limsup_{t\to\infty} \max_{x\in\Omega} N(x,t) \leq 1$.

Having in mind that for a given $\epsilon > 0$ there exists a $T_\epsilon > 0$ such that $N(x,t) \leq 1 + \epsilon$ for any $x \in \Omega$ and $t \geq T_\epsilon$, and by using the second equation of (2.1), we get

$$\frac{\partial P}{\partial t} - d_2 \Delta P \leq \delta P(-r + \frac{1+\epsilon}{P}) = -\delta r P + \delta(1+\epsilon),$$

for any $x \in \Omega$ *and* $t \geq T_\epsilon$.

Let z *be the solution of the following initial value problem*

$$z'(t) = -\delta r z(t) + \delta(1+\epsilon), \qquad z(T_\epsilon) = \max_{x\in\Omega} P(x, T_\epsilon).$$

After straightforward computation we get

$$z(t) \leq \frac{1+\epsilon}{r} + z(T_\epsilon)e^{-\delta r(t-T_\epsilon)}, \quad \forall t \geq T_\epsilon.$$

Finally, by using the comparison principle we know that $P(x,t) \leq z(t)$ *as long* P *is defined as function of* t. *This together with the previous inequality implies that*

$$\limsup_{t\to\infty} \max_{x\in\Omega} P(x,t) \leq \frac{1}{r}.$$

Which completes the proof.

3 Analysis of the model without diffusion

In this section we will study the system (2.1) without diffusion, i.e.,

$$N'(t) = F_1(N,P), \;\; P'(t) = F_2(N,P). \tag{3.1}$$

In particular, we will focus our attention to the existence of equilibria and their local stability. This information will be crucial in the next section where we study the effect of the diffusion parameters on the stability of the steady states.

The equilibria of the system (3.1) are given by the solution of the following equations

$$N(1 - N - \frac{sP}{P+N}) = 0 \quad , \quad \delta P(-r + \frac{N}{P+N}) = 0.$$

The system (3.1) has in the first quadrant the equilibrium points $(0,0)$ and $(1,0)$ for all parameters values. If $0 < r < 1$ and $0 < s < 1/(1-r)$, then (3.1) admits a nontrivial equilibrium, which is given by

$$(N^*, P^*) = \left(s(r-1)+1, \frac{(1-r)[s(r-1)+1]}{r} \right).$$

We point out that for $r = 1$ we get that $(N^*, P^*) = (1, 0)$.

Hereafter, we will assume that $(r,s) \in D$, where D is the region given by

$$D = \left\{ (r,s) : 0 < r < 1, 0 < s < \frac{1}{1-r} \right\}.$$

In the system (3.1) the origin is a non analytical complicated equilibrium point. The structure of a neighborhood of point $(0,0)$ in the first quadrant of the plane (x,y) and the asymptotes of trajectories for $x, y \longrightarrow 0$ depend on parameter values and change in an essential way with a change of parameter. See [6].

A straightforward computation shows us that the equilibrium point $(1,0)$ is locally asymptotically stable for $r>1$, and unstable if $0<r<1$.

Linearizing the system (3.1) around the nontrivial equilibrium (N^*,P^*), we obtain that the characteristic equation is given by

$$\lambda^2 - \mathrm{trace}A\,\lambda + \det A = 0.$$

where

$$A = \begin{pmatrix} s(1-r^2)-1 & -sr^2 \\ \delta(1-r)^2 & -\delta r(1-r) \end{pmatrix}.$$

Taking into account that $\mathbb{R}e\lambda<0$ if and only if $\mathrm{trace}A<0$ and $\det A>0$, we get that (N^*,P^*) is locally asymptotically stable if and only if $r,s,\delta\in D_s$, where D_s is the set determined by the following inequalities:

$$0<r<1, \qquad 0<s<\frac{1}{1-r^2}+\frac{\delta r}{1+r}, \qquad s<\frac{1}{1-r}, \qquad \delta>0. \tag{3.2}$$

Let us set $f(r)=\dfrac{1}{1-r}$ and $g_\delta(r)=\dfrac{r\delta}{1+r}+\dfrac{1}{1-r^2}$, where δ is a positive parameter. We represent in Fig. 1a and 1b the regions of asymptotic stability of the nontrivial equilibrium.

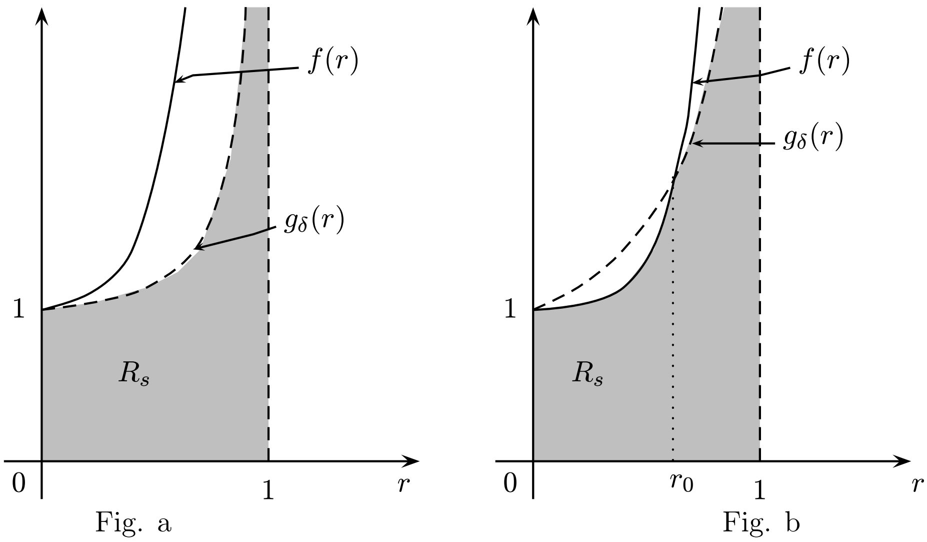

Figure 1: Fig. a R_s: Region of local asymptotic stability for $0<\delta\le 1$. Fig. b R_s:Region of local asymptotic stability for $\delta>1$.

4 Turing instability

It is obvious that the equilibria of the system (3.1) are solutions of (2.1). We shall focus our attention on the nontrivial equilibrium $U^*=(N^*,P^*)$ of the system (3.1). More concretely, in this section we will analyze the stability of nontrivial steady-state solutions of (2.1).

Definition 1 *(see [14]) The equilibrium U^* of* (2.1) *is said to be diffusionally (Turing) unstable if it is an asymptotically stable equilibrium of* (3.1) *but it is unstable with respect to* (2.1).

The stability of a homogeneous stationary solution U^* of (3.1) will be studied via linearized stability analysis (see for instance [10], pp. 68-70). Setting $W = U - U^*$ and recalling that $A = F'(U^*)$, as given previously, the linearized system of the reaction diffusion equation (2.1) around U^* is given by

$$\frac{\partial W}{\partial t} = D\Delta W + AW, \qquad \frac{\partial W}{\partial \eta}(x,t) = 0,\ x \in \partial\Omega,\ t > 0. \tag{4.1}$$

The trivial solution, $W = 0$, is asymptotically stable if and only if every solution of (4.1) decays to zero as $t \longrightarrow \infty$.

Let $\phi_j(x)$ denote the jth eigenfunction of the Laplacian operator $-\Delta$ on Ω with no-flux boundary conditions. That is,

$$\Delta\phi_j + \lambda_j\phi_j = 0, \quad x \in \Omega, \qquad n.\nabla\phi_j = 0,\ x \in \partial\Omega,$$

for scalars λ_j satisfying

$$0 = \lambda_0 < \lambda_1 < \lambda_2 < ....$$

The determination of the pairs $(\phi_j, \lambda j)$ is a standard problem (see for instance [9], pp. 205-208). The differential operator $-\Delta$, with no-flux boundary conditions, is self-adjoint in $L_2(\Omega)$, that is

$$\int_\Omega -\Delta\psi_1 \cdot \psi_2 dx = \int_\Omega -\Delta\psi_2 \cdot \psi_1 dx,$$

and it is easy to see that,

$$\lambda_j = \frac{\int_\Omega \mid \nabla\phi_j \mid^2 dx}{\int_\Omega \phi_j^2 dx} > 0 \text{ for all } j \geq 1.$$

We may suppose without loss of generality that the $\phi_{j's}$ are normalized so that $\parallel \phi_j \parallel_{L_2(\Omega)} = 1$. Moreover, the set ϕ_j form an orthogonal basis for $L_2(\Omega)$ and any function may be expanded as a Fourier series or eigenfunction expansion

$$u(x) = \sum_{j=0}^{\infty} u_j\phi_j(x).$$

Using these preliminaries, we may solve (4.1) by expanding our solution W via

$$W(x,t) = \sum_{j=0}^{\infty} s_j(t)\phi_j(x) \tag{4.2}$$

where each $s_j(t) \in \mathbb{R}^2$. Substituting (4.2) in (4.1) and equating the coefficients of each ϕ_j, we have

$$\frac{ds_j}{dt} = B_j s_j,$$

where B_j is the matrix

$$B_j = A - \lambda_j D.$$

Now the trivial solution $W = 0$ of (4.1) is asymptotically stable if and only if each $s_j(t)$ decays to zero as $t \longrightarrow \infty$. This is equivalent to the condition that each B_j has two eigenvalues with negative real parts for all j. The eigenvalues of the matrix B_j are given by

$$\det[B_j - \rho I] = \rho^2 - \text{trace}B_j\rho + \det B_j = 0.$$

Hereafter, we are going to assume that parameters $r, s, \delta \in D_s$; i.e. r, s, δ belong to the region where the nontrivial equilibrium U^* of the system (3.1) is asymptotically stable. Now we shall study the stability of U^* with respect to the system (2.1) in the (d_1, d_2)-plane.

Taking into account that $r, s, \delta \in D_s$, it follows that trace$A < 0$ and det$A > 0$. Therefore, traceB_j = trace$A - \lambda_j(d_1 + d_2) < 0$, due to $\lambda_j \geq 0$, $j = 0, 1, 2, ...,$ and $d_1, d_2 > 0$. Henceforth, in order that occur the Turing instability, it should be satisfied that $\det B_j \leq 0$, for some $j \geq 1$, where $\det B_j = (A_{11} - \lambda_j d_1)(A_{22} - \lambda_j d_2) - A_{12}A_{21}$.

For fixed λ let us denote the hyperbola in the (d_1, d_2)-plane by

$$H_\lambda : (\lambda d_1 - A_{11})(\lambda d_2 - A_{22}) - A_{12}A_{21} = 0.$$

We know that $A_{22} = -\delta r(1 - r) < 0$ on the admissible region. Hence, the location of the graph of the hyperbola H_λ on the (d_1, d_2)-plane is dictated by the sign of $A_{11} = s(1 - r^2) - 1$. A straightforward computation gives us that the graph of the function $h(r) = 1/(1 - r^2)$ lies strictly below of the boundary of the region of asymptotic stability for any $\delta > 0$, see Fig.2a and Fig. 2b.

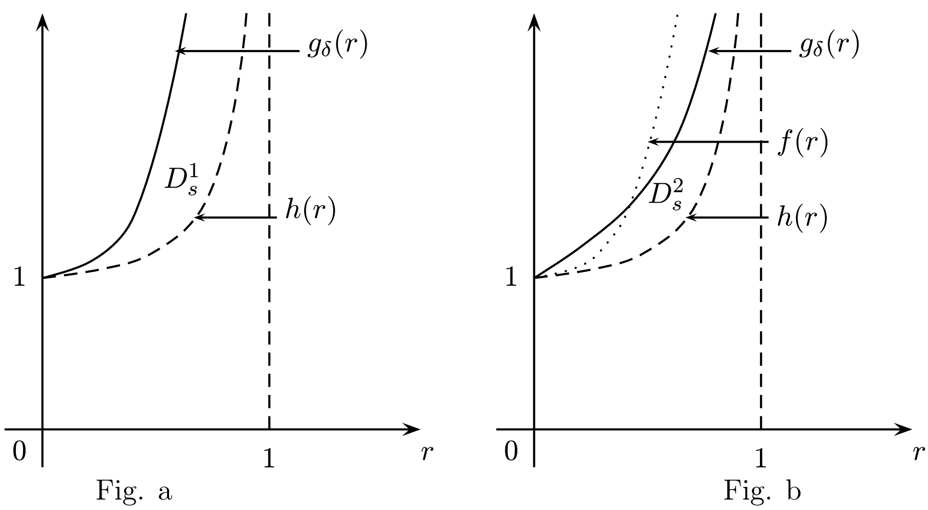

Figure 2: Fig. a $0 < \delta \leq 1$. Fig. b $\delta > 1$.

Let us suppose that $A_{11} < 0$. In this case $\det B_j > 0$ for any $j \geq 0$ and $d_1 > 0$, $d_2 > 0$. We disregard this situation due to we are looking for Turing instability conditions, see Fig.3a. Assuming that $A_{11} > 0$, we obtain that there exists positive parameters d_1 and d_2 where U^* is diffusionally unstable. That region is depicted in Fig.3b.

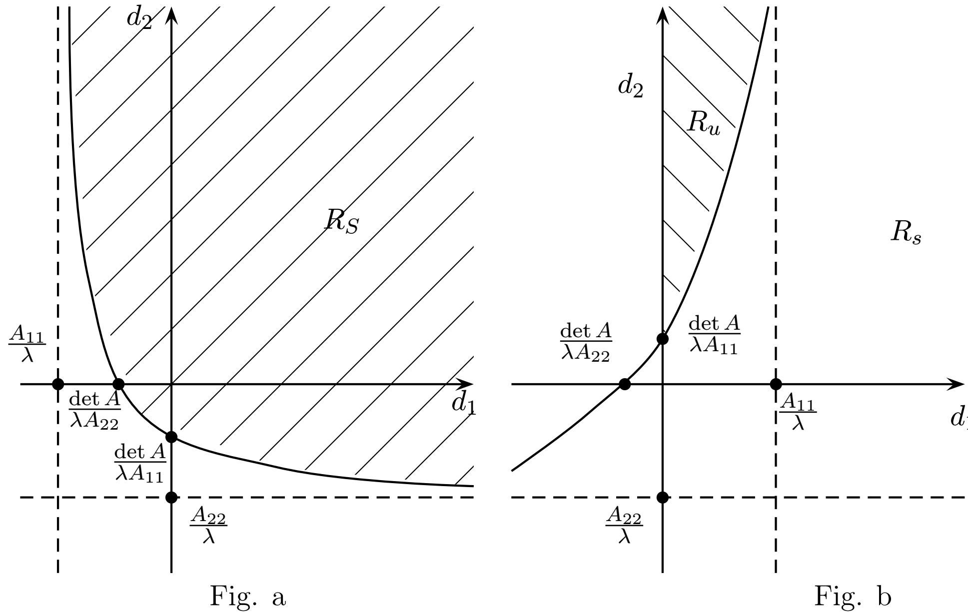

Figure 3: Fig. a. R_s-Stability region, when $A_{11} < 0$; $r, s, \delta \in D_s$ and $\lambda > 0$. Fig. b. R_s-Stability region, R_u-Instability region, when $A_{11} > 0$, $r, s, \delta \in D_s$, and $\lambda > 0$.

From Figure 3b, it follows that the set of $(d_1, d_2) \in \mathbb{R}^2_+$ satisfying that $\det B_j \leq 0$ for some $j \in \mathbb{N}$ consists of all points which are above the graph of the hyperbola H_{λ_j}. Clearly, for each $j \in \mathbb{N}$ this set is nonempty and therefore we always can choose $(d_1, d_2) \in \mathbb{R}^2_+$ in such a way that U^* is diffusionally unstable. Let us fix $d_2 > 0$. Since $\lambda_j \to \infty$ as $j \to \infty$, then there exists a $k \in \mathbb{N}$ such that $d_k^* = \dfrac{\det A}{\lambda_k A_{11}} < d_2$. Therefore, the point (d_A, d_2) belongs to the hyperbola H_{λ_k}, where $d_A = \dfrac{A_{11}\lambda_k d_2 - \det A}{\lambda_k(\lambda_k d_2 - A_{22})}$. Moreover if $0 < d_1 < d_A$, then (d_1, d_2) will lie above of the graph of H_{λ_k} and the homogeneous steady-state solution $U^* = (N^*, P^*)$ will be diffusionally unstable. We can also remark that if $d_2 \longrightarrow \infty$ we have

$$\frac{A_{11}\lambda_k d_2 - \det A}{\lambda_k(\lambda_k d_2 - A_{22})} \to \frac{A_{11}}{\lambda_k}.$$

5 Pattern Formation.

In this section we shall show how the diffusion-driven instability phenomenon gives rise to non-homogeneous steady-state solutions of (2.1) that bifurcate from the uniform stationary solution. For this purpose, we start by introducing a definition. Consider the following reaction diffusion system

$$\frac{\partial U}{\partial t} = D\Delta U + F(U), \quad \frac{\partial U}{\partial \eta}(x,t) = 0, \quad x \in \partial\Omega,\ t > 0 \tag{5.1}$$

where $U \in \mathbb{R}^2$, D is 2×2 nonnegative diagonal matrix and $F : \mathbb{R}^2 \longrightarrow \mathbb{R}^2$ is a smooth function, where $\dfrac{\partial}{\partial \eta}$ denotes the normal derivate. Assume that U^* is an uniform stationary solution of (5.1), i.e., $F(U^*) = 0$.

Definition 2 *We say that U^* undergoes a Turing bifurcation at $\mu_0 \in (0,\infty)$ if the solution U^* changes its stability at μ_0 and in some neighborhood of μ_0 there exists a one-parameter family of nonconstant stationary solution of systems* (5.1).

Now we use the theorem 13.5 in [17] for to determine the nonhomogeneous stationary solutions of (5.1), in this case take d_2 as bifurcation parameter.

Theorem 2 *Let υ_{1k} and υ_{2k} be the eigenvectors of B_k corresponding to the eigenvalues λ_{1k} and λ_{2k}, respectively. Assume that*

i. $r, s, \delta \in D_s^i$, $i = 1, 2$.

ii. $\upsilon_{1k} = \begin{pmatrix} \xi_1 \\ \xi_2 \end{pmatrix}$ *and υ_{2k} is not parallel to* $\begin{pmatrix} \xi_1 \\ 0 \end{pmatrix}$,

iii. $0 < d_1 < D^*$, *where* $D^* = \dfrac{A_{11}}{\lambda_k}$,

Then there exists a $k \in \mathbb{N}$ such that at

$$d_2^* = \frac{A_{22}\lambda_k d_1 - detA}{\lambda_k(\lambda_k d_1 - A_{11})}$$

the uniform steady-state solution U^* of (5.1) *undergoes a Turing bifurcation*

Proof 2 *Hereafter, the role of the space X will be played by*

$$X = \left\{ W \in C(\Omega, \mathbb{R}^2) \times C(\Omega, \mathbb{R}^2) : \frac{\partial W}{\partial \eta}(x,t) = 0,\ t > 0\ x \in \partial\Omega \right\}$$

with the supremum norm involving the first and second derivatives, while $Y = C(\Omega, \mathbb{R}^2)$ with the usual supremum norm. However, when choosing the subspace Z, we shall use the orthogonality induced by the scalar product

$$\langle V, W \rangle = \int_\Omega (V_1(x)W_1(x) + V_2(x)W_2(x))dx,$$

where $V = (V_1, V_2)$ y $W = (W_1, W_2)$.

Setting $W = U - U^*$, *where* U^* *is a nontrivial homogeneous steady-state solution of* (5.1) *can be rewritten as follows*

$$W_t = D\Delta W + AW + G(W), \quad \frac{\partial W}{\partial \eta}(x,t) = 0, \quad t > 0, \quad x \in \partial\Omega \tag{5.2}$$

where A *is the Jacobian matrix of* F *in* U^* *y* $G(W) = F(U^* + W) - AW$.

For any nonhomogeneous stationary solution U *of* (5.1), $W = U - U^*$ *satisfies the elliptic equation*

$$D\Delta W + AW + G(W) = 0, \quad \frac{\partial W}{\partial \eta}(x,t) = 0, \; t > 0 \; x \in \partial\Omega \tag{5.3}$$

Taking into account this observation, define the function $f : \mathbb{R} \times X \longrightarrow Y$ *and linear operator* L_0 *considered in Theorem 13.5 ([17]) as follows*

$$f(d_2, W) = D\Delta W + AW + G(W) \;\; \text{and} \;\; L_0 = D_2 f(d_2^*, 0) = \frac{\partial f(d_2^*, 0)}{\partial W}$$

where d_2 *is the diffusion coefficient of the susceptible class. The spectrum of the linear operator* L_0 *is given by the eigenvalues* λ_{ij} *of the matrices*

$$B_j = A - \lambda_j D$$

evaluated at $d_2 = d_2^*$, *where* $i = 1, 2$, *and* $j = 0, 1, 2, \ldots..$ *Since* $0 < d_1 < D^*$, *there exists a unique* $k \in \mathbb{N}$ *such that* (d_1, d_2^*) *belongs to the hyperbola* H_{λ_k}.

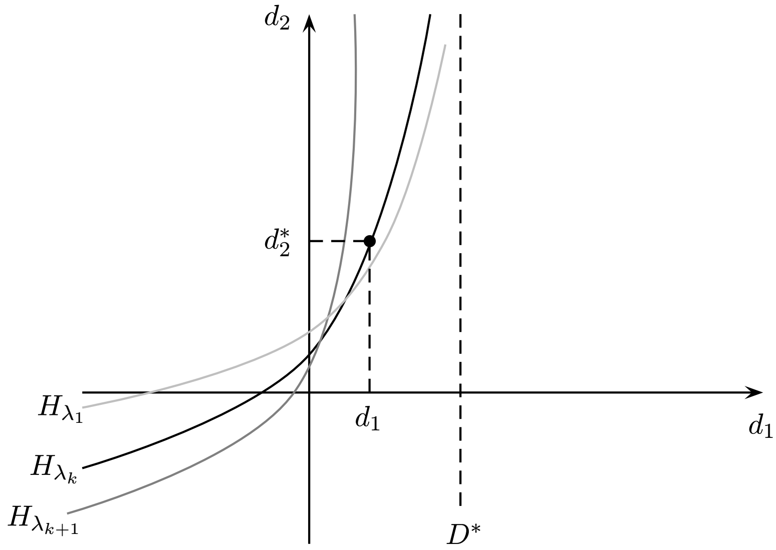

Figure 4: Turing Bifurcation. When $d_1 < D^*$, the uniform steady-state solution U^* of (5.1) undergoes a Turing bifurcation at $d_2 = d_2^*$

In other words, $\det B_j > 0$ *for* $j \neq k$ *and* $\det B_j = 0$ *just for* $j = k$. *Therefore, for* $i = 1, 2$ *and* $j = 0, 1, 2, ..., k-1, k+1, ...$ *all eigenvalues* λ_{ij} *have negative real part. For* $j = k$, *one eigenvalue, say* λ_{1k}, *is zero and the other one is negative, i.e.,* $\lambda_{2k} < 0$.

Since υ_{1k} is the eigenvector of B_k corresponding to the zero eigenvalue λ_{1k}, the eigenfunction of the linear operator L_0 corresponding to $\lambda_{1k} = 0$ is given by $\psi_k = \upsilon_{1k}\Phi_k(x)$ which is a nonuniform stationary solution of the linearized system (4.1)*, i.e.,*

$$D\Delta\psi_k(x) + A\psi_k(x) = 0, \quad \frac{\partial\psi_k}{\partial\eta}(x) = 0, \ x \in \partial\Omega.$$

Therefore, the null subspace $N(L_0)$ of the operator $D_2f(d_2^*, 0)$ is one-dimensional, spanned by ψ_k. Because of the orthogonality of the system, $\Phi_n(x)$, $n = 0, 1, 2, ...$ obtained by solving the eigenvalue problem

$$\Delta\Phi_n(x) + \lambda_n\Phi_n(x) = 0, \ x \in \Omega, \ \mathbf{n}.\nabla\Phi_n(x) = 0, \ x \in \partial\Omega.$$

The range $R(L_0)$ of this operator is given by

$$\begin{aligned} R(L_0) = \{&U \in [C(\Omega, \mathbb{R})]^2 : \textit{The Fourier expansion of} \\ &U \textit{ does no contain the term } \ \Phi_n(x)\} \bigcup \{\upsilon_{2k}\Phi_n(x)\}, \end{aligned}$$

and has codimension one. So conditions (i) and (ii) of Theorem 13.5 [17] are satisfied. It still remains to verify condition (iii). Let

$$L_1 = D_1D_2f(d_2^*, 0) = \frac{\partial}{\partial d}\left(\frac{\partial f}{\partial W}\right)(d_2^*, 0).$$

Then

$$L_1 = \begin{pmatrix} \Delta & 0 \\ 0 & 0 \end{pmatrix}$$

and

$$L_1\psi_k = \begin{pmatrix} \Delta & 0 \\ 0 & 0 \end{pmatrix} \upsilon_{1k}\Phi_n(x) = -\lambda_n \begin{pmatrix} \xi_1 \\ 0 \end{pmatrix} \Phi_n(x),$$

with $\xi_1 \neq 0$, and $\begin{pmatrix} \xi_1 \\ 0 \end{pmatrix}$ not being parallel to υ_{2k}. Then, $L_1\psi_{1k} \notin R(L_0)$ and condition (iii) of theorem 13.5 [17] is satisfied. So by choosing $Z = R(L_0)$ we conclude that there exists a $\gamma > 0$ and a C^1 curve

$$(d, \phi) : (-\gamma, \gamma) \longrightarrow \mathbb{R} \times Z$$

with $d(0) = d_2^*$ and $\phi(0) = 0$ such that

$$W(x, s) = s\upsilon_{1k}\Phi_n(x) + s\phi(x, s)$$

is a solution of the elliptic equation (5.3) *with $d_2 = d(s)$, $s \in (-\gamma, \gamma)$.*

Finally, taking into account that $W = U - U^*$, we obtain that

$$U(x, s) = U^* + s\upsilon_{1k}\Phi_n(x) + \mathrm{O}(s^2)$$

are non-uniform stationary solutions of (5.1) *with $d_2 = d(s)$, and $s \in (-\gamma, \gamma)$.*

Therefore, at $d_2 = d_2^*$, the uniform steady-state solution U^* undergoes a Turing bifurcation.

6 Stability of bifurcating solution

In this section we will study the stability of the one parameter family of non uniform stationary solution $U(x,s)$ of the system (2.1) that arise from the bifurcation of the homogeneous steady state U^*.

We showed that λ_{1k} is a L_1-simple eigenvalue of L_0, where $L_1 = D_1D_2f(d_2^*,0)$ and $L_0 = D_2f(d_2^*,0)$. On the other hand, for $|\varepsilon|$ and $|s|$ small enough, the operators $D_2f(d_2^*+\varepsilon,0)$ and $D_2f(d(s),s\psi_k+s\phi(x,s))$ are close to L_0. Applying Lemma 13.7 in [17], we obtain that there exist functions

$$d \longmapsto (\rho(d),\psi_c(d)), \;\; s \longmapsto (\eta(s),\psi_b(s))$$

defined on neighborhoods of d_2^* and 0, respectively, such that

$$D_2f(d,0)\psi_c(d) = \rho(d)\psi_c(d)$$

$$D_2f(d(s),s\psi_k+s\phi(x,s))\psi_b(s) = \eta(s)\psi_b(s)$$

and

$$(\rho(d_2^*),\psi_c(d_2^*)) = (0,\psi_k) = (\eta(0),\psi_b(0)).$$

Note that the functions

$$\eta(s) = \eta(D_2f(d(s),s\psi_k+s\phi(x,s))),$$
$$\psi_b(s) = \psi_b(D_2f(d(s),s\psi_k+s\phi(x,s))),$$

$$\rho(d) = \eta(D_2f(d,0)), \;\; \psi_c(d) = \psi_b(D_2f(d,0))$$

given by Lemma 13.7, [17], are smooth functions.

The following result is the Crandall- Rabinowitz's Theorem 1.16 p.165 which is proved in [8].

Theorem 3 *Let the assumptions of Theorem 13.5 in [17] holds, and let the functions $\rho(d)$ and $\eta(s)$ be defined as above. Then $\rho'(d_2^*) \neq 0$, and if $\eta(s) \neq 0$ for s close to 0, then*

$$\lim_{s\to 0} \frac{sd'(s)\rho'(d_2^*)}{\eta(s)} = -1. \tag{6.1}$$

First we determine $\rho'(d_2^*)$. It is known that $\rho(d_2)$ satisfies the equation

$$\rho^2(d_2) - \text{trace}B_k\rho(d_2) + \det B_k = 0.$$

Differentiating implicitly the former equation with respect to d_2, we have

$$\rho'(d_2) = \frac{\lambda_k A_{11} - \lambda_k^2 d_1 - \lambda_k \rho(d_2)}{2\rho(d_2) - \text{trace}B_k}.$$

Evaluating at d_2^*, we obtain

$$\rho'(d_2^*) = \frac{\lambda_k^2 d_1 - \lambda_k A_{11}}{\text{trace}A - \lambda_k(d_1+d_2^*)} = \frac{\lambda_k(\lambda_k d_1 - A_{11})}{\text{trace}A - \lambda(d_1+d_2^*)}.$$

Since $A_{11} > 0$ and $0 < d_1 < \dfrac{A_{11}}{\lambda_k}$ then $\lambda_k d_1 - A_{11} < 0$ and $\text{trace}A - \lambda_k(d_1+d_2^*) < 0$. Therefore,

$$\rho'(d_2^*) > 0.$$

Proposition 1 *Let $(d(s), U(x,s))$ be the one parameter family of bifurcating solutions given by*

$$U(x,s) = W^* + s v_{1k} \Phi_n(x) + \mathrm{O}(s^2).$$

Assume that the conditions of Theorem 2 are satisfied, $d'(0) \neq 0$, and that the eigenvalues $\eta(s)$ of the nonhomogeneous steady state bifurcating from the critical value $\lambda_{1k} = 0$ are nonzero for small $|s| \neq 0$. Then if $d(s) < d_2^*$ the corresponding solution $U(x,s)$ is stable and if $d(s) > d_2^*$, the corresponding solution $U(x,s)$ is unstable.

Proof 3 *We know that $\rho'(d_2^*) > 0$. Let us determine the sign of $\eta(s)$. Since $d'(0) \neq 0$, we may assume that $d'(0) > 0$. Then by continuity we have that $d'(s) > 0$ for $|s|$ small enough. Therefore, using (6.1), it follow that $\eta(s) < 0$ for $s > 0$ small enough, which in turn implies that the bifurcating solution is asymptotically stable. For small $s < 0$, $\eta(s) > 0$. Hence, the bifurcating nonhomogeneous stationary solution is unstable.*

The case $d(s) < 0$ can be analyzed similarly . This completes the proof of our claim.

7 Discussion

In this paper, we discussed the main mathematical features exhibited by the reaction-diffusion system (1.1). More concretely, we showed that when $A_{11} = s(1 - r^2) - 1$ is positive nontrivial geotemporal dynamics of the reaction diffusion ratio-dependent predator-prey model (1.1) can be obtained. In the case when the $0 < d_1 < A_{11}/\lambda_j$ we showed that for a wide range of parameter values and diffusion coefficients d_1 and d_2, see fig.3-b, the nonlinear system (1.1) can exhibit stable spatially heterogeneous solutions which arise from Turing bifurcations. It is worth to point out that a Turing bifurcation can not occur for large diffusive coefficient of the prey, nevertheless the diffusive coefficient of the predator can be large enough.

The existence of this pattern formation for system (1.1) shows that the reaction diffusion ratio-dependent predator-prey model exhibits features which were not possible for the classical model. More specifically, one can show that for a classical Lotka Volterra prey-predator system with diffusion on a finite domain and zero flux boundary condition cannot give rise to temporally or spatially inhomogeneous solutions asymptotically as $t \to \infty$.

In conclusion, the mathematical analysis of model (1.1) shows how reaction diffusion ratio-dependent predator-prey model can stably regulate its growth around either spatially homogeneous or heterogeneous solutions through a Turing instability mechanism.

ACKNOWLEDGEMENTS

We are deeply indebted to Professor Miklos Farkas for detailed criticism that helped us improve this paper.

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