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An Investigation of the Effects of Diffusion on a Competition Model

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Abstract

We present a reaction-diffusion competition model, to describe the spatial spread of two competing species. Standard analysis of the model using the travelling wave procedure was employed to determine the existence of travelling wave solutions and the stability of the equilibrium points. The result shows that the zero equilibrium point is stable, contrary to that of a diffusion-free competition model. The result is further confirmed using the normal modes analysis. This result is however more general than the special case considered by Okubo, et al (1989). The remaining three steady states are saddle points, thus guaranteeing the existence of travelling wave solutions in form of heteroclinic connections among the equilibrium points.

1. Introduction

The classic Lotka-Volterra competition model of the red and Grey squirrels provides a background for many mathematical models of competition amongst species in an ecosystem. There have been many articles on non-diffusive competition models similar to the Lotka-Volterra model. A good example of such research work is that of Fassoni, et al (2014), which was concerned with investigating the effects of parameter values on the size and shape of the basins of attraction of stable equilibrium points. Apart from the basins of attraction, they

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found that the survival or extinction of competing species depends on the relative strengths of their competition. It is clear from the analysis of most non-diffusive competition models that the competing species cannot both go into extinction simultaneously (Kot, 2001), which is also consistent with what happens in reality.

Many research work have been carried out on competition models with diffusion of the competing species. Examples include the work of Okubo, *et al* (1989), where they showed that for a special case of a diffusive model of two competing species, the species can both go into extinction simultaneously. In a similar work, Gerhard, *et al* (1996) and Murray (2002), used the travelling wave solution approach to analyse the model and obtained estimates for the minimal travelling wave speed needed for the survival of the engineered species. Seno (2007), carried out similar work to that of Gerhard *et al* (1996), where they considered two dispersing species in a Lotka-Volterra system with a temporally periodic interruption of the inter-specific competitive relationship. They obtained conditions for coexistence of these species, which is determined by the time-averaged strength of the competition. The expression for the traveling wave speed was also obtained. The results of the work of Flores (1998), Mansour (2006) and Ndam, *et al* (2012) all showed the existence of travelling wave solutions for the reaction-diffusion systems. It has also been shown that diffusion has an effect on the stability of the the equilibrium points (Okubo, 2002 and Ndam *et al*, 2012). More recently, Benlong Xu and Hongyan Jiang (2017) considered a diffusion-advection competition model and determined conditions under which coexistence of competing species could be achieved. In a similar work, Shuling Yan and Shangjiang Guo (2018) investigated a diffusive Lotka-Volterra competion model and examined only the stability of the semi-trivial solutions. From the works we have reviewed, we realised that not much has been done on the effects of diffusion on the stability of the steady states of a competition model. We are particularly concerned about the stability of the the zero equilibrium point which is normally unstable in a diffusion-free competition model. The instability of the zero equilibrium point in a competition model is consistent with what happens in the physical sense. For instance, in a soccer competition, one team or the other wins or they draw, but both cannot lose. However, there are suggestions to the contrary from literature, one of which is in the work of Okubo et al. (1989), where they concluded that diffusion can alter the stability of the zero equilibrium point of a competition model. This conclusion was however based on a special case of the model. In this work, we intend to examine the effect of diffusion on the stability of the zero equilibrium point in a more general consideration. We intend to demonstrate that diffusion induces the simultaneous extinction of the competing species, not only in a special case. The remaining parts of this paper are organised as follows: Section 2 is dedicated to the formulation of the model, while the travelling wave solution of the diffusive model will be the subject of section 3. The normal modes analysis of the model is considered in section 4, the results of the analysis is the subject of section 5, while the conclusions is done in section 6.

2. Mathematical Formulation

The governing equations for the diffusive competition of the two species is given by:

$$\frac{\partial p}{\partial t} = D_1 \frac{\partial^2 p}{\partial x^2} + pr_1 \left[1 - \left(\frac{p + \alpha_{12} q}{K_1} \right) \right] \tag{1}$$

$$\frac{\partial q}{\partial t} = D_2 \frac{\partial^2 q}{\partial x^2} + qr_2 \left[1 - \left(\frac{\alpha_{21} p + q}{K_2} \right) \right] \tag{2}$$

where p and q are species 1 and 2 respectively, D_1 and D_2 are diffusion coefficients, K_1 and K_2 are the carrying capacities for species p and q respectively, α_{12} is the effect of competition of p on q, α_{21} is the effect of competition of q on p, while r_1 and r_2 are the growth rates of species p and q respectively.
We now introduce the following non-dimensional quantities to reduce the number of parameters thus: $p = K_1 p^*$, $q = K_2 q^*$, $x = \sqrt{\frac{D_1}{r_1}} x^*$ and $t = \frac{t^*}{r_1}$.
Substituting the new variables in (1) and (2) and dropping asterisks, we have,

$$\frac{\partial p}{\partial t} = \frac{\partial^2 p}{\partial x^2} + p[1 - (p + \gamma q)] \tag{3}$$

and

$$\frac{\partial q}{\partial t} = \delta \frac{\partial^2 q}{\partial x^2} + \theta q[1 - (\beta p + q)] \tag{4}$$

where $\alpha_{12} \frac{K_2}{K_1} = \gamma$, $\frac{D_2}{D_1} = \delta$, $\frac{r_2}{r_1} = \theta$ and $\alpha_{21} \frac{K_1}{K_2} = \beta$.

3. Travelling wave solution of the diffusive model

Here, we assume a travelling wave variable of the form $z = x - ct$, where c is the wave speed propagating from left to right. Using the travelling wave variable, the partial differential equations are then transformed into ordinary differential equations thus:

$$p'' + cp' + p(1 - p - \gamma q) = 0 \tag{5}$$

$$\delta q'' + cq' + \theta q(1 - \beta p - q) = 0 \tag{6}$$

which yields the first order system of equations

$$p' = u \tag{7}$$

$$u' = -cu - p(1 - p - \gamma q) \tag{8}$$

$$q' = v \tag{9}$$

$$v' = \frac{-cv - \theta q(1-\beta p - q)}{\delta} \tag{10}$$

We then obtain the following equilibrium points:

$$(p,u,q,v) = (0,0,0,0), (0,0,1,0), (1,0,0,0), \left(\frac{\gamma-1}{\beta\gamma-1}, 0, \frac{\beta-1}{\beta\gamma-1}, 0\right).$$

In order to determine the nature of the equilibrium point $(0,0,0,0)$ of system (7-10), we determine the eigenvalues of the Jacobian matrix. The Jacobian matrix of the system of equations is given by

$$J(p,u,q,v) = \begin{pmatrix} 0 & 1 & 0 & 0 \\ -1+2p+\gamma q & -c & 0 & 0 \\ 0 & 0 & 0 & 1 \\ \frac{\beta\theta q}{\delta} & 0 & \frac{-\theta+\beta\theta p+2\theta q}{\delta} & \frac{-c}{\delta} \end{pmatrix}$$

and

$$J(0,0,0,0) = \begin{pmatrix} 0 & 1 & 0 & 0 \\ -1 & -c & 0 & 0 \\ 0 & 0 & 0 & 1 \\ 0 & 0 & \frac{-\theta}{\delta} & \frac{-c}{\delta} \end{pmatrix}.$$

This yields the characteristic polynomial

$$\lambda^4 + \frac{c\delta+\theta}{2}\lambda^3 + \frac{c\theta+c+\delta}{4\delta}\lambda^2 + \frac{c^2+\theta}{\delta}\lambda + \frac{c}{16\delta} = 0$$

with the eigenvalues

$$\lambda_{1,2} = \frac{-c \pm \sqrt{c^2-4}}{2}, \lambda_{3,4} = \frac{-c \pm \sqrt{c^2-4\delta\theta}}{2\delta}.$$

The parameters γ, β, θ and δ are all positive, hence the point $(0,0,0,0)$ is a stable node for $c \geq 2$ and $c \geq 2\sqrt{\delta\theta}$.

Theorem 1: The zero equilibrium point is asymptotically stable for $c \geq 2$ and $c \geq 2\sqrt{\delta\theta}$.

Proof: As shown above. For the equilibrium point $(0,0,1,0)$,

$$|J - \lambda I| = \begin{vmatrix} -\lambda & 1 & 0 & 0 \\ -1+\gamma & -c-\lambda & 0 & 0 \\ 0 & 0 & -\lambda & 1 \\ \frac{\beta\theta}{\delta} & 0 & \frac{\theta}{\delta} & \frac{-c}{\delta}-\lambda \end{vmatrix} = 0$$

Hence, the characteristic polynomial is

$$\lambda^4 + \frac{c\delta + c}{2\delta}\lambda^3 + \frac{c^2 - \delta\gamma + \delta - \theta}{4\delta}\lambda^2 + \frac{c - c\gamma - c\theta}{8\delta}\lambda + \frac{\gamma\theta - \theta}{16\delta} = 0,$$

while the eigenvalues are given by

$$\lambda_{1,2} = \frac{-c \pm \sqrt{c^2 + 4\delta\theta}}{2\delta}, \lambda_{3,4} = \frac{-c \pm \sqrt{c^2 - 4(1-\gamma)}}{2}.$$

Thus the point $(0, 0, 1, 0)$ is a saddle for $c > 2\sqrt{1-\gamma}, \gamma < 1$ as well as for $\gamma > 1$. For the equilibrium point $(1, 0, 0, 0)$, we obtain

$$|J - \lambda I| = \begin{vmatrix} -\lambda & 1 & 0 & 0 \\ 1 & -c-\lambda & 0 & 0 \\ 0 & 0 & -\lambda & 1 \\ 0 & 0 & \frac{\beta\theta - \theta}{\delta} & \frac{-c}{\delta} - \lambda \end{vmatrix} = 0$$

which yields the characteristic polynomial

$$\lambda^4 + (\frac{c\delta + c}{2\delta})\lambda^3 + (\frac{c^2 - \delta + \theta - \beta\theta}{4\delta})\lambda^2 + (\frac{c\theta - c\beta\theta - c}{8\delta})\lambda + \frac{\beta\theta - \theta}{16\delta} = 0$$

and the eigenvalues

$$\lambda_{1,2} = \frac{-c \pm \sqrt{c^2 + 4}}{2}, \lambda_{3,4} = \frac{-c \pm \sqrt{c^2 - 4\theta(\gamma - \delta\beta)}}{2\delta},$$

which shows that $(1, 0, 0, 0)$ is a saddle for $c > 2\sqrt{\theta(\gamma - \delta\beta)}, \gamma > \delta\beta$ and also for $\gamma < \delta\beta$. Finally, we consider the point $\left(\frac{\gamma-1}{\beta\gamma-1}, 0, \frac{\beta-1}{\beta\gamma-1}, 0\right)$, which has the characteristic equation

$$|J - \lambda I| = \begin{vmatrix} -\lambda & 1 & 0 & 0 \\ \frac{\gamma-1}{\beta\gamma-1} & -c-\lambda & 0 & 0 \\ 0 & 0 & -\lambda & 1 \\ \frac{\beta^2\theta - \beta\theta}{\beta\gamma\delta - \delta} & 0 & \frac{\beta\theta - \theta}{\beta\gamma\delta - \delta} & -\frac{c}{\delta} - \lambda \end{vmatrix} = 0$$

and we obtain the eigenvalues

$$\lambda_{1,2} = \frac{c\delta(\beta\gamma - 1) \pm \sqrt{[c^2\delta^2(1 - 2\beta\gamma + \beta\gamma) + 4\delta^2\theta(1 + \beta^2\gamma)] - [4\delta^3\beta\theta(1+\gamma)]}}{\delta^2(1 - \beta\gamma)}$$

and

$$\lambda_{3,4} = \frac{-c(\beta\gamma - 1) \pm \sqrt{[c^2(\beta\gamma^2 - 2\beta\gamma + 1) + 4(\beta\gamma^2 + 1)] - [4(\gamma + \beta\gamma)]}}{2(\beta\gamma - 1)}.$$

Again, the point $\left(\frac{\gamma-1}{\beta\gamma-1}, 0, \frac{\beta-1}{\beta\gamma-1}, 0\right)$ is easily seen to be a saddle when

$$(c^2 + 4)(\beta\gamma^2 + 1) > 2\gamma(c^2\beta + 2\beta + 2).$$

It could be observed from the analysis above that the origin is a stable equilibrium point with three other saddle points. Okubo, *et al* (1989), in their model for the spatial spread of Grey squirrels in Britain, considered a special case which shows that the zero equilibrium becomes stable.

4. Nomal Modes Analysis

To further confirm the effects of diffusion on the stability of the steady states, we consider a small perturbation of the equilibrium points following Jones and Sleeman (2003) as

$$p(x,t) = p_e + \xi_1(x,t), q(x,t) = q_e + \xi_2(x,t).$$

Equations (3) and (4) can be recast as

$$\frac{\partial P}{\partial t} = \frac{\partial^2 P}{\partial x^2} + f_1(p,q) \tag{11}$$

and

$$\frac{\partial Q}{\partial t} = \delta\frac{\partial^2 Q}{\partial x^2} + f_2(p,q) \tag{12}$$

where $f_1(p,q) = P[1-(P+Q\gamma)$ and $f_2(p,q) = Q\theta[1-(P\beta+Q)]$. Expanding $f_i(p,q)$ as a Taylor series about the steady states (p_e, q_e), we obtain

$$f_i(p,q) = f_i(p,q) + \xi_1\frac{\partial f_i}{\partial p} + \xi_2\frac{\partial f_i}{\partial q} + \cdots \tag{13}$$

where $|\xi_i| \ll 1, i = 1,2$. Linearising (13) about the steady state produces the system of equations

$$\frac{\partial \xi_1}{\partial t} = \frac{\partial^2 \xi_1}{\partial x^2} + a_{11}\xi_1 + a_{12}\xi_2 \tag{14}$$

and

$$\frac{\partial \xi_2}{\partial t} = \sigma\frac{\partial^2 \xi_2}{\partial x^2} + a_{21}\xi_1 + a_{22}\xi_2 \tag{15}$$

Using the normal modes

$$\xi_i = \alpha_i e^{\lambda t}\cos kx, i = 1,2 \tag{16}$$

where α_i, λ and k are constants, and substituting into (14) and (15) yield the system

$$\alpha_1\lambda = C_{11}\alpha_1 + C_{12}\alpha_2 - k^2\alpha_1 \tag{17}$$

$$\alpha_2\lambda = C_{21}\alpha_1 + C_{22}\alpha_2 - \sigma k^2\alpha_2 \tag{18}$$

Hence at the steady state $(p_e, q_e) = (0,0), f_1(0,0) = \xi_1$ and $f_2(0,0) = \theta\xi_2$, and the system has a non-trivial solution if

$$\begin{vmatrix} \lambda - 1 + k^2 & 0 \\ 0 & \lambda - \theta + \sigma k^2 \end{vmatrix} = 0.$$

In the absence of diffusion, that is, $k = 0$, we obtain the eigenvalues $\lambda_1 = 1, \lambda_2 = \theta$, confirming the point $(0,0)$ to be unstable. In the presence of diffusion, we have $\lambda_1 = 1 - k^2$ and $\lambda_2 = \theta - \sigma k^2$. Hence diffusion induced stability occurs when $Re\lambda_i (i = 1,2) < 0$. In a similar vein, we obtain the eigenvalues $\lambda_1 = (1-\gamma) - k^2$ and $\lambda_2 = -\theta - \sigma k^2$ for the equilibrium point $(0,1)$. In the absence of diffusion, $(0,1)$ is stable if $\gamma > 1$. However, the point is stable if $Re\lambda_i < 0$ and unstable otherwise. For the point $(1,0)$, we obtain the eigenvalues $\lambda_1 = -1 - k^2$ and $\lambda_2 = \theta(1-\beta) - \sigma k^2$. Hence the equilibrium point is stable for $Re\lambda_i < 0$. Similarly, the eigenvalues for the interior equilibrium point $\left(\frac{\gamma-1}{\beta\gamma-1}, \frac{\beta-1}{\beta\gamma-1}\right)$ are obtained. However, they are unwieldy and are not displayed here.

5. Results

A diffusive Lotka-Volterra competition model is constructed and analyzed using the travelling wave solution approach. Standard analysis shows the stability of the zero equilibrium point with three other saddle points and so we established the existence of traveling wave solutions for the model in the form of heteroclinic orbits linking the points $(0,0,1,0)$, $\left(\frac{\gamma-1}{\beta\gamma-1}, 0, \frac{\beta-1}{\beta\gamma-1}, 0\right)$, $(1,0,0,0)$ and $(0,0,0,0)$. While the zero equilibrium point is unstable in the non-diffusive model, the reverse is the case in the diffusive model, confirming the result of Okubo, *et al* (1989). Though they showed this for a special case of the model, we have shown that it is true in general. This therefore implies that it is possible for the competing species to simultaneously go into extinction, a scenario that is not possible in the non-diffusive model. Hence diffusion induces extinction of both species at the same time.

Numerical simulations were also carried out to illustrate the result. Figure 1 depicts the stability of the zero equilibrium point, where the population densities of the two species approach zero as time $t \to \infty$. In the diffussion-free competition model, we observe that the zero steady state is unstable as shown in Figure 2, as the same parameter values were used. Figures 3-6 illustrate the stabilities of the equilibrium points of the standard competition model in the absence of diffusion. Figure 6 in particular indicates the existence of two stable steady states, a phenomenon known as bistability.

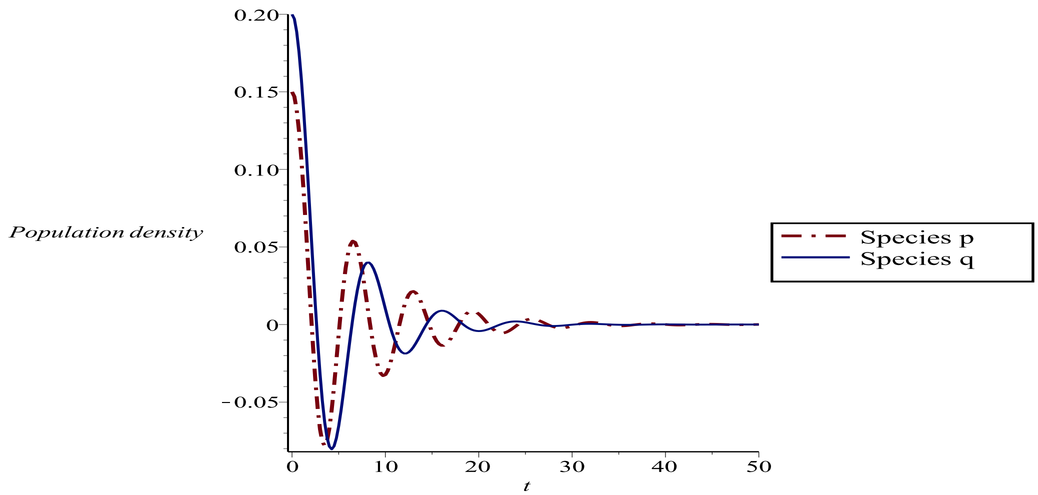

Figure 1: Time course solution for
$\beta = 0.5, \delta = 0.75, \theta = 0.5, \gamma = 0.98, c = 2\sqrt{1-\gamma}$

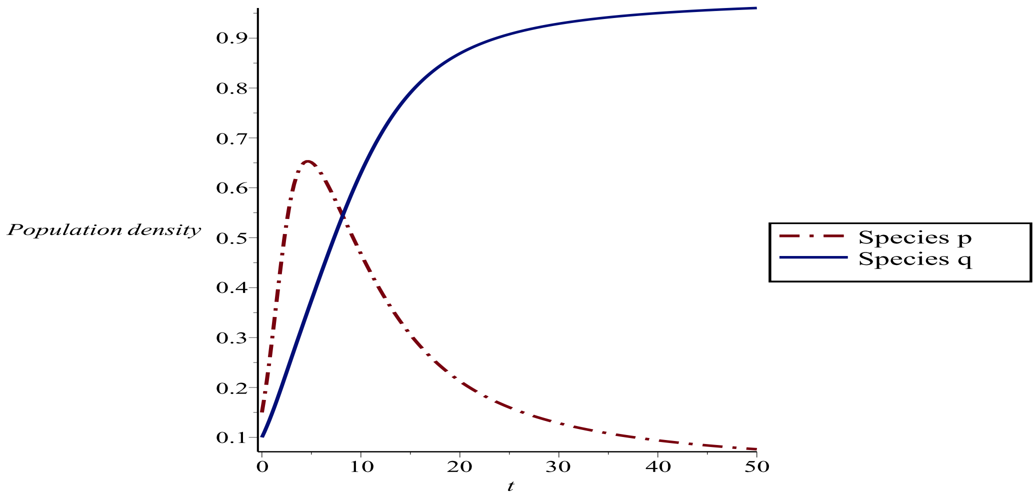

Figure 2: Time course solution for $\beta = 0.5, \theta = 0.5, \gamma = 0.98$

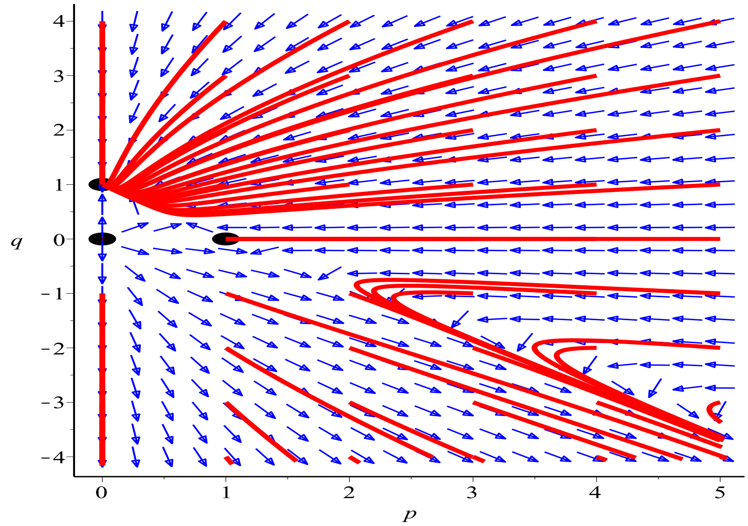

Figure 3: $\theta > 1$, $\gamma > 1$, $\beta < 1$

For the parameter values above, $(0,0)$ is unstable, $(0,1)$ is stable, $(1,0)$ is saddle, parameter values are unrealistic for $\left(\frac{\gamma-1}{\beta\gamma-1}, \frac{\beta-1}{\beta\gamma-1}\right)$

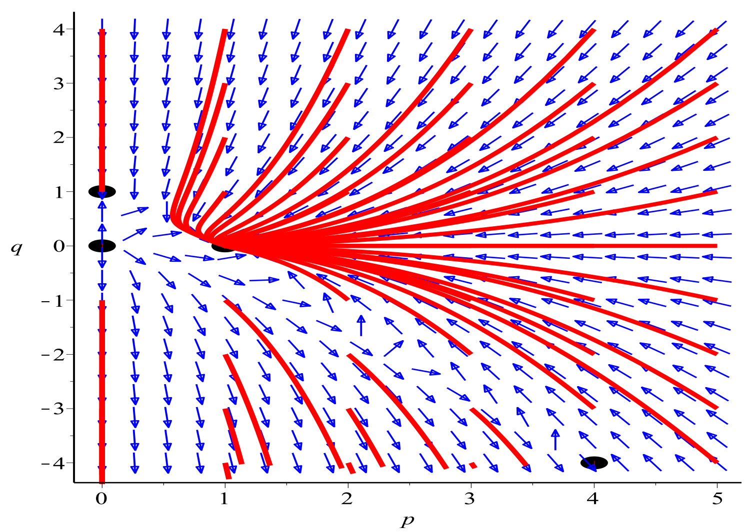

Figure 4: $\theta > 1$, $\gamma < 1$, $\beta > 1$

From the figure above, $(0,0)$ is unstable, $(0,1)$ is stable, $(1,0)$ is saddle, parameter values are unrealistic for $\left(\frac{\gamma-1}{\beta\gamma-1}, \frac{\beta-1}{\beta\gamma-1}\right)$. We notice that θ which is the parameter for the ratio of growth rates has no significant implication on the stability of the critical points.

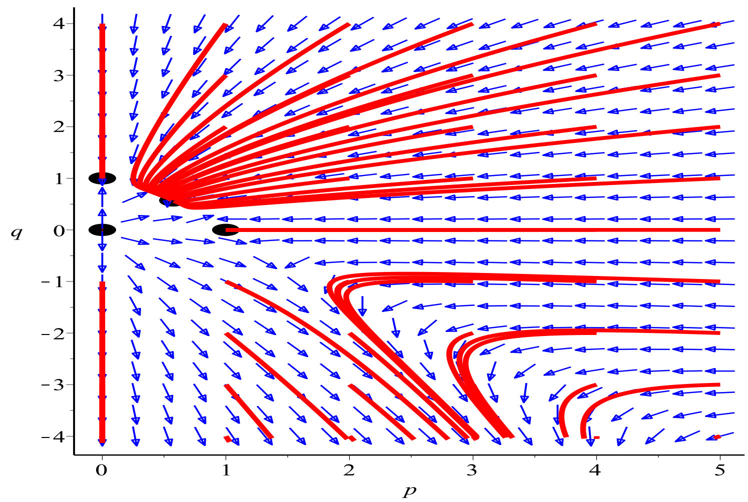

Figure 5: $\gamma < 1$, $\beta < 1$

From the figure above, $(0,0)$ and $(1,0)$ are unstable, $(0,1)$ is a saddle and $\left(\frac{\gamma-1}{\beta\gamma-1}, \frac{\beta-1}{\beta\gamma-1}\right)$ is stable.

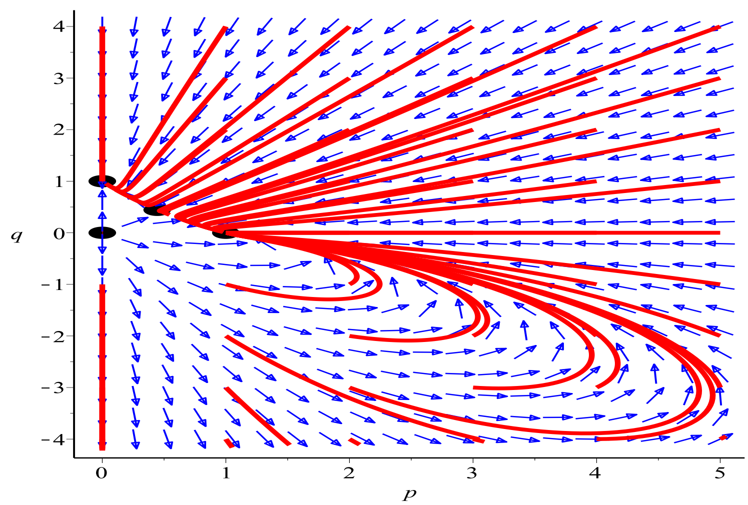

Figure 6: $\gamma > 1$, $\beta > 1$

The phase-portrait indicates that $\left(\frac{\gamma-1}{\beta\gamma-1}, \frac{\beta-1}{\beta\gamma-1}\right)$ is a saddle, while $(1,0)$ and $(0,1)$ are stable nodes, hence we have a case of bi-stability.

5.1. **The effects of diffusion.**

(1) The steady state $(0,0)$ is unstable from standard analysis, but (0,0,0,0) is clearly stable for any $c \geq 2$ due to diffusion.
(2) For the case without diffusion, $(0,1)$ is stable when $\gamma > 1$ and a saddle if $\gamma < 1$, but (0,0,1,0) is a saddle for $\gamma > 0$.
(3) While (1,0) is stable for $\beta > 1$, (1,0,0,0) is a saddle for $\gamma > 0$.
(4) While $\left(\frac{\gamma-1}{\beta\gamma-1}, \frac{\beta-1}{\beta\gamma-1}\right)$ is stable for some values of $\gamma, \beta < 1$, $\left(\frac{\gamma-1}{\beta\gamma-1}, 0, \frac{\beta-1}{\beta\gamma-1}, 0\right)$ is stable for varying or some values of $\gamma, \beta > 0$.
(5) The normal modes analysis was used to confirm the effects of diffusion on the stability of the steady states of a competition model obtained through standard analysis.

Conclusions

We have considered a mathematical model for the spatial spread of two competing species using the diffusive Lotka-Volterra competition model. Travelling wave solution procedure was used to analyse the model. Of the four steady states obtained, we had an unstable origin with three other conditionally stable states. With diffusion, the nature of the equilibrium points differ from those the diffusion-free model. Due to diffusion, the origin $(0,0,0,0)$ is stable, which exhibits the possibility of a traveling wave from $(0,0,1,0)$ into $(0,0,0,0)$, from $\left(\frac{\gamma-1}{\beta\gamma-1}, 0, \frac{\beta-1}{\beta\gamma-1}, 0\right)$ into $(0,0,1,0)$ and $(1,0,0,0)$, and from $(1,0,0,0)$ into $(0,0,0,0)$. The effect of diffusion on the stability of the steady states was confirmed using the normal modes analysis. The result is in agreement with the special case considered by Okubo, *et al.* (1989). Hence we conclude that diffusion induces the simultaneous extinction of the the competing species.

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