Population Dynamics in a Patchy Space and Turing Bifurcation

A Thesis by
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1 Introduction

The Turing bifurcation is the basic bifurcation generating spatial pattern, wherein an equilibrium of a nonlinear system is asymptotically stable in the absence of diffusion but unstable in the presence of diffusion. This lies at the heart of almost all mathematical models for patterning in ecology, embryology and elsewhere in biology and chemistry.

The classical approach to modeling ecological systems (Volterra 1931, Lotka 1924) simplifies by ignoring space completely and in essence assumes that the per capita growth rates of the participating species are linear functions of the quantities (densities) of the species.

The classical Lotka-Volterra model takes the form:

$$\dot{u}_1 = u_1(r_1 - a_{11}u_1 - a_{12}u_2),\ \dot{u}_2 = u_2(-r_2 + a_{21}u_1 - a_{22}u_2), \tag{1}$$

where $r_i > 0$ is the growth or death rate, a_{ii} is the coefficient of intra-specific competition, $a_{ij}(i \neq j)$ is the coefficient of inter-specific competition.

A predator-prey model has received great attention in the last forty years in mathematical ecology due to its universal existence and importance.

A predator-prey model in which the predator consumes the prey with Holling type functional response (or ratio-dependent) take the form.

$$\dot{u}_1 = u_1(r_1 - a_{11}u_1 - \frac{u_2}{a + u_1}),\quad \dot{u}_2 = u_2(-r_2 + \frac{bu_1}{a + u_1} - a_{22}u_2). \tag{2}$$

where $r_1 > 0$ and $-r_2 < 0$ are the intrinsic growth rate and intrinsic mortality of the respective species, $a_{11} > 0$ and $a_{22} > 0$ represent the strength of the intraspecific competition (the competition within the species, $\frac{r_1}{a_{11}}$ is the carrying capacity for the prey), $b > 0$, $a > 0$ are the maximum birth rate and the half saturation constant of the predator, respectively. The meaning of the half saturation constant is that at $u_1 = a$ the specific growth rate $\frac{bu_1}{a+u_1}$ (called also a Holling type functional response) of the predator is equal to half its maximum b. The Holling type terms are more realistic than those in a Lotka-Volterra system because they increase with u_1 but do not tend to infinity and are concave down.

A predator-prey system of Cavani-Farkas type takes the form:

$$\dot{u}_1 = \varepsilon u_1(1 - \frac{u_1}{K}) - \frac{\beta u_1 u_2}{\beta + u_1}, \dot{u}_2 = -\frac{u_2(\gamma + \delta u_2)}{1 + u_2} + \frac{\beta u_1 u_2}{\beta + u_1}, \tag{3}$$

where $\varepsilon > 0$ is the specific growth rate of the prey in the absence of predation and without environmental limitation, $\beta > 0$, $K > 0$ are the conversion rate and carrying capacity with respect to the prey, respectively, $\gamma > 0$ and $\delta > 0$ are the minimal mortality and the limiting mortality of the predator, respectively (the natural assumption is $\gamma < \delta$). The advantage of this model over the more often used models is that here the predator mortality is neither a constant nor an unbounded function, still, it is increasing with the predator abundance.

2 The Aims and The Strategy

Because the relation between the organisms and the space seems to be essential to stability of an ecological system, the effect of diffusion on the possibility of species coexistence in an ecological community has been an important subject in population biology. The effects of self and cross-diffusion, Turing bifurcation and pattern formation are the subjects of this thesis.

One of the fundamental issues in spatial ecology is how explicit considerations of space alter the prediction of population models. Classical theories, such as diffusion-driven instability and meta-population dynamics which are developed via simple spatial population models, have profoundly increased our understanding of the issue. In this thesis I scrutinize these theories by considering more complicated processes of spatial interaction of populations. For this purpose I consider spatio-temporal models as systems of ODE which describe two-identical patch-two-species systems linked by migration, where the phenomenon of the Turing bifurcation occurs. In the models it is assumed that either the migration rate of each species is influenced only by its own density (self-diffusion) or that not only by its own but also by the other one's density (cross diffusion). I show that the equilibrium of a standard (self-diffusion) system may be either stable or unstable, a cross-diffusion response can stabilize an unstable equilibrium of standard system and destabilize a stable equilibrium of standard system. For the models I show that at a critical value of the bifurcation parameter the system undergoes a Turing bifurcation and numerical studies show that if the bifurcation parameter is increased through a critical value the spatially homogeneous equilibrium loses its stability and two new stable equilibria emerge. I conclude that the cross migration response is an important factor that should not be ignored when pattern emerges.

3 Main Results of My Work

I have checked how the strength and the type of the self-and cross-diffusion response affect the stability of these three type of interactions.

3.1 The Effect of a Self-Diffusion Response

I have considered a two-species model in a habitat of two identical patches linked by migration in which the migration rate of each species is influenced only by its own density, i.e. there is no response to the density of the other one described by the equations:

Let $u_i(t,j) :=$ density of species i in patch j at time t, $i = 1,2$; $j = 1,2$; $t \in R$

$$\begin{aligned}
\dot{u}_1(t,1) &= u_1(t,1)f_1(u_1(t,1), u_2(t,1)) + d_1(u_1(t,2) - u_1(t,1)),\\
\dot{u}_2(t,1) &= u_2(t,1)f_2(u_1(t,1), u_2(t,1)) + d_2(u_2(t,2) - u_2(t,1)),\\
\dot{u}_1(t,2) &= u_1(t,2)f_1(u_1(t,2), u_2(t,2)) + d_1(u_1(t,1) - u_1(t,2)),\\
\dot{u}_2(t,2) &= u_2(t,2)f_2(u_1(t,2), u_2(t,2)) + d_2(u_2(t,1) - u_2(t,2)),
\end{aligned} \tag{4}$$

where $f_i(i = 1,2)$ is continuously differentiable, $d_i > 0(i = 1,2)$ is a constant characterizing the rate of migration when individuals of species i migrate from a certain patch according to Fick's law.

Lotka-Volterra system:

I have shown that instability of a uniform state can not arise via the well known Turing mechanism of diffusion driven instability.

Predator-prey model with Holling type II functional response:

Theorem 3.1.1: *If*

$$\Theta_1 - 2d_1 > 0 \text{ and } d_2 > d_{2crit} = \frac{(\Theta_2\Theta_3 - \Theta_1\Theta_4 + 2d_1\Theta_4)}{2(\Theta_1 - 2d_1)}, \tag{5}$$

then Turing instability occurs.

Remark 3.1.1: *If*

$$\Theta_1 - 2d_1 < 0, \tag{6}$$

then self-diffusion never destabilizes the equilibrium $(\overline{u}_1, \overline{u}_2, \overline{u}_1, \overline{u}_2)$.

Where

$$\Theta_1 = \frac{\overline{u}_1}{a_{11}(a+\overline{u}_1)}[(\frac{r_1}{a_{11}} - a) - 2\overline{u}_1], \Theta_2 = \frac{\overline{u}_1}{a+\overline{u}_1}, \quad \Theta_3 = \frac{ab\overline{u}_2}{(a+\overline{u}_1)^2}, \quad \Theta_4 = a_{22}\overline{u}_2. \tag{7}$$

A predator-prey system of Cavani-Farkas type:

Theorem 3.1.2: *If*

$$\Phi_1 - 2d_1 > 0 \text{ and } d_2 > d_{2crit} = \frac{(\Phi_2\Phi_3 - \Phi_1\Phi_4 + 2d_1\Phi_4)}{2(\Phi_1 - 2d_1)}, \tag{8}$$

then Turing instability occurs.

Remark 3.1.2: *If*

$$\Phi_1 - 2d_1 < 0, \tag{9}$$

then self-diffusion never destabilizes the equilibrium $(\overline{u}_1, \overline{u}_2, \overline{u}_1, \overline{u}_2)$.

Where

$$\Phi_1 = \frac{\varepsilon\overline{u}_1(K-\beta-2\overline{u}_1)}{K(\beta+\overline{u}_1)}, \; \Phi_2 = \frac{\beta\overline{u}_1}{\beta+\overline{u}_1}, \Phi_3 = \frac{\beta^2\overline{u}_2}{(\beta+\overline{u}_1)^2}, \quad \Phi_4 = \frac{(\delta-\gamma)\overline{u}_2}{(1+\overline{u}_2)^2}. \tag{10}$$

3.2 The Effect of a Cross-Diffusion Response

I have considered a two-species models in a habitat of two identical patches linked by migration in which the per capita migration rate of each species is influenced not only by its own but also by the other one's density, i.e. there is cross diffusion present described by the equations:

Let $u_i(t,j) :=$ density of species i in patch j at time t, $i = 1,2$; $j = 1,2$; $t \in R$.

$$\begin{aligned}
\dot{u}_1(t,1) &= u_1(t,1)f_1(u_1(t,1),u_2(t,1)) + d_1(\rho_1(u_2(t,2))u_1(t,2) - \rho_1(u_2(t,1))u_1(t,1)),\\
\dot{u}_2(t,1) &= u_2(t,1)f_2(u_1(t,1),u_2(t,1)) + d_2(\rho_2(u_1(t,2))u_2(t,2) - \rho_2(u_1(t,1))u_2(t,1)),\\
\dot{u}_1(t,2) &= u_1(t,2)f_1(u_1(t,2),u_2(t,2)) + d_1(\rho_1(u_2(t,1))u_1(t,1) - \rho_1(u_2(t,2))u_1(t,2)),\\
\dot{u}_2(t,2) &= u_2(t,2)f_2(u_1(t,2),u_2(t,2)) + d_2(\rho_2(u_1(t,1))u_2(t,1) - \rho_2(u_1(t,2))u_2(t,2)),
\end{aligned} \tag{11}$$

where $f_i(i = 1, 2)$ is continuously differentiable, $d_i > 0(i = 1, 2)$ is a constant characterizing the rate of migration when individuals of species i migrate from a certain patch according to Fick's law, $\rho_i(u)(i = 1, 2)$ is a positive function of u characterizing the decrease or the increase of the rate of migration if it depends on the densities of the species.

Lotka-Volterra system:

Theorem 3.2.1: For competitive (or cooperative) type interaction: *the equilibrium point* $(\overline{u}_1, \overline{u}_2, \overline{u}_1, \overline{u}_2)$ *is asymptotically stable if* $\frac{\rho_1'}{\rho_1}, \frac{\rho_2'}{\rho_2}, \frac{\rho_1'\rho_2'}{\rho_1\rho_2}, d_1$ *and* d_2 *are sufficiently small; if* $\frac{\rho_1'}{\rho_1}, \frac{\rho_2'}{\rho_2}, \frac{\rho_1'\rho_2'}{\rho_1\rho_2}$ *and either* d_1 *or* d_2 *are sufficiently large the* $(\overline{u}_1, \overline{u}_2, \overline{u}_1, \overline{u}_2)$ *loses its stability by a Turing bifurcation.*

Predator-prey model with Holling type II functional response:

Theorem 3.2.2: *If*

$$\Theta_1 - 2d_1\rho_1 > 0, \tag{12}$$

and $\rho_2(\overline{u}_1)$ *is sufficiently large then Turing instability occurs.*

Remark 3.2.1: *As I have mentioned in section 3.1, if* $\Theta_1 - 2d_1 < 0$, *holds and there is no cross-diffusion then the equilibrium remains stable for any* $d_2 > 0$. *Still* $\Theta_1 - 2d_1\rho_1 > 0$ *may hold, i.e. in this case only the cross-diffusion effect may destabilize the equilibrium.*

A predator-prey system of Cavani-Farkas type:

Theorem 3.2.3: *If*

$$\Phi_1 - 2d_1\rho_1 > 0, \tag{13}$$

and $\rho_2(\overline{u}_1)$ *is sufficiently large then Turing instability occurs.*

Remark 3.2.2: *As I have mentioned in section 3.1, if* $\Phi_1 - 2d_1 < 0$, *holds and there is no cross-diffusion then the equilibrium remains stable for any* $d_2 > 0$. *Still* $\Phi_1 - 2d_1\rho_1 > 0$ *may hold, i.e. in this case only the cross-diffusion effect may destabilize the equilibrium.*

4 Conclusions

- I have considered spatio-temporal models as systems of ODE which describe two-identical patch-two-species systems linked by migration, where the phenomenon of the Turing bifurcation occurs.
- I have presented a simple and straightforward way of deducing the characteristic polynomial of matrix in a form that can be applied to calculate the all eigenvalues analytical to determine the stability.
- I have shown that the equilibrium of a standard (self-diffusion) system may be either stable or unstable, a cross-diffusion response can stabilize an unstable equilibrium of standard system and destabilize a stable equilibrium of standard system. For the models I show that at a critical value of the bifurcation parameter the system undergoes a Turing bifurcation and numerical studies show that if the bifurcation parameter is increased through a critical value the spatially homogeneous equilibrium loses its stability and two new stable equilibria emerge, i.e. a cross migration response is an important factor that should not be ignored when pattern emerges.

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