DIFFUSION-MEDIATED PERSISTENCE OF MATHEMATICAL MODELS IN POPULATION ECOLOGY

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ABSTRACT

We consider a model composed of two patches and analyze two cases. One patch has two competitors in one case and three competing species forming a heteroclinic cycle in the other case. Another patch is a refuge for one of the two or three species, which one can diffuse between the two patches. The remaining competitors are confined to the competitive patch and cannot diffuse. It is proved that the system with two competitors can be made persistent under appropriate diffusion conditions that ensure the instability of boundary equilibria, even if the competitive patch is not persistent without diffusion. With respect to the three-competitors case, a new heteroclinic cycle can exist in the model and the underlying one in the competitive patch cannot appear with a positive diffusion rate. It is proved that the model of the latter case also can be made persistent under appropriate diffusion conditions, even if the underlying heteroclinic cycle is an attractor in the competitive patch.

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1 INTRODUCTION

One of the most important problems in mathematical ecology concerns the survival of species. (Strong) persistence and permanence are well known concepts for dealing with this problem and exclude the possibility of extinction of species and therefore ensure the coexistence of the species in the system. With respect to references on persistence, see Butler, Freedman and Waltman [4] and Freedman and Waltman [9], which give a method to check persistence by examining limit sets on the boundary of the phase space. Concerning permanence, see Hofbauer [10,11], Hutson [14], Hutson and Vickers [15], Hofbauer and Sigmund [12].

When the system is not persistent, several authors considered the possibility to make the system persistent by introducing predators [12,13,15,17,18] or by partitioning the system into patches and connecting them by diffusion [1,19,23,24,25].

When the system has two competitors and it is described by a Lotka-Volterra model, three typical dynamical behaviours ,*Coexistence*, *Bistability* and *Dominance* are possible (see, for example, Freedman[6]).

Hutson and Vickers[15] showed that the coexistence is possible when a common predator is introduced if the system is coexistent or dominant. For the bistable case, the introduction of one predator is not enough to make the system persistent. We need *two* predators (Kirlinger[18]). Further, it is known that the bistable system cannot be made persistent by the introduction of *any one* species (a predator or a competitor) if the whole system is described by Lotka-Volterra model (see Hofbauer and Sigmund[12]).

When the system has three cyclically competing species, it can have a so called *heteroclinic cycle*, whose existence was shown originally in May and Leonard [20] and the system was investigated in detail in Coste et al. [5] and Schuster et al. [21]. The system with a heteroclinic cycle has three two-species competitive subsystems

and each subsystem has a dominant species. When the cycle is an attractor, the system is not persistent since the cycle belongs to the boundary of the phase space. This system can be made permanent by the introduction of a suitable predator or a suitable fourth competitor (Hofbauer and Sigmund [13]).

Concerning the possibility of *diffusion-mediated persistence*, the following is known. The system is composed of two Lotka-Volterra patches, each of which has two competitors, connected by diffusion. The system can be made persistent under appropriate diffusion conditions (Takeuchi [23]). But we need the heterogeneity for patch structures, which means that two competitive patches are not identical, to establish persistence of the system when both patches are bistable [19,23]. The result in [23] can be extended to the system composed of two competitors, one of which can diffuse between the two patches but the other is confined to one of the patches.

From the above consideration, it may be natural to ask whether it is possible to establish persistence for two competitors or three cyclically competing species by the introduction of one of the species' ability for the species to diffuse between patches. In this paper we consider a system with two patches. One of the patches is composed of two or three competitors. The other patch is composed of only one competitor and the one-species patch may be regarded as a kind of *refuge* for a dispersable competitor, since there exist no rivals in the patch. Therefore, the question can be stated as follows: is it possible to establish persistence if a refuge for one of the two or three species is introduced, when persistence is impossible without that refuge? It is proved that the system can be made persistent by choosing the diffusion parameter appropriately, even if the competitive patch is not persistent without diffusion.

2 MODEL

We consider the following models:

For two-competitors case;

$$\dot{x}_1 = x_1(r_1 - x_1 - \alpha_2 x_2) + \epsilon(y - x_1)$$

$$\dot{y} = y(R - y) + \epsilon(x_1 - y)$$

$$\dot{x}_2 = x_2(r_2 - \beta_1 x_1 - x_2)$$

(1)

For three-species model;

$$\dot{x}_1 = x_1 r_1(1 - x_1 - \alpha_2 x_2 - \beta_3 x_3) + \epsilon(y - x_1)$$

$$\dot{y} = yR(1 - y) + \epsilon(x_1 - y)$$

$$\dot{x}_2 = x_2 r_2(1 - \beta_1 x_1 - x_2 - \alpha_3 x_3)$$

(2)

$$\dot{x}_3 = x_3 r_3(1 - \alpha_1 x_1 - \beta_2 x_2 - x_3)$$

with all coefficients positive.

Here x_i $(i=1,2,3)$ are the numbers of competitors i in patch X; y is the number of species 1 in patch Y; α_i, β_j $(i,j=1,2,3)$ describe the effects of competition in patch X; r_i $(i=1,2,3)$ (or R) are carrying capacities for species i (or 1) in patch X (or Y); and ϵ is the diffusion coefficient between the two patches for species 1.

The system is composed of two patches X and Y which are connected by diffusion. Only species 1 can diffuse between the patches. For species 1, patch Y may be better than patch X in the sense that patch Y has no rivals. Therefore, patch Y can be regarded as a *refuge* for species 1.

We call system (1) (or (2)) *persistent* if all solutions to (1) (or (2)) with positive initial values satisfy $\liminf_{t \to \infty} x_i(t) > 0$ (for all i) and $\liminf_{t \to \infty} y(t) > 0$. Namely, the system is persistent if all species in the system can survive for all future times. The key for proving persistence of system (1) (or (2)) is the *Butler-McGehee lemma* (see [9] and its extentions and applications can be found, for example, in [4,7,18,22,23,24]), which can be stated as follows in our system (2):

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Let P be a point in $R^4_+ = \{(x_1, y; x_2, x_3) : x_i \geq 0 (i = 1, 2, 3), y \geq 0\}$ and Q be an equilibrium point. Then if $Q \in \Omega(P)$ (the omega-limit set of the orbit thorough P), then either (i) $Q = \Omega(P)$ or (ii) there exist Q^+ and Q^- such that $Q^+ \in W^+(Q) \backslash \{Q\}$, $Q^- \in W^-(Q) \backslash \{Q\}$, and $Q^+(Q^-) \in \Omega(P)$, where $W^+(Q)(W^-(Q))$ is the strong stable (unstable) manifold of Q.

First we consider the existence of nonnegative equilibria of system (1) (or (2)). Let us denote them by E^1_1, E^1_{12}, E_3 etc., the subscripts referring to the species with positive densities in patch X and the superscript to species 1 in patch Y.

Clearly, system (1) has three equilibrium points $E_0 = (0, 0; 0)$, $E_2 = (0, 0; r_2)$ and $E^1_1 = (\hat{x}_1(\epsilon), \hat{y}(\epsilon); 0)$.

On the other hand, $E_0 = (0, 0; 0, 0)$ is always an equilibrium for system (2). Also there exists $E^1_1 = (1, 1; 0, 0)$, which is globally stable for any $\epsilon > 0$ with respect to the two-dimensional space $\{x_1 > 0, y > 0; x_2 = x_3 = 0\}$ [7,8]. Further, there exist $E_2 = (0, 0; 1, 0)$ and $E_3 = (0, 0; 0, 1)$. The E^1_{13} does not exist for any $\epsilon > 0$, since no positive equilibria exist on the face $\{x_2 = 0\}$. E^1_{12} and E^1_{123}, the last one is a positive equilibrium point in R^4_+, may exist.

Hereafter we consider only generic case where all equilibrium points have hyperbolic Jacobian matrices, that is, no eigenvalue of the matrices has its real part equal to zero.

3 TWO-COMPETITORS CASE

For dispersable species 1, patch Y may be better than patch X, since patch X has a rival species 2. If $r_1 \leq R$, the best strategy for species 1 may be to stay in rich patch Y and avoid severe competition with species 2. In fact, it can be shown that any choice of ϵ cannot make the system persistent for the particular cases satisfying

that $r_1 \leq R$. Therefore we suppose that

$$r_1 > R \tag{3}$$

which means that patch X is more abundant for species 1 than patch Y. There is a conflict for species 1 between the need to choose more food and the need to avoid competition.

We can prove the following persistence theorem [24]:

THEOREM 1

If both E_1^1 and E_2 are unstable, then system (1) is persistent.

The instabilities of E_1^1 and E_2 are ensured under the assumption (3) if we choose $\epsilon > 0$ satisfying the following theorem [24]:

THEOREM 2

E_1^1 is unstable if ϵ satisfies one of the indicated conditions:

(i) any $\epsilon > 0$ for $r_2 - \beta_1 r_1 \geq 0$,

(ii) $\epsilon > \epsilon^*$ for $r_2 - \beta_1 r_1 \leq 0$.

Here ϵ^* is a value of ϵ satisfying $r_2 - \beta_1 \hat{x}_1(\epsilon^*) = 0$ and it exists if and only if

$$r_2 - \beta_1 (r_1 + R)/2 > 0. \tag{4}$$

E_2 is unstable if ϵ satisfies one of the indicated conditions:

(iii) any $\epsilon > 0$ for $r_1 - \alpha_2 r_2 + R \geq 0$,

(iv) $\epsilon < R(r_1 - \alpha_2 r_2)/(r_1 - \alpha_2 r_2 + R) = \bar{\epsilon}$ for $r_1 - \alpha_2 r_2 + R < 0$.

In the following subsections, it is shown that for system (1) the value of the diffusion parameter $\epsilon > 0$ can be chosen so that E_1^1 and E_2 are unstable *simultaneously*, regardless of the patch dynamics without diffusion.

3.1   Coexistence case

First suppose that patch X without diffusion is coexistent, that is,

$$r_1 - \alpha_2 r_2 > 0 \qquad and \qquad r_2 - \beta_1 r_1 > 0. \qquad (5)$$

By Theorem 2 (i), E_1^1 is unstable for any $\epsilon > 0$ and by Theorem 2 (iii), so is E_2 for any $\epsilon > 0$. Therefore, system (1) is always persistent for any diffusion rate when two competitors are coexistent without diffusion.

When $\epsilon = 0$, $E_1^1 = (r_1, R; 0)$ and $E_2 = (0, 0; r_2)$ are unstable. Therefore, they continue to be unstable for sufficiently small $\epsilon > 0$ and the system is persistent for small $\epsilon > 0$. The above analysis shows that persistence is ensured for *any* $\epsilon > 0$ when the competitive patch is coexistent.

3.2   Dominance case

First, Let us consider the case where species 2 is dominant in patch X, that is,

$$r_1 - \alpha_2 r_2 \leq 0 \qquad and \qquad r_2 - \beta_1 r_1 \geq 0. \qquad (6)$$

By Theorem 2 (i), E_1^1 is unstable for any $\epsilon > 0$ and by Theorem 2 (iii) and (iv), so is E_2 for any $\epsilon > 0$ if $r_1 - \alpha_2 r_2 + R \geq 0$ or for $\epsilon < \bar{\epsilon}$ if $r_1 - \alpha_2 r_2 + R < 0$. Therefore system (1) is persistent for any $\epsilon > 0$ if $r_1 - \alpha_2 r_2 + R \geq 0$ or for $\epsilon < \bar{\epsilon}$ if $r_1 - \alpha_2 r_2 + R < 0$.

Next, we consider the case where species 1 is dominant in patch X, that is,

$$r_1 - \alpha_2 r_2 \geq 0 \qquad and \qquad r_2 - \beta_1 r_1 \leq 0. \qquad (7)$$

This case is qualitatively different from the former dominance case. For case (6), E_1^1 and E_2 are unstable at $\epsilon = 0$ and so are they for sufficiently small $\epsilon > 0$. Therefore, the system is persistent for small $\epsilon > 0$ when species 2 is dominant. Concerning case (7), E_1^1 is stable for sufficiently small $\epsilon > 0$. Therefore, we need *large* $\epsilon > 0$ to establish persistence for the system when species 1 is dominant. By Theorems 1 and

2, E_1^1 and E_2 are unstable and the system is persistent if $\epsilon > \epsilon^*$. A necessary and sufficient condition for $\epsilon^* > 0$ to exist is given by (4).

3.3 Bistability case

Finally, consider the case where patch X is bistable, that is,

$$r_1 - \alpha_2 r_2 < 0 \qquad and \qquad r_2 - \beta_1 r_1 < 0. \tag{8}$$

Similarly to the last dominance case, E_1^1 is unstanle at $\epsilon = 0$. Therefore, we need again large $\epsilon > 0$ to attain persistence for the system.

By Theorems 1 and 2, the system is persistent for $\epsilon > \epsilon^*$ if $r_2 - \alpha_2 r_2 + R \geq 0$ or for $\epsilon^* < \epsilon < \bar{\epsilon}$ if $r_2 - \alpha_2 r_2 + R < 0$. The former case implies that the system is persistent for sufficiently large diffusion, but for the latter case so is the system for moderate diffusion $\epsilon^* < \epsilon < \bar{\epsilon}$. This may be reasonable from the biological point of view. Since for the former case the total carrying capacity for species 1 in two patches (that is, $r_1 + R$) can be large, species 1 can disperse frequently between the patches. But for the latter case, $r_1 + R$ is less than $\alpha_2 r_2$ and the frequent dispersal does not give much benefit for species 1. Another explanation seems to be possible. Parameter α_2 represents the competitive effect by species 2 on species x. For the former case $\alpha_2 \leq (r_1 + R)/r_2$, but for the latter $\alpha_2 > (r_1 + R)/r_2$. That is, for the former case species 1 can disperse between the patches without worrying about competition with species 2.

4 THREE-COMPETITORS CASE

Now we consider system (2) and assume that

$$0 < \beta_i < 1 < \alpha_i \qquad i = 1, 2, 3. \tag{9}$$

It is known that patch X of system (2) satisfying (9) represents *cyclic competition* with a *heteroclinic cycle* γ_0 on the boundary of the phase space [5,12,13,20,21]. We suppose that the heteroclinic cycle γ_0 is an attractor, that is,

$$\prod_{i=1}^{3}(\alpha_i - 1) > \prod_{i=1}^{3}(1 - \beta_i) \tag{10}$$

Therefore, system (2) is not permanent (persistent) [12,13] without diffusion.

Further we suppose that

$$\alpha_2 \beta_1 < 1, \tag{11}$$

$$\alpha_1 \beta_3 < 1. \tag{12}$$

Condition (11) ensures the global stability of E_{12}^1 with respect to the positive $x_1 y x_2$ face for system (2), if it exists [24]. Further, $E_1^1 = (1, 1; 0, 0)$ is globally stable in the $x_1 y x_3$ face if (12) is satisfied [24].

It is easy to show that E_{12}^1 exists [25] if and only if

$$(\alpha_2 - 1)r_1 - R \le 0 \qquad \text{for any } \epsilon > 0 \tag{13}$$

or

$$(\alpha_2 - 1)r_1 - R > 0 \qquad \text{for } \epsilon < \epsilon^* = \frac{Rr_1(\alpha_2 - 1)}{(\alpha_2 - 1)r_1 - R}. \tag{14}$$

Now we give conditions for persistence of system (2). We consider two cases, one is the case where E_{12}^1 exists and the other is the case where there exists no E_{12}^1.

4.1 Persistence for the case where E_{12}^1 exists

First suppose that E_{12}^1 exists. Then, E_2 is unstable with respect to $\{(x_1, y; x_2, x_3) : x_1 \ge 0, y \ge 0, x_2 > 0, x_3 = 0\}$.

THEOREM 3.

Suppose that an equilibrium point $E_{12}^1 = (\bar{x}_1, \bar{y}; \bar{x}_2, 0)$ exists for system (2). Then system (2) is persistent if and only if E_{12}^1 is unstable with respect to $\{(x_1, y; x_2, x_3) : x_1 > 0, y > 0, x_2 > 0, x_3 \geq 0\}$.

The necessity of Theorem 3 is obvious, since some solutions starting near E_{12}^1 converge to it if it is stable.

Note that the equilibrium point $\tilde{E}_{12}^1 = (\bar{x}_1, \bar{y}; \bar{x}_2)$ is globally stable with respect to $\{(x_1, y; x_2) : x_1 > 0, y > 0, x_2 > 0\}$ [24]. Therefore, the instability of E_{12}^1 implies that the solution starting near the equilibrium point (not on the boundary of R_+^4) tends to go into the interior of R_+^4. In fact, it can be shown that E_{12}^1 is unstable with respect to $\{(x_1, y; x_2, x_3) : x_1 > 0, y > 0, x_2 > 0, x_3 \geq 0\}$ if and only if

$$1 - \alpha_1 \bar{x}_1 - \beta_2 \bar{x}_2 > 0. \tag{15}$$

Condition (15) implies that E_{12}^1 is not *saturated*, that is, that the eigenvalue corresponding to the x_3-direction is positive [12].

4.2 Persistence for the case where E_{12}^1 does not exist

Next, let us consider the case where E_{12}^1 does not exist and E_2 is stable with respect to $\{(x_1, y; x_2, x_3) : x_1 \geq 0, y \geq 0, x_2 > 0, x_3 = 0\}$. From (13) and (14), the following must be satisfied.

$$(\alpha_2 - 1)r_1 - R > 0 \quad \text{and} \quad \epsilon > \epsilon^*. \tag{16}$$

In this case, a new heteroclinic cycle $E_1^1 \rightarrow E_2 \rightarrow E_3 \rightarrow E_1^1 \rightarrow \cdots$ exists for system (2), which we denote by γ. We can prove the following:

THEOREM 4.

Suppose that system (2) does not have an equilibrium point E_{12}^1. Then a heteroclinic cycle γ exists for (2). System (2) is persistent if and only if γ is a repellor.

Example. Let $\alpha_i = 3, \beta_i = 0.2, r_i = R = 1(i = 1, 2, 3)$ which satisfy (9), (11) and (12). Further condition (10) is also satisfied. Therefore, an attracting heteroclinic cycle γ_0 appears in system (2) with $\epsilon = 0$ and patch X is not persistent. These parameters satisfy (14) if $\epsilon < \epsilon^* = 2$ and E_{12}^1 exists for any $\epsilon < 2$. The instability condition (15) on E_{12}^1 is trivially satisfied for small $\epsilon > 0$ and system (2) is persistent by Theorem 3. Numerical simulations suggest that the condition (15) is satisfied for any $\epsilon < 2$ and system (2) may be persistent.

On the other hand, for $\epsilon \geq 2$, E_{12}^1 does not exist and a heteroclinic cycle γ exists in system (2) by Theorem 4. Numerical simulations show that γ is a repellor for $2 < \epsilon < 2.5$ and the system is persistent by Theorem 4.

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