

Metapopulation Dynamics with Migration and Local Competition

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Abstract

Many patch-based metapopulation models assume that the local population within each patch is at its equilibrium and independent of changes in patch occupancy. We study a metapopulation model which explicitly incorporates the local population dynamics of two competing species. Singular perturbation method is used to separate the fast dynamics of the local competition and the slow process of patch colonization and extinction. Our results show that the coupled system leads to much more complex outcomes than simple patch models that do not include explicit local dynamics.

Key words and phrases: Bifurcation, Competing species, Metapopulation, Singular perturbation

MSC2000: primary 34D15, 34D23, 92B05; secondary 34K60, 34E13, 92D40.

*Partially supported by NSF grant DMS-9974389 and NSF grant ESE-0119908

†Partially supported by NSF grant DMS-9803581

‡Partially supported by a Canadian NSERC postdoctoral fellowship

1 Introduction

There is a large body of literature dealing with species competitions using Lotka-Volterra type of models. Most of these models assume homogeneous environments and do not consider the impact of habitat fragmentation. The implications of habitat fragmentation have been studied using metapopulation models. A metapopulation is viewed as a network of idealized habitat patches (fragments) in which different species occur as discrete local populations connected by dispersal [4]. The first metapopulation model due to Levins [7] has the form

$$\frac{dp}{dt} = cp(1-p) - ep, \quad (1.1)$$

where p denotes the proportion of the occupied patches, c is the colonization rate of the empty patches, and e is the extinction rate of the occupied patches. This model has been generalized to include multiple species and habitat destruction (e.g., [1],[5],[9],[10]). However, most of these models do not take into consideration the local population dynamics within each patch. In [6], Hanski and Zhang developed a model that explicitly couples the local population changes and the metapopulation dynamics to examine the effect of migration on metapopulation persistence, with the goal of providing further insights into conditions for the metapopulation persistence which cannot be obtained from the simple patch models.

In this paper, we generalize the model in [6] by including two symmetric competitors in the local population dynamics. Differing from the patch models without local population dynamics, our model exhibits multiple interior equilibria. The fact that local competitions occur on a much faster time scale than changes in patch occupancy allows us to use the method of singular perturbations to separate the model dynamics into two time scales. A complete analysis of the slow dynamics will be conducted and the dynamical response to the incorporation of local competitions will be analyzed. The existence and uniqueness of an interior attractor will be also shown under the coexistence conditions.

2 Model

In [6], Hanski and Zhang proposed the following patch based metapopulation model:

$$\begin{cases} \frac{dN}{dt} &= rN\left(1 - \frac{N}{K}\right) - mN + \alpha mNp, \\ \frac{dp}{dt} &= \beta \alpha mNp(1-p) - ep, \end{cases} \quad (2.1)$$

where $p \in [0, 1]$ is the fraction of the occupied habitat patches, $N \in [0, \infty)$ is the average size of existing local populations with $r > 0$ as the averaged per capita birth rate and $K > 0$ as the carrying capacity, $m > 0$ is the per capita emigration rate, $\alpha > 0$ is the fraction of migrating individuals that survived and reached a new patch, $\beta > 0$ is the

per capita rate at which a new local population is created in an empty patch by arriving individuals, and $e > 0$ is the extinction rate of local populations.

We generalize the model (2.1) by considering the situation in which the local dynamics involve two competing species of Lotka-Volterra type. Let N_1 and N_2 denote the number of the species 1 and 2, respectively, and, let p_1 and p_2 denote the fractions of the patches occupied by species 1 and 2, respectively. Denote d/dt by “.” and use the subscript i to represent the species i , for $i = 1, 2$. Then the generalized model reads:

$$\begin{cases} \dot{N}_1 &= r_1 N_1 \left(1 - \frac{N_1}{K_1} - a_{12} \frac{N_2}{K_1}\right) - m_1 N_1 + \alpha_1 m_1 N_1 p_1, \\ \dot{N}_2 &= r_2 N_2 \left(1 - \frac{N_2}{K_2} - a_{21} \frac{N_1}{K_2}\right) - m_2 N_2 + \alpha_2 m_2 N_2 p_2, \\ \dot{p}_1 &= \beta_1 \alpha_1 m_1 N_1 p_1 (1 - p_1) - e_1 p_1, \\ \dot{p}_2 &= \beta_2 \alpha_2 m_2 N_2 p_2 (1 - p_2) - e_2 p_2, \end{cases} \quad (2.2)$$

where, for each $i, j = 1, 2$, $i \neq j$, a_{ij} is the competition coefficient between the species i and j , and, all other parameters have the similar meanings as their respective ones in (2.1).

Since the changes in patch occupancy occur on a slower time scale than the local population dynamics, the parameters β_i (patch creation) and e_i (patch extinction), $i = 1, 2$, are much smaller than all other parameters. This allows us to set N_1, N_2 at the equilibrium (N_1 and N_2 are then functions of p_1 and p_2) and study the respective dynamics of p_1 and p_2 .

Assume that

$$\beta_i = \varepsilon \hat{\beta}_i, \quad e_i = \varepsilon \hat{e}_i, \quad i = 1, 2,$$

where $\varepsilon > 0$ is small. Then system (2.2) can be rewritten as

$$\begin{cases} \dot{p}_1 &= \varepsilon p_1 f_1(p_1, N_1), \\ \dot{p}_2 &= \varepsilon p_2 f_2(p_2, N_2), \\ \dot{N}_1 &= N_1 g_1(p_1, N_1, N_2), \\ \dot{N}_2 &= N_2 g_2(p_2, N_1, N_2), \end{cases} \quad (2.3)$$

where

$$\begin{aligned} f_1(p_1, N_1) &= -\hat{e}_1 + \hat{\beta}_1 \alpha_1 m_1 N_1 (1 - p_1), \\ f_2(p_2, N_2) &= -\hat{e}_2 + \hat{\beta}_2 \alpha_2 m_2 N_2 (1 - p_2), \\ g_1(p_1, N_1, N_2) &= r_1 \left(1 - \frac{N_1}{K_1} - a_{12} \frac{N_2}{K_1}\right) - m_1 + \alpha_1 m_1 p_1, \\ g_2(p_2, N_1, N_2) &= r_2 \left(1 - \frac{N_2}{K_2} - a_{21} \frac{N_1}{K_2}\right) - m_2 + \alpha_2 m_2 p_2. \end{aligned}$$

The fast dynamics of (2.3) are given by

$$\begin{cases} \dot{N}_1 &= N_1 g_1(p_1, N_1, N_2), \\ \dot{N}_2 &= N_2 g_2(p_2, N_1, N_2). \end{cases} \quad (2.4)$$

As is in [6], we are only concerned with the case when both species are present, which, in the absence of metapopulation dynamics, is expected if and only if the competition

intensity is weak, i.e., $a_{12}, a_{21} < 1$. On the fast time scale, all solutions of (2.2) are hyperbolically asymptotic to the equilibrium (N_1^*, N_2^*) , where (N_1^*, N_2^*) is determined by

$$g_1(p_1, N_1, N_2) = 0, \quad g_2(p_1, N_1, N_2) = 0,$$

i.e.,

$$\begin{cases} r_1(1 - \frac{N_1}{K_1} - a_{12}\frac{N_2}{K_1}) - m_1 + \alpha_1 m_1 p_1 = 0, \\ r_2(1 - \frac{N_2}{K_2} - a_{21}\frac{N_1}{K_2}) - m_2 + \alpha_2 m_2 p_2 = 0. \end{cases} \quad (2.5)$$

Solving (N_1, N_2) from (2.5), we obtain the two-dimensional critical manifold (or slow manifold) characterized by

$$\begin{aligned} N_1^* &= k_{10} + k_{11}p_1 - k_{12}p_2, \\ N_2^* &= k_{20} - k_{21}p_1 + k_{22}p_2, \end{aligned} \quad (2.6)$$

where

$$\begin{aligned} k_{10} &= \frac{1}{1 - a_{12}a_{21}} \left[K_1(1 - \frac{m_1}{r_1}) - a_{12}K_2(1 - \frac{m_2}{r_2}) \right], \\ k_{11} &= \frac{\alpha_1 m_1}{r_1(1 - a_{12}a_{21})} K_1, \\ k_{12} &= \frac{a_{12}\alpha_2 m_2}{r_2(1 - a_{12}a_{21})} K_2, \\ k_{20} &= \frac{1}{1 - a_{12}a_{21}} \left[K_2(1 - \frac{m_2}{r_2}) - a_{21}K_1(1 - \frac{m_1}{r_1}) \right], \\ k_{21} &= \frac{\alpha_2 m_2}{r_1(1 - a_{12}a_{21})} K_1, \\ k_{22} &= \frac{\alpha_1 m_1}{r_2(1 - a_{12}a_{21})} K_2. \end{aligned}$$

Define

$$\mathbb{D}_1 = \left\{ (p_1, p_2) \mid 0 \leq p_1 \leq 1, \frac{k_{21}}{k_{22}}p_1 - \frac{k_{20}}{k_{22}} \leq p_2 \leq \frac{k_{11}}{k_{12}}p_1 + \frac{k_{10}}{k_{12}} \right\}. \quad (2.7)$$

Then $(p_1, p_2) \in \mathbb{D}_1$ if and only if $0 \leq p_1 \leq 1$ and

$$\begin{aligned} N_1^* &= k_{10} + k_{11}p_1 - k_{12}p_2 \geq 0, \\ N_2^* &= k_{20} - k_{21}p_1 + k_{22}p_2 \geq 0. \end{aligned} \quad (2.8)$$

Since only nonnegative equilibria make biological sense, only parameter values for which \mathbb{D}_1 is non-empty need to be considered.

Denote $\tau = t/\varepsilon$ and $d/d\tau = "r"$. Then the slow dynamics of (2.3) are determined by

$$\begin{cases} p_1' &= p_1 f_1(p_1, N_1^*), \\ p_2' &= p_2 f_2(p_2, N_2^*), \end{cases} \quad (2.9)$$

or

$$\begin{cases} p_1' &= p_1[-\hat{e}_1 + (1 - p_1)(\hat{k}_{10} + \hat{k}_{11}p_1 - \hat{k}_{12}p_2)], \\ p_2' &= p_2[-\hat{e}_2 + (1 - p_2)(\hat{k}_{20} - \hat{k}_{21}p_1 + \hat{k}_{22}p_2)], \end{cases} \quad (2.10)$$

where $\hat{k}_{ij} = \hat{\beta}_i \alpha_i m_i k_{ij}$, $i = 1, 2$ and $j = 0, 1, 2$. For convenience, we rewrite the system (2.10) as

$$\begin{cases} p_1' &= \hat{k}_{12} p_1 (1 - p_1) [-p_2 + h_1(p_1)], \\ p_2' &= \hat{k}_{21} p_2 (1 - p_2) [-p_1 + h_2(p_2)], \end{cases} \quad (2.11)$$

where

$$\begin{aligned} h_1(p_1) &= \alpha_{10} + \alpha_{11} p_1 - \frac{\alpha_{12}}{1 - p_1}, \\ h_2(p_2) &= \alpha_{20} + \alpha_{22} p_2 - \frac{\alpha_{21}}{1 - p_2}, \end{aligned} \quad (2.12)$$

and $\alpha_{1i} = \frac{\hat{k}_{1i}}{\hat{k}_{12}}$, $i = 0, 1$, $\alpha_{2j} = \frac{\hat{k}_{2j}}{\hat{k}_{21}}$, $j = 0, 2$, and $\alpha_{12} = \frac{\hat{e}_1}{\hat{k}_{12}}$, $\alpha_{21} = \frac{\hat{e}_2}{\hat{k}_{21}}$.

We note that both isoclines $p_2 = h_1(p_1)$, $p_1 = h_2(p_2)$ are hyperbolas with two branches each. The isocline $p_2 = h_1(p_1)$ has a vertical asymptote $p_1 = 1$ and a slang asymptote $L_1 : p_2 = \alpha_{10} + \alpha_{11} p_1$. The isocline $p_1 = h_2(p_2)$ has a horizontal asymptote $p_2 = 1$ and a slang asymptote $L_2 : p_1 = \alpha_{20} + \alpha_{22} p_2$. Moreover, it follows from (2.8) that $N_1^*(p_1, p_2) > 0$ if and only if (p_1, p_2) is below L_1 , and $N_2^*(p_1, p_2) > 0$ if and only if (p_1, p_2) is above L_2 . Hence, \mathbb{D}_1 has non-empty interior if and only if there is an open sub-interval of $p_1 \in (0, 1)$ over which L_1 is above L_2 .

3 Dynamics of the slow system

The equilibria for the slow system (2.11) are determined by

$$\begin{cases} p_1 [-p_2 + h_1(p_1)] &= 0, \\ p_2 [-p_1 + h_2(p_2)] &= 0. \end{cases} \quad (3.1)$$

Besides the equilibria at the origin, there can be equilibria on both axes, determined by $\{h_1(p_1) = 0, p_2 = 0\}$ and $\{p_1 = 0, h_2(p_2) = 0\}$, and equilibria lying inside of the unit square

$$\mathbb{D}_2 = \left\{ (p_1, p_2) \mid 0 \leq p_1, p_2 \leq 1 \right\},$$

determined by the intersections of two isoclines $p_2 = h_1(p_1)$ and $p_1 = h_2(p_2)$.

Since $p_1, p_2 \in [0, 1]$ and (2.8) must hold, dynamics of the slow system (2.11) should be considered within the region

$$\mathbb{D} = \mathbb{D}_1 \cap \mathbb{D}_2.$$

A primary step is of course to analyze all equilibria and their stabilities in \mathbb{D} . This would require *a priori* the classification of \mathbb{D} as well as its position in the unit square \mathbb{D}_2 , which, however, would not be an easy task because the determination of the positions of the slang asymptotes L_1, L_2 alone depends on four parameters and the determination of the positions of the two isoclines (for the analysis of equilibria) depends on another two parameters. To avoid such complication, we will take a different approach by first considering all possible slow dynamics lying in the unit square \mathbb{D}_2 then identifying conditions which lead to interesting slow dynamics in \mathbb{D} .

Proposition 3.1. *Both \mathbb{D} (if exists) and \mathbb{D}_2 are positively invariant and attracting with respect to the slow system (2.11).*

Proof. We note that both axes $p_1 = 0$ and $p_2 = 0$ are invariant. Moreover, $p'_i|_{\{p_i=1\} \cup L_i} = -\hat{e}_i p_i < 0$ for all $i = 1, 2$. The proposition easily follows. \square

Although we are mainly interested in the coexistence scenario (i.e., the existence of equilibria in the interior of \mathbb{D}) for the slow system (2.11), the investigation of stabilities of possible boundary equilibria will provide useful information for the study of interior ones.

We first exam the threshold conditions for the stability of the origin $(p_1, p_2) = (0, 0)$. Rewrite system (2.11) as

$$\begin{cases} p'_1 &= -(\hat{e}_1 - \hat{k}_{10})p_1 + (\hat{k}_{11} - \hat{k}_{10})p_1^2 - \hat{k}_{12}p_1p_2 - \hat{k}_{11}p_1^3 + \hat{k}_{12}p_1^2p_2, \\ p'_2 &= -(\hat{e}_2 - \hat{k}_{20})p_2 - \hat{k}_{21}p_1p_2 + (\hat{k}_{22} - \hat{k}_{20})p_2^2 + \hat{k}_{21}p_1p_2^2 - \hat{k}_{22}p_2^3. \end{cases} \quad (3.2)$$

The eigenvalues at the origin are $\hat{k}_{10} - \hat{e}_1$ and $\hat{k}_{20} - \hat{e}_2$. Let

$$\delta_i = k_{i0} - \frac{\hat{e}_i}{\hat{\beta}_i \alpha_i m_i}, \quad i = 1, 2. \quad (3.3)$$

As summarized in Table 1, depending on the values of δ_1 and δ_2 , the origin can be an attracting node, repelling node, or a saddle, which can also be degenerate.

	$\delta_1 > 0$	$\delta_1 = 0$	$\delta_1 < 0$
$\delta_2 > 0$	repelling node	repelling saddle-node	saddle
$\delta_2 = 0$	repelling saddle-node	degenerate saddle-node	attracting saddle-node
$\delta_2 < 0$	saddle	attracting saddle-node	attracting node

Table 1: Stability of the origin

We note that δ_1 and δ_2 provide threshold conditions for both the stability of the origin and the number of equilibria on the coordinate axes as well as in \mathbb{D}_2 . In particular, when both δ_1 and δ_2 vanish, the origin becomes degenerate with respect to the system (3.2).

Let

$$\theta_i = k_{ii} - k_{i0}, \quad i = 1, 2. \quad (3.4)$$

A straightforward calculation yields

$$\begin{aligned} \theta_1 &= = \frac{\hat{\beta}_1 \alpha_1 m_1}{1 - a_{12} a_{21}} [a_{12} (1 - \frac{m_2}{r_2}) K_2 - (1 - (1 + \alpha_1) \frac{m_1}{r_1}) K_1], \\ \theta_2 &= = \frac{\hat{\beta}_2 \alpha_2 m_2}{1 - a_{12} a_{21}} [a_{21} (1 - \frac{m_1}{r_1}) K_1 - (1 - (1 + \alpha_2) \frac{m_2}{r_2}) K_2], \end{aligned} \quad (3.5)$$

and hence the system (3.2) becomes

$$\begin{cases} p'_1 &= \hat{\beta}_1 \alpha_1 m_1 \theta_1 p_1^2 - \hat{k}_{12} p_1 p_2 - \hat{k}_{11} p_1^3 + \hat{k}_{12} p_1^2 p_2, \\ p'_2 &= -\hat{k}_{21} p_1 p_2 + \hat{\beta}_2 \alpha_2 m_2 \theta_2 p_2^2 + \hat{k}_{21} p_1 p_2^2 - \hat{k}_{22} p_2^3. \end{cases} \quad (3.6)$$

Since we are interested in the dynamics in the interior of \mathbb{D}_2 , the local bifurcation of the system (3.6) at the origin will not be considered in this work. It is interesting to note that since the origin can even be a saddle node of co-dimension three it can generate a rich set of local bifurcations.

For $i = 1, 2$, we note that the quantity $\hat{\beta}_i \alpha_i m_i k_{i0}$ measures the colonization ability of the empty patches by the i th population scaled by the local population size. The condition $\delta_i < 0$, or equivalently, $\hat{e}_i < \hat{\beta}_i \alpha_i m_i k_{i0}$, is in consistent with the conditions obtained from the simple patch models, i.e., the patch colonization rate needs to exceed the patch extinction rate in order for the metapopulation to persist. However, the scaling factor in our condition allows an assessment on how the local competition parameters may affect the metapopulation persistence.

3.1 Equilibria on the coordinate axes

By equilibria on the coordinate axes, we mean those lying in the unit interval $[0, 1]$ of the p_1 and the p_2 axes. They are determined by equations $p_2 = 0$, $h_1(p_1) = 0$ and $p_1 = 0$, $h_2(p_2) = 0$, respectively. Let $i = 1, 2$. A straightforward calculation shows that the equilibria p_{ij}^* , $j = 1, 2$, on the p_i axis satisfy

$$k_{i2} p_i^2 - \theta_i p_i - \delta_i = 0. \quad (3.7)$$

Hence if

$$\Delta_i = \theta_i^2 + 4k_{i2}\delta_i \geq 0, \quad (3.8)$$

then

$$p_{i1}^* = \frac{\theta_i - \sqrt{\Delta_i}}{2k_{i2}}, \quad p_{i2}^* = \frac{\theta_i + \sqrt{\Delta_i}}{2k_{i2}}$$

are real roots of (3.7). Since $p_i = 1$ is one of the asymptotes of the isoclines $h_i(p_i)$, and k_{12} and k_{21} are positive, we have $p_{i1}^* \leq p_{i2}^* < 1$.

There are three possibilities:

- If $\delta_i > 0$ or $\delta_i = 0$ but $\theta_i > 0$, then (3.7) has a unique positive root p_{i2}^* which corresponds to the unique equilibrium Q_{i2} on the positive p_i axis.
- If $\delta_i < 0$, $\theta_i > 0$ and $\Delta_i \geq 0$, then (3.7) has two positive roots (counting multiplicity) p_{ij}^* , $j = 1, 2$, which correspond to two equilibria Q_{ij} , $j = 1, 2$, on the positive p_i axis.
- If $\delta_i < 0$, $\theta_i < 0$ and $\Delta_i \geq 0$, or $\Delta_i < 0$, then (3.7) has no root in $(0, 1)$ since the isocline $h_i(p_i)$ lies outside of \mathbb{D}_2 . In this case, there are no equilibria on the positive p_1 and p_2 axes.

Putting the above cases together, Table 2 shows all possible nine cases of the equilibria on the positive axes.

	$\delta_1 \geq 0$	$\delta_1 < 0, \theta_1 > 0, \Delta_1 \geq 0$	$\delta_1 < 0, \theta_1 < 0, \Delta_1 \geq 0$ or $\Delta_1 < 0$
$\delta_2 \geq 0$	<p>Case I</p>	<p>Case II</p>	
$\delta_2 < 0$ $\theta_2 > 0$ $\Delta_2 \geq 0$	<p>Case III</p>	<p>Case IV</p>	
$\delta_2 < 0$ $\theta_2 < 0$ $\Delta_2 \geq 0$ or $\Delta_2 < 0$			

Table 2: Equilibria on the positive axes and phase portraits for the 5 simple cases

We now discuss the stabilities of these equilibria when they exist. Let $j = 1, 2$ and

$$\gamma_{1j} = \hat{k}_{12} [h_2(0) - p_{1j}^*], \quad \gamma_{2j} = \hat{k}_{21} [h_1(0) - p_{2j}^*]. \quad (3.9)$$

A straightforward calculation based on (2.12) yields

$$\begin{aligned} \gamma_{1j} &= \delta_2 - \frac{1}{2}[\theta_1 + (-1)^j \sqrt{\Delta_1}], \\ \gamma_{2j} &= \delta_1 - \frac{1}{2}[\theta_2 + (-1)^j \sqrt{\Delta_2}]. \end{aligned} \quad (3.10)$$

Using γ_{1j} , we can express the variational matrix of the equilibrium $Q_{1j} = (p_{1j}^*, 0)$ as

$$V(Q_{1j}) = \begin{pmatrix} \hat{k}_{12} \left[(1 - 2p_{1j}^*)h_1(p_{1j}^*) + p_{1j}^*(1 - p_{1j}^*)h_1'(p_{1j}^*) \right] & -\hat{k}_{21}p_{1j}^*(1 - p_{1j}^*) \\ 0 & \gamma_{1j} \end{pmatrix}. \quad (3.11)$$

Similarly, the variational matrix corresponding to the equilibrium $Q_{2j} = (0, p_{2j}^*)$ reads

$$V(Q_{2j}) = \begin{pmatrix} \gamma_{2j} & 0 \\ -\hat{k}_{21}p_{2j}^*(1 - p_{2j}^*) & \hat{k}_{21} \left[(1 - 2p_{2j}^*)h_2(p_{2j}^*) + p_{2j}^*(1 - p_{2j}^*)h_2'(p_{2j}^*) \right] \end{pmatrix}. \quad (3.12)$$

The existence and stabilities of of the equilibria Q_{ij} will depend on the sign of γ_{ij} , $j = 1, 2$, as showing in the following.

Proposition 3.2. 1) *If $\delta_i > 0$ or $\delta_i = 0$ and $\theta_i > 0$, then there is a unique equilibrium Q_{i2} on the p_i axis, which is a*

- a) *saddle, if $\gamma_{i2} > 0$;*
- b) *a saddle node, if $\gamma_{i2} = 0$; and*
- c) *an attracting node, if $\gamma_{i2} < 0$.*

2) *If $\Delta_i > 0$ and $\theta_i > 0$ ($\delta_i < 0$), then there are two equilibria Q_{i1} and Q_{i2} on the positive p_i axis. Moreover,*

- a) *if $\gamma_{i2} > 0$, then Q_{i1} is a repelling node and Q_{i2} is a saddle;*
- b) *if $\gamma_{i2} = 0$, then Q_{i1} is a repelling node and Q_{i2} is a saddle node ;*
- c) *if $\gamma_{i2} < 0 < \gamma_{i1}$, then Q_{i1} is a repelling node and Q_{i2} is an attracting node ;*
- d) *if $\gamma_{i1} = 0$, then Q_{i1} is a saddle node and Q_{i2} is an attracting node ;*
- e) *if $\gamma_{i1} < 0$, then Q_{i1} is a saddle and Q_{i2} is an attracting node.*

3) *If $\Delta_i = 0$ and $\theta_i > 0$ ($\delta_i < 0$), then Q_{i1} and Q_{i2} coalesce to become a saddle node (hence $\gamma_{i1} = \gamma_{i2}$), which is*

- a) *unstable, if $\gamma_{i1} \geq 0$; and*
- b) *stable, if $\gamma_{i1} < 0$.*

Moreover, there are five cases without interior equilibria of \mathbb{D}_2 whose respective phase portraits are as in Table 2.

The phase portraits for the remaining four cases (i.e., Cases I-IV) involving interior equilibria of \mathbb{D}_2 will be given in the next section together with discussions on the number and stabilities of the interior equilibria. One can see that the total number of the possible cases is very large if we include all the saddle-node bifurcations of the equilibria on the positive axes. Since all saddle-node bifurcations come from the tangency of the isoclines with their respective axes, we will omit their phase portraits since they can be easily obtained from their corresponding cases before the tangency occur.

3.2 Interior equilibria

The interior equilibria of \mathbb{D}_2 are the intersections of the two isoclines $p_2 = h_1(p_1)$ and $p_1 = h_2(p_2)$ in \mathbb{D}_2 . Since such an intersection necessarily lies below L_1 and above L_2 hence lies in \mathbb{D} , \mathbb{D}_2 and \mathbb{D} admit exactly the same set of interior equilibria. In the sequel, we will not specify the regions \mathbb{D}_2 or \mathbb{D} when referring to interior equilibria.

The p_1 coordinate of any interior equilibrium clearly satisfies the equation

$$p_1 = h_2(h_1(p_1)). \quad (3.13)$$

A straightforward calculation using *Maple* shows that (3.13) has the form

$$d_0 p_1^4 + d_1 p_1^3 + d_2 p_1^2 + d_3 p_1 + d_4 = 0, \quad (3.14)$$

where

$$\begin{aligned} d_0 &= -\frac{\alpha_1 m_1 (\alpha_2 m_2)^2 K_1 K_2^2}{r_1 r_2^2 (1 - a_{12} a_{21})^2} \neq 0, \\ d_1 &= -2\hat{k}_{11}\hat{k}_{22}^2 + \hat{k}_{12}\hat{k}_{21}^2 + \hat{k}_{10}\hat{k}_{21}\hat{k}_{22} - \hat{k}_{11}\hat{k}_{22}\hat{k}_{21} + 2\hat{k}_{11}\hat{k}_{20}\hat{k}_{22} \\ &\quad + 2\hat{k}_{12}\hat{k}_{21}\hat{k}_{22} - \hat{k}_{12}\hat{k}_{21}\hat{k}_{20}, \\ d_2 &= -2\hat{k}_{12}\hat{k}_{21}^2 + \hat{k}_{11}\hat{k}_{20}^2 + \hat{k}_{11}\hat{k}_{22}^2 + \hat{e}_1\hat{k}_{21}^2 - \hat{k}_{10}\hat{k}_{21}^2 - 2\hat{k}_{10}\hat{k}_{21}\hat{k}_{22} \\ &\quad + \hat{k}_{10}\hat{k}_{21}\hat{k}_{20} + 2\hat{k}_{11}\hat{k}_{22}\hat{k}_{21} - \hat{k}_{11}\hat{k}_{20}\hat{k}_{21} + 2\hat{k}_{11}\hat{k}_{22}\hat{e}_2 - 4\hat{k}_{11}\hat{k}_{20}\hat{k}_{22} \\ &\quad + 2\hat{k}_{12}\hat{k}_{21}\hat{k}_{20} - \hat{k}_{12}\hat{k}_{21}\hat{k}_{22} - \hat{k}_{12}\hat{k}_{21}\hat{e}_2, \\ d_3 &= \hat{k}_{12}\hat{k}_{21}^2 + 2\hat{k}_{10}\hat{k}_{21}^2 - 2\hat{e}_1\hat{k}_{21}^2 - 2\hat{k}_{10}\hat{k}_{21}\hat{k}_{20} + \hat{k}_{10}\hat{k}_{21}\hat{k}_{22} + \hat{k}_{10}\hat{k}_{21}\hat{e}_2 \\ &\quad - \hat{k}_{11}\hat{e}_2\hat{k}_{21} + 2\hat{k}_{11}\hat{k}_{20}\hat{e}_2 + 2\hat{k}_{11}\hat{k}_{20}\hat{k}_{21} - 2\hat{k}_{11}\hat{k}_{22}\hat{e}_2 - \hat{k}_{11}\hat{k}_{22}\hat{k}_{21} \\ &\quad + 2\hat{k}_{11}\hat{k}_{20}\hat{k}_{22} - \hat{k}_{12}\hat{k}_{21}\hat{k}_{20} + \hat{k}_{12}\hat{k}_{21}\hat{e}_2 - 2\hat{k}_{11}\hat{k}_{20}^2, \\ d_4 &= -\hat{k}_{10}\hat{k}_{21}\hat{e}_2 + \hat{e}_1\hat{k}_{21}^2 - \hat{k}_{11}\hat{k}_{20}\hat{k}_{21} + \hat{k}_{11}\hat{e}_2\hat{k}_{21} + \hat{k}_{10}\hat{k}_{21}\hat{k}_{20} \\ &\quad - 2\hat{k}_{11}\hat{k}_{20}\hat{e}_2 + \hat{k}_{11}\hat{k}_{20}^2 + \hat{k}_{11}\hat{e}_2^2 - \hat{k}_{10}\hat{k}_{21}^2. \end{aligned}$$

Hence the two isoclines admit at most four intersections (counting multiplicity) in the region \mathbb{D}_2 . Denote the discriminant of (3.14) by

$$\begin{aligned} \Delta &= -4d_3^3 d_0 d_3^2 - 4d_1^3 d_3^3 - 27d_1^4 d_4^2 - 128d_0^2 d_4^2 d_2^2 \\ &\quad + 16d_2^4 d_0 d_4 - 192d_0^2 d_4^2 d_1 d_3 - 6d_0 d_4 d_1^2 d_3^2 + 144d_0 d_4^2 d_2 d_1^2 \\ &\quad + 144d_0^2 d_4 d_2 d_3^2 + 18d_1 d_0 d_3^3 d_2 + d_2^2 d_1^2 d_3^2 - 4d_2^3 d_1^2 d_4 \\ &\quad + 256d_0^3 d_4^3 - 27d_0^2 d_3^4 - 80d_1 d_0 d_3 d_2^2 d_4 + 18d_1^3 d_3 d_2 d_4. \end{aligned} \quad (3.15)$$

Then $\Delta = 0$ defines a hypersurface in the parameter space. For any parameter value on the surface, a tangency of the two isoclines occurs. Such a tangency involves not only the two branches lying inside of \mathbb{D}_2 but also those lying outside of \mathbb{D}_2 .

For $i = 1, 2$, we note that $h_i''(p_i) < 0$, $p_i \in (0, 1)$, hence the function $h_i(p_i)$ on $(0, 1)$ admits a unique maximum at

$$p_{iM}^* = 1 - \sqrt{\frac{\alpha_{i2}}{\alpha_{i1}}} \quad (3.16)$$

with the maximal value

$$h_i(p_{iM}^*) = \alpha_{i0} - 2\sqrt{\alpha_{i1}\alpha_{i2}} + \alpha_{i1}. \quad (3.17)$$

As shown in Figure 1, we define

$$\begin{aligned} \mu_1 &= h_1(p_{1M}^*) - p_{2M}^*, \\ \mu_2 &= h_2(p_{2M}^*) - p_{1M}^*. \end{aligned} \quad (3.18)$$

Then the following holds.

Proposition 3.3. *If*

$$\mu_1 > 0, \quad \mu_2 > 0, \quad (3.19)$$

then the slow system (2.11) admits at least one interior equilibrium.

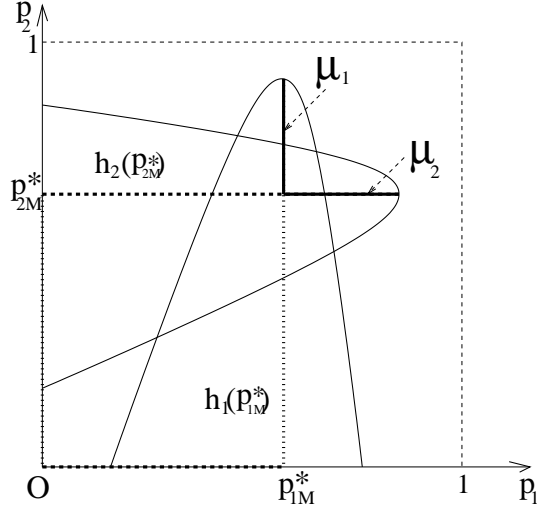


Figure 1: 4 interior equilibria: $\mu_1 > 0$ and $\mu_2 > 0$

Proof. Under the condition (3.19), the slow system (2.11) admits four equilibria in the unit square \mathbb{D}_2 . Since (2.11) can only have up to three equilibria on the coordinate axes, there is at least one interior equilibrium. \square

Due to the complexity of the expressions of d_i , $i = 0, 1, 2, 3, 4$, we will determine the number of interior equilibria geometrically and use Δ as the key quantity to determine the existence of an attracting interior equilibrium. When $\Delta > 0$, Proposition 3.3 will be used to separate the cases with and without interior equilibria.

We now state some properties concerning the stabilities of possible interior equilibria.

Proposition 3.4. *For any choice of the parameter values such that $\alpha_{ij} > 0$, $i, j = 1, 2$, the two isoclines $p_2 = h_1(p_1)$ and $p_1 = h_2(p_2)$ defined in (2.12) have up to 4 intersections (counting multiplicity) in the region \mathbb{D}_2 . In the case that exactly four interior equilibria present, two of them are hyperbolic saddles, one is an attracting node, and the other one is a repelling node (see Figure 2). Moreover, as parameters vary, the movement of the two isoclines give rise to 4, 3, 2, 1 and 0 interior equilibria, whose stabilities can be determined accordingly.*

Proof. Let $Q = (\bar{p}_1, \bar{p}_2)$ be any interior equilibrium. Then the variational matrix at Q is simply

$$V(Q) = \begin{pmatrix} \hat{k}_{12}\bar{p}_1(1-\bar{p}_1)h'_1(\bar{p}_1) & -\hat{k}_{12}\bar{p}_1(1-\bar{p}_1) \\ -\hat{k}_{21}\bar{p}_2(1-\bar{p}_2) & \hat{k}_{21}\bar{p}_2(1-\bar{p}_2)h'_2(\bar{p}_2) \end{pmatrix} \quad (3.20)$$

whose eigenvalues λ_1, λ_2 satisfy

$$\begin{aligned} \lambda_1 + \lambda_2 &= \hat{k}_{12}\bar{p}_1(1-\bar{p}_1)h'_1(\bar{p}_1) + \hat{k}_{21}\bar{p}_2(1-\bar{p}_2)h'_2(\bar{p}_2), \\ \lambda_1 \lambda_2 &= \hat{k}_{12}\hat{k}_{21}\bar{p}_1\bar{p}_2(1-\bar{p}_1)(1-\bar{p}_2)[h'_1(\bar{p}_1)h'_2(\bar{p}_2) - 1]. \end{aligned} \quad (3.21)$$

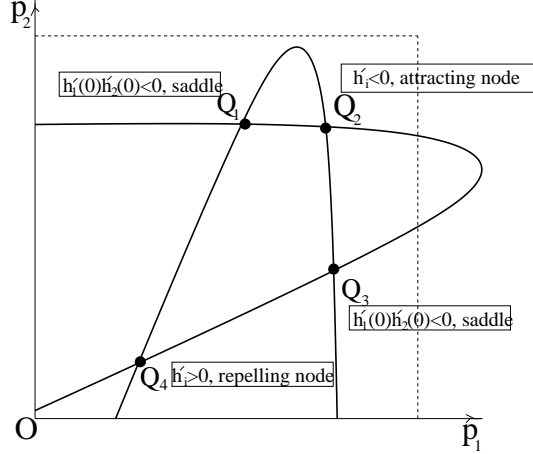


Figure 2: Stability of the interior equilibria

Now suppose that there are exactly four interior equilibria $Q_i = (\bar{p}_{1i}, \bar{p}_{2i})$, $i = 1, 2, 3, 4$, as shown in Figure 2, where $\bar{p}_{1i} \in (0, 1)$ are distinct roots of (3.14) and $\bar{p}_{2i} = h_1(\bar{p}_{1i})$.

Since $h'_1(\bar{p}_{1i})h'_2(\bar{p}_{2i}) < 0$, $i = 1, 3$, it follows from (3.21) that Q_1 and Q_3 are hyperbolic saddles. Also, since

$$\begin{aligned} h'_1(\bar{p}_{12}) &< \frac{1}{h'_2(\bar{p}_{22})} < 0, \\ h'_1(\bar{p}_{14}) &> \frac{1}{h'_2(\bar{p}_{24})} > 0, \end{aligned}$$

we have $h'_1(\bar{p}_{1i})h'_2(\bar{p}_{2i}) > 1$, $i = 2, 4$. It follows from (3.21) that Q_2 and Q_4 are nodes. Furthermore, since $h'_i(\bar{p}_{i2}) < 0$, $h'_i(\bar{p}_{i4}) > 0$, $i = 1, 2$, it is clear that Q_2 is attracting and Q_4 is repelling. \square

Depending on the positions of the equilibria on the axes and the sign of γ_{ij} , $i, j = 1, 2$, the two isoclines can only intersect in the Cases I-IV listed in Table 2. Also, the sign of Δ is crucial in determining the number and stability nature of the interior equilibria in each of these cases. In the proposition below, we only consider the bifurcating dynamics of (2.11), i.e., in the cases that $\gamma_{ij} \neq 0$, $i, j = 1, 2$, and $\Delta \neq 0$. Again, for a critical case in which one or more quantities above become 0, the corresponding phase portrait can be easily obtained from their respective bifurcating phase portraits (as we will see, only saddle-node bifurcations can occur for all parameter values).

- Proposition 3.5.**
- 1) Consider Case I, i.e., $\delta_1 \geq 0$ and $\delta_2 \geq 0$ (if $\delta_i = 0$, assume that $\theta_i > 0$, $i = 1, 2$). Then depending on the signs of $\gamma_{12}, \gamma_{22}, \Delta$, there is a total of seven sub-cases whose phase portraits are as in Table 3.
 - 2) Consider Case II, i.e., $\delta_1 < 0, \theta_1 > 0, \Delta_1 \geq 0$ and $\delta_2 \geq 0$. Then depending on the signs of $\gamma_{11}, \gamma_{12}, \Delta$, there is a total of seven sub-cases whose phase portraits are as in Table 4.
 - 3) Consider Case III, i.e., $\delta_1 \geq 0$ and $\delta_2 < 0, \theta_2 > 0, \Delta_2 \geq 0$. Then depending on the signs of $\gamma_{21}, \gamma_{22}, \Delta$, there is a total of seven sub-cases whose phase portraits are the same as Table 4 with the indexes 1, 2 reversed for all listed quantities.

- 4) Consider Case VI, i.e, $\delta_i < 0, \theta_i > 0$ and $\Delta_i \geq 0$, for $i = 1, 2$. Then depending on the sign of Δ , there is a total of four sub-cases whose respective phase portraits are as in Table 5.

Moreover, in all cases above, if $\Delta > 0, \mu_1 > 0$ and $\mu_2 > 0$ for some parameter value, then system (2.11) has a unique interior attracting node. All possible basins of attraction of the attracting nodes are indicated in the shaded regions in Tables 3- 5.

Proof. The result can be easily seen from the number, stability and positions of the equilibria on the positive axes summarized in Proposition 3.2 and Table 2, based on Theorem 3.6 below which simply says that the system (2.11) admits neither period orbits nor homoclinic loops in \mathbb{D}_2 . We note that in Case I, there exists a unique equilibrium Q_{12} on the p_1 axis and a unique equilibrium Q_{22} on the p_2 axis. The seven sub-cases are characterized by all possible sign changes of γ_{12}, γ_{22} and Δ . From Table 3, it is clear that in each of the sub-cases with $\Delta > 0$ system (2.11) admits a unique attracting interior equilibrium. We note that in all the subcases with $\Delta > 0$, the conditions $\mu_1 > 0, \mu_2 > 0$ hold automatically. In Case II (and similarly Case III), there exist two equilibria Q_{11} and Q_{12} on the p_1 axis and a unique equilibrium Q_{22} on the p_2 axis. Since γ_{22} is necessarily negative for $\delta_1 < 0$, the seven sub-cases are characterized by all possible sign changes of γ_{11}, γ_{12} and Δ . We note that $\gamma_{11} < 0$ and $\Delta > 0$ correspond to two types of phase portraits with none or four interior equilibria respectively. But Proposition 3.3 guarantees the existence of exactly four interior equilibria under the additional conditions that $\mu_1 > 0, \mu_2 > 0$, among which only one interior equilibrium is an attracting node, according to Proposition 3.4. In Case IV, for each $i = 1, 2$, there exist exactly two equilibria Q_{i1} and Q_{i2} on the positive p_i axis. Since in this case the quantities $\gamma_{ij}, i, j = 1, 2$, are always negative, the four sub-cases are characterized by the sign changes of Δ . Again, $\Delta > 0$ corresponds to two types of phase portraits with none or two interior equilibria respectively, and in the subcase that two interior equilibria present, one of them must be an attracting node. With an application of Proposition 3.3, the conditions $\mu_1 > 0, \mu_2 > 0$ again exclude the subcase having none interior equilibria. \square

3.3 Global dynamics of the slow system

Theorem 3.6. *For any choice of the positive parameters, system (2.11) admits neither periodic orbits nor homoclinic loops in the interior of \mathbb{D}_2 .*

Proof. The theorem is clearly true if there is no interior equilibrium. In general, the system (2.11) can have up to four interior equilibria, which, except for the critical cases, include two hyperbolic saddle and two nodes - one attracting and one repelling. We note that since \mathbb{D}_2 is positively invariant, if there exists a closed orbit (including both periodic orbit and homoclinic loop) in \mathbb{D}_2 , then it must surround one of the node.

We first consider the case when there exist exactly four interior equilibria, say, $Q_i = (\bar{p}_{1i}, \bar{p}_{2i}), i = 1, 2, 3, 4$, as shown in Figure 2.

$\gamma_{12} > 0, \gamma_{22} > 0 (\Delta > 0)$	
$\gamma_{12} < 0, \gamma_{22} > 0, \Delta < 0$	$\gamma_{12} < 0, \gamma_{22} > 0, \Delta > 0$
$\gamma_{12} > 0, \gamma_{22} < 0, \Delta < 0$	$\gamma_{12} > 0, \gamma_{22} < 0, \Delta > 0$
$\gamma_{12} < 0, \gamma_{22} < 0, \Delta < 0$	$\gamma_{12} < 0, \gamma_{22} < 0, \Delta > 0$

Table 3: Phase portraits of **Case I**: $\delta_1 \geq 0$ and $\delta_2 \geq 0$

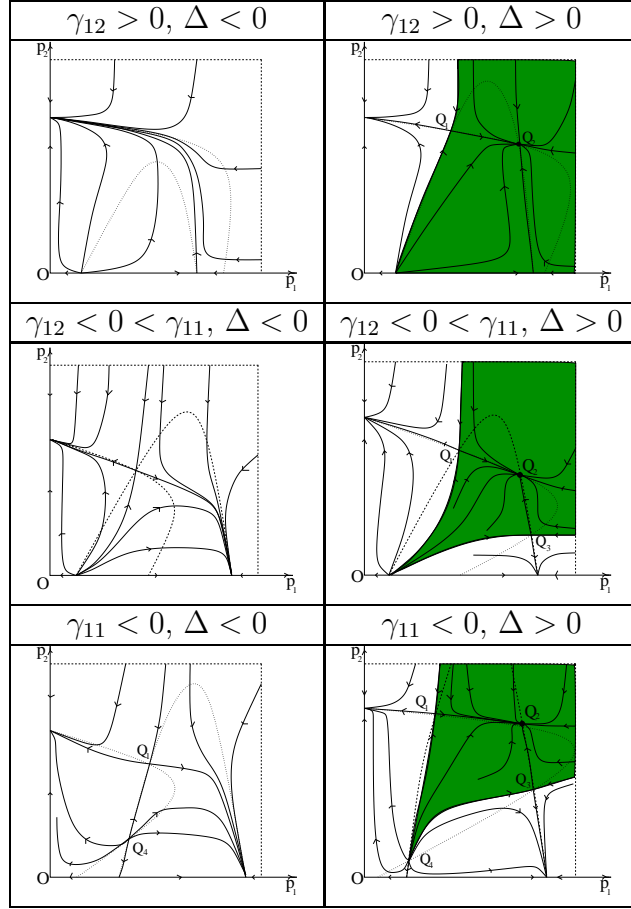


Table 4: Phase portraits of **Case II**: $\delta_1 < 0, \theta_1 > 0, \Delta_1 \geq 0$ and $\delta_2 \geq 0$, where $\gamma_{22} < 0$

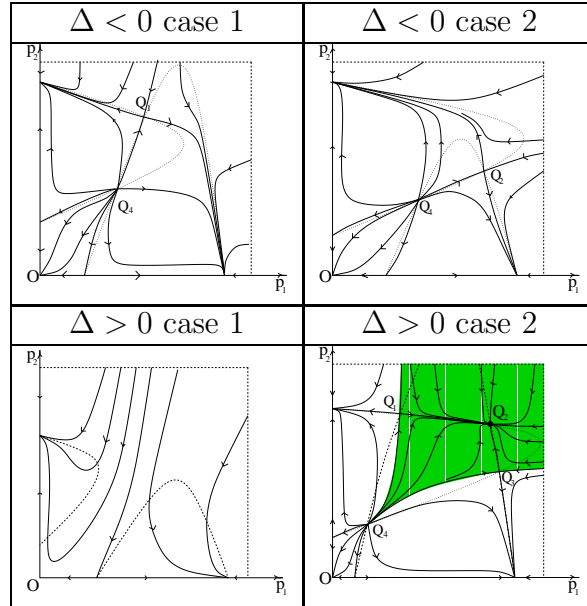


Table 5: Phase portraits of **Case IV**: $\delta_i < 0, \theta_i > 0$ and $\Delta_i \geq 0$ ($i = 1, 2$) and $\gamma_{ij} < 0$

Suppose that there is a closed orbit inside \mathbb{D}_2 which surrounds Q_2 . Let

$$\hat{p}_{1m} = \max\{0, \bar{p}_{11}\}, \quad \hat{p}_{1M} = \min\left\{1, \max_{p_2 \in (0,1)} h_2(p_2)\right\}. \quad (3.22)$$

Since interior equilibria exist, we have $\hat{p}_{1M} > 0$. Therefore, the closed orbit must lie in the open rectangle $\mathbb{D}^* = (\hat{p}_{1m}, \hat{p}_{1M}) \times (0, 1)$.

Within this open rectangle, we can rewrite system (2.11) as

$$\begin{cases} p_1' &= -\hat{k}_{12}p_1(1-p_1)[p_2 - h_1(p_1)], \\ p_2' &= -\hat{k}_{22}p_2[p_2 - g_1(p_1)][p_2 - g_2(p_1)], \end{cases} \quad (3.23)$$

where the functions $p_2 = g_1(p_1)$, and $p_2 = g_2(p_1)$, $p_1 \in (\hat{p}_{1m}, \hat{p}_{1M})$, are the two roots of

$$p_2^2 - \frac{\theta_2 + k_{21}p_1}{k_{22}}p_2 - \frac{\delta_2 - k_{21}p_1}{k_{22}} = 0. \quad (3.24)$$

Hence,

$$g_i(p_1) = \frac{1}{2k_{22}} \left[\theta_2 + k_{21}p_1 + (-1)^i \sqrt{(\theta_2 + k_{21}p_1)^2 + 4k_{22}(\delta_2 - k_{21}p_1)} \right], \quad i = 1, 2. \quad (3.25)$$

We note that $g_1(p_1) < g_2(p_1)$ for all $p_1 \in (\hat{p}_{1m}, \hat{p}_{1M})$.

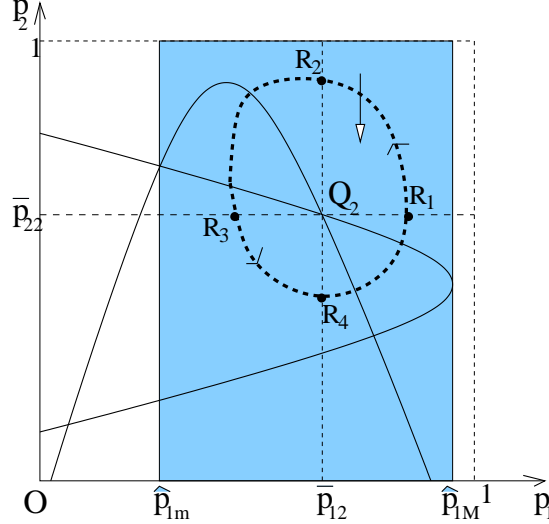


Figure 3: Auto bifurcation diagram

Define the functions $F_1(p_1)$ and $F_2(p_2)$ as the solutions to the following initial value problems:

$$\hat{k}_{12}p_1(1-p_1)\frac{dF_1}{dp_1} = g_2(p_1) - g_1(p_1), \quad F_1(\bar{p}_{12}) = 0, \quad (3.26)$$

$$\hat{k}_{22}p_2\frac{dF_2}{dp_2} = 1, \quad F_2(h_1(\bar{p}_{12})) = 0. \quad (3.27)$$

Let $F(p_1, p_2) = F_1(p_1) + F_2(p_2)$. Then a straightforward calculation yields that

$$\frac{dF}{d\tau} = -[(g_2(p_1) - g_1(p_1))[p_2 - h_1(p_1)] + (p_2 - g_1(p_1))(p_2 - g_2(p_1))]. \quad (3.28)$$

Denote by R_i , $i = 1, 2, 3, 4$, as the intersections of the closed orbit with the lines $p_1 = \bar{p}_{12}$ and $p_2 = \bar{h}_1(p_{12})$, as shown in Figure 3. On one hand, since

$$F(R_i) > 0, \quad i = 1, 2; \quad F(R_j) < 0, \quad j = 3, 4, \quad (3.29)$$

the direction of the closed orbit must be counterclockwise.

On the other hand, let (p_1, p_2) be any orbit of (3.23) in \mathbb{D}^* which stays in the cone $\{p_2 > g_2(p_1)\}$ during a time interval. Since by the second equation of (3.23)

$$p_2' = -\hat{k}_{22}p_2[p_2 - g_1(p_1)][p_2 - g_2(p_1)] < 0$$

for all τ in the time interval, it follows that the orbit must go downward during the same time interval. In particular, since the closed orbit passes through the cone, it has to go counterclockwise, a contradiction.

The above argument has shown that no closed orbit surrounding Q_2 can exist. The same holds for the interior equilibrium Q_4 .

In the case that there is an interior node and a less number (< 4) of interior equilibria, one can use the same argument as the above to show the non-existence of a closed orbit surrounding the node. \square

Based on the local and global analysis above, we conclude that away from the origin the only bifurcations which can occur in the slow system (2.11) are the saddle-node bifurcations and they can only occur when (i) the hypersurface $\Delta = 0$ is crossed; (ii) there is a tangency of the two isoclines with the coordinate axes; and (iii) the number of equilibria changes by ± 2 .

We now turn to the dynamics of the slow system (2.11) in \mathbb{D} . Since the equilibria on the coordinate axes represent the extinction of either p_1 or p_2 , in the cases that no attracting interior equilibrium is in present, all orbits in \mathbb{D} will tend to extinction. It is therefore of most interests focusing on the cases where an attracting interior equilibrium exists. Based on all the local and global dynamical studies above, the following theorem summarizes all the structurally stable cases with an interior attractor.

Theorem 3.7. *Consider the slow system (2.11). If $\Delta > 0$, $\mu_1 > 0$ and $\mu_2 > 0$, then \mathbb{D} has a non-empty interior and admits a unique stable interior node as the interior attractor.*

The above results on the dynamics of the slow system (2.11) can be easily extended to the full model (2.3). We note that the slow manifold

$$M = \{(N_1^*(p_1, p_2), N_2^*(p_1, p_2), p_1, p_2) : (p_1, p_2) \in \mathbb{D}\}$$

is normally hyperbolically stable and positively invariant with respect to (2.3) as $\varepsilon = 0$. It follows from the geometric theory of singular perturbation ([3]) that such a manifold is persistent for ε sufficiently small, i.e., given a positive integer r , there is a $\varepsilon_0 > 0$ such that (2.3) admits a family of normally hyperbolically stable invariant manifolds M_ε , $0 < \varepsilon \leq \varepsilon_0$, called center manifolds, which are C^r diffeomorphic and C^r close to M . Now, since the global bifurcating dynamics on \mathbb{D} (hence on M) are structurally stable, they are preserved on M_ε . In particular, if $\Delta > 0$, $\mu_1 > 0$ and $\mu_2 > 0$, then there exists a unique stable node which is an interior attractor on M_ε hence the unique attractor of (2.2) or (2.3), as ε sufficiently small. The geometric theory of singular perturbation along with the Tiknov-O'Malley matching principle ([8]) can also yield two scale asymptotic expansions for all solutions near the center manifolds M_ε (see [2] for more discussions).

To compare the results of our model with those of simple patch models, let us examine the following simple patch model for two competing species:

$$\begin{cases} \dot{p}_1 &= c_1 p_1 (1 - p_1 - a_{12} p_2) - e_1 p_1, \\ \dot{p}_2 &= c_2 p_2 (1 - p_2 - a_{21} p_1) - e_2 p_2. \end{cases} \quad (3.30)$$

If one species is absent then the system (3.30) reduces to the Levins model (1.1). It is known that (3.30) has at most one interior equilibrium and at most one non-trivial boundary equilibrium on each coordinate axis in the biological feasible region. Moreover, the interior equilibrium of (3.30) exists if $a_{12} a_{21} < 1$ and is always stable.

4 Discussion

We have formulated a metapopulation model that explicitly incorporates local competition dynamics of two species. This model generalizes the Hanski-Zhang model (2.1) by introducing two symmetric competing species under the assumption that patch colonizations are related to migration of local individuals. Our model apparently generates much richer dynamics than the ones produced by simple patch models without local population dynamics.

Using the method of singular perturbations to separate the fast local population dynamics and the slow changes in patch occupancy, we have conducted a detailed analysis of the slow system and identified threshold conditions for the existence and stability of feasible equilibria. It is shown that while multiple interior equilibria are possible, only one can be stable. It is clear that the outcomes predicted by our model and other simple patch models are qualitatively different. For example, the model (3.30) permits a unique interior equilibrium and a unique non-trivial boundary equilibrium where only one species is present, whereas our model is capable of generating multiple equilibria both in the interior and on the boundary. Our results also predict that in some cases two or three non-trivial equilibria can be stable for the same set of parameters (see Tables 3–5). These scenarios are also absent in simple patch models such as the one in (3.30). The implications of these different dynamics and possible uses of our model in the estimation of competition parameters will be discussed in a separate paper.

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