

Stability analysis of a two-species model with transitions between population interactions

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Abstract

Stability of a simple two-species system is investigated. This model assumes that the kind of inter-specific interactions is not fixed, and that it depends on the system state, i.e., undergoes transitions between different population interactions due to variation in population densities. The main goal is to show the effects of the transitions between different population interactions on the two-species coexistence, and on the stability conditions of multiple equilibria.

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1. Introduction

As pointed out by Murray (1993), for inter-specific interactions, there are three main types, i.e., host–parasite (or predator–prey), competition, and mutualism (or symbiosis). The classical two-species Lotka–Volterra equation provides a basic model to understand inter-specific interactions. In general, the standard two-species Lotka–Volterra equation is given by

$$\frac{dN_1}{dt} = N_1(\beta_1 - \alpha_{11}N_1 - \alpha_{12}N_2),$$
$$\frac{dN_2}{dt} = N_2(\beta_2 - \alpha_{21}N_1 - \alpha_{22}N_2),$$

where N_1 and N_2 denote the population densities of species 1 and species 2, respectively, and the parameters α_{12} and α_{21} are the coefficients of inter-specific interactions, i.e., if both α_{12} and α_{21} are positive then the populations are in a competition situation; if both α_{12} and α_{21} are negative then the populations are in a mutualism (or symbiosis) situation; and if α_{12} is

positive and α_{21} negative, or α_{12} is negative and α_{21} positive, then the populations are in a predator–prey situation.

Hernandez (1998) pointed out that the theoretical models about the populations showing one kind of interaction at one moment of time and then switching to another, i.e., undergoing transitions between different interactions, are very rare. But in nature this occurs often. Hernandez (1998) reviewed also some interesting instances for this phenomenon. Gibert (1983) showed that at low densities, interactions between Mullerian mimics are mutualistic as they facilitate the training of predators in recognizing unpalatable prey, and that at high densities they become competitors because they share resources. The interactions between some ant and aphid species can be beneficial at low aphid densities, but either detrimental or just neutral as this density increases (Addicott, 1979; Cushman and Addicott, 1991). Wahl and Hay (1995) investigated the epibiotic associations between host seaweed and some plant and animal epibionts, and showed that associations included both positive and negative effects. The outcome, ‘associated resistance’ or ‘shared doom’, was highly influenced by the relative densities of the species involved. Phillips et al. (1995) reported that

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seaweed flies, *Coelopa frigida* and *C. pilipes*, can interact either as competitors or as amensalists, etc.

Hernandez (1998) developed a theoretical model to study the stability properties of a two-species system that undergoes transitions between different population interactions. In this model, the inter-specific interaction is defined as a nonlinear function, called the α -function. Recently, Zhang (2003) presented a similar model to explain the effect of mutualism on coexistence among the competitors. In fact, there are many theoretical models for the inter-specific interactions that are mostly based on the modified Lotka–Volterra equations (May, 1981; Gillman and Hails, 1997). Addicott (1981) and Wolin and Lawor (1984) considered the variation in the outcome of the inter-specific interaction. Addicott (1981) compared three different mutualistic models, and studied the stability properties after perturbations on the equilibrium. Wolin and Lawor (1984) investigated the density-dependent effects on mutualistic interaction. It is different from the models that are concerned mainly with only one kind of inter-specific interaction, Hernandez’s (1998) model assumes that the inter-specific relationship depends on the system state, i.e., the inter-specific interaction coefficients α_{ij} ($i \neq j$) in the Lotka–Volterra equations are reinterpreted as nonlinear functions of population densities modulated by environmental parameters, which offer the possibility of a change in sign of α_{ij} due to the variation in population densities. Using a graphical stability analysis, Hernandez’s (1998) results show that multiple equilibria are possible. Zhang (2003) considered a theoretical model that is based on the classical Lotka–Volterra competition model, where he assumed that the interaction of one species to the other is flexible instead of always negative. Similarly to Hernandez (1998), Zhang (2003) used also the graphical stability analysis to emphasize that mutualism or cooperation among competitors promotes coexistence and competitive ability. Recently, Neuhauser and Fargione (2004) considered interactions between a symbiont and its host in the framework of the familiar Lotka–Volterra predator–prey model, modified to allow the symbiont to benefit the host. This model includes both benefits and costs to the interaction and spans the mutualism–parasitism continuum. Neuhauser and Fargione (2004) used this model to explore the shift from mutualism to parasitism in plant–mycorrhizae interactions across gradients of soil fertility.

In this paper, following Hernandez (1998) and Zhang (2003), a simple two-species system based on the classical Lotka–Volterra competition model is investigated. In this model, we assume that transitions between different population interactions are possible due to variation in population densities. We mainly focus our attention on the dynamical stability of the system in general, and we provide a complete stability analysis. Our main goal is to show the effects of transitions between different population interactions on the two-species coexistence, and on the stability of multiple equilibria.

2. Model and analysis

2.1. Basic model

Let us consider a simple two-species system,

$$\begin{aligned} \frac{dx}{dt} &= x(r - kx + (a - cy)y), \\ \frac{dy}{dt} &= y(R - Ky + (b - dx)x), \end{aligned} \tag{1}$$

where $x(t)$ and $y(t)$ denote the population densities of species 1 and species 2 at time t , respectively; the parameters r and R are the intrinsic growth rates of species 1 and species 2, respectively; k and K the coefficients of intra-specific competition of species 1 and species 2, respectively; and the term $a - cy$ represents the inter-specific interaction of species 2 to species 1; similarly, the term $b - dx$ the inter-specific interaction of species 1 to species 2. We also assume that the parameters $a - d$ are non-negative, i.e., $a, b, c, d \geq 0$. This implies that mutualism will happen at low density, but competition will happen at high density (Wolin and Lawor, 1984; Hernandez, 1998; Zhang, 2003).

Biologically, similarly to Hernandez (1998) and Zhang (2003), Eq. (1) is an expansion of the classic Lotka–Volterra competition equation, and we assume that both intrinsic growth rates R and r are positive, i.e., Eq. (1) can be not used to represent exactly a real prey–predator system. In this model, the kind of inter-specific interaction is assumed to be not fixed, and it depends on the system state (system state-dependent), i.e., the term $a - cy$ is positive if $y < \frac{a}{c}$ and negative if $y > \frac{a}{c}$; and the term $b - dx$ is positive if $x < \frac{b}{d}$ and negative if $x > \frac{b}{d}$. Three possible situations for the inter-specific relationship can be shown easily on the x – y phase plane (see Fig. 1), where the inter-specific relationship is called competition if $y > \frac{a}{c}$ and $x > \frac{b}{d}$, denoted by “(–, –)”; mutualism if $y < \frac{a}{c}$ and $x < \frac{b}{d}$, denoted by “(+, +)”; and host–parasite (prey–predator) if $y < \frac{a}{c}$ and $x > \frac{b}{d}$, denoted by “(+, –)”, or if $y > \frac{a}{c}$ and $x < \frac{b}{d}$, denoted by “(–, +)”.

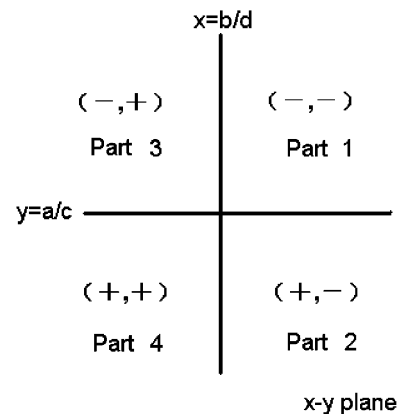


Fig. 1. Four possible kinds of population interactions are shown on the x – y phase plane.

As mentioned in Section 1, a similar model was developed by Hernandez (1998), where the inter-specific interaction is defined as a nonlinear function of the system state, called the α -function. Recently, Zhang (2003) used also a similar model to emphasize the effects of mutualism or cooperation among the competitors on the coexistence and competitive ability. But, it is necessary to point out that both Hernandez's (1998) and Zhang's (2003) results are based only on a graphic stability analysis.

2.2. Boundary equilibria

It is easy to see that in Eq. (1) three possible boundary equilibria are $(0, 0)$, $(\frac{r}{k}, 0)$ and $(0, \frac{R}{K})$, respectively, where $(0, 0)$ is called the trivial boundary.

Theorem 1. For the stabilities of the boundary equilibria in Eq. (1): (i) the trivial boundary equilibrium $(0, 0)$ must be unstable; (ii) the boundary equilibrium $(\frac{r}{k}, 0)$ is locally asymptotically stable if and only if $R + \frac{r}{k}(b - \frac{rd}{k}) < 0$; and, similarly, (iii) the boundary equilibrium $(0, \frac{R}{K})$ is locally asymptotically stable if and only if $r + \frac{R}{K}(a - \frac{Rc}{K}) < 0$.

Proof. (i) Note that the Jacobian matrix of Eq. (1) about $(0, 0)$ is $\begin{pmatrix} r & 0 \\ 0 & R \end{pmatrix}$ with positive eigenvalues r and R . Thus, the trivial boundary equilibrium $(0, 0)$ must be unstable. (ii) The Jacobian matrix of Eq. (1) about the boundary equilibrium $(\frac{r}{k}, 0)$ is

$$\begin{pmatrix} -r & \frac{ra}{k} \\ 0 & R + \frac{r}{k}(b - \frac{rd}{k}) \end{pmatrix}$$

with eigenvalues $-r$ and $R + \frac{r}{k}(b - \frac{rd}{k})$. Obviously, if $R + \frac{r}{k}(b - \frac{rd}{k}) > 0$, then $(\frac{r}{k}, 0)$ must be unstable and if the inequality is reversed, then $(\frac{r}{k}, 0)$ is stable. On the other hand, for the situation with $R + \frac{r}{k}(b - \frac{rd}{k}) = 0$, the boundary equilibrium $(\frac{r}{k}, 0)$ is unstable (see Appendix A). (iii) For the stability of the boundary equilibrium $(0, \frac{R}{K})$, the proof is similar to (ii). \square

The stability conditions for the non-trivial boundary equilibria provide a basic insight for the two-species coexistence, i.e., if both the boundary equilibria $(\frac{r}{k}, 0)$ and $(0, \frac{R}{K})$ are unstable, then the coexistence will be always possible when the initial values of $x(t)$ and $y(t)$, denoted by x_0 and y_0 , are positive, i.e., $x_0 > 0$ and $y_0 > 0$.

2.3. Interior equilibria

Clearly, an interior equilibrium of Eq. (1), denoted by (x^*, y^*) with $x^* > 0$ and $y^* > 0$, is the solution of the equations

$$\begin{aligned} r - kx + (a - cy)y &= 0, \\ R - Ky + (b - dx)x &= 0. \end{aligned} \tag{2}$$

On the x - y phase plane, the curve determined by the equation $r - kx + (a - cy)y = 0$ is the zero isocline for

$dx/dt = 0$, denoted by L_1 , and the curve determined by the equation $R - Ky + (b - dx)x = 0$ the zero isocline for $dy/dt = 0$, denoted by L_2 . For convenience, the slopes of two zero isoclines L_1 and L_2 at an interior equilibrium (x^*, y^*) are denoted by $\frac{dy}{dx}(L_1^*)$ and $\frac{dy}{dx}(L_2^*)$, respectively, i.e.,

$$\begin{aligned} \frac{dy}{dx}(L_1^*) &= \frac{k}{a - 2cy^*}, \\ \frac{dy}{dx}(L_2^*) &= \frac{b - 2dx^*}{K}. \end{aligned} \tag{3}$$

According to the signs of $\frac{dy}{dx}(L_1^*)$ and $\frac{dy}{dx}(L_2^*)$, three possible types of the interior equilibria are defined.

Definition. (i) (x^*, y^*) is a competitive equilibrium, denoted by CP, if $\frac{dy}{dx}(L_1^*) < 0$ and $\frac{dy}{dx}(L_2^*) < 0$; (ii) (x^*, y^*) is a mutualistic equilibrium, denoted by MP, if $\frac{dy}{dx}(L_1^*) > 0$ and $\frac{dy}{dx}(L_2^*) > 0$; and (iii) (x^*, y^*) is a host-parasite (predator-prey) equilibrium, denoted by HP, if $\frac{dy}{dx}(L_1^*) > 0$ and $\frac{dy}{dx}(L_2^*) \leq 0$, or if $\frac{dy}{dx}(L_1^*) < 0$ and $\frac{dy}{dx}(L_2^*) \geq 0$ (see Fig. 2a-c).

Notice that for the curve L_1 the solutions of the equation $r + (a - cy)y = 0$ are

$$\begin{aligned} y' &= \frac{1}{2c}(a + \sqrt{a^2 + 4cr}) > 0, \\ y'' &= \frac{1}{2c}(a - \sqrt{a^2 + 4cr}) < 0, \end{aligned}$$

and the point (x_1, y_1) with $x_1 = \frac{1}{k}(r + \frac{a^2}{4c})$ and $y_1 = \frac{a}{2c}$ corresponds to the maximum of the parabola

$$x = \frac{r + (a - cy)y}{k} \Leftrightarrow r - kx + (a - cy)y = 0.$$

Similarly, for the curve L_2 the solutions of equation $R + (b - dx)x = 0$ are

$$\begin{aligned} x' &= \frac{1}{2d}(b + \sqrt{b^2 + 4dR}) > 0, \\ x'' &= \frac{1}{2d}(b - \sqrt{b^2 + 4dR}) < 0, \end{aligned}$$

and the point (x_2, y_2) with $x_2 = \frac{b}{2d}$ and $y_2 = \frac{1}{K}(R + \frac{b^2}{4d})$ corresponds to the maximum of the parabola

$$y = \frac{R + (b - dx)x}{K} \Leftrightarrow R - Ky + (b - dx)x = 0.$$

This implies that at most three interior equilibria can exist in Eq. (1), i.e., if $x' > \frac{r}{k}$ and $y' > \frac{R}{K}$, then at least one, and at most three interior equilibria exist; if $x' < \frac{r}{k}$ and $y' < \frac{R}{K}$, then there must be a unique interior equilibrium; and if $x' > \frac{r}{k}$ and $y' < \frac{R}{K}$, or $x' < \frac{r}{k}$ and $y' > \frac{R}{K}$, then there is no interior equilibrium, or there are one or two interior equilibria. From theorem 1, the boundary equilibrium $(\frac{r}{k}, 0)$ is locally asymptotically stable if and only if $\frac{r}{k} < x'$; the

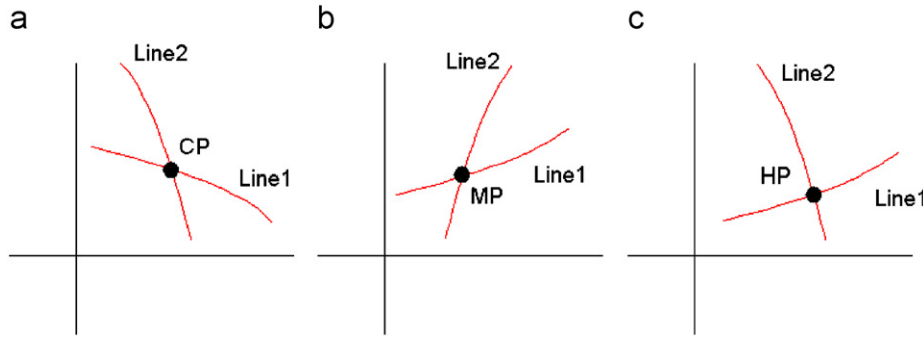


Fig. 2. Three types of interior equilibria are defined: (a) for $\frac{dy}{dx}(L_1^*) < 0$ and $\frac{dy}{dx}(L_2^*) < 0$, the interior equilibrium is CP; (b) for $\frac{dy}{dx}(L_1^*) > 0$ and $\frac{dy}{dx}(L_2^*) > 0$, the interior equilibrium is MP; and (c) for $\frac{dy}{dx}(L_1^*) < 0$ and $\frac{dy}{dx}(L_2^*) > 0$, or $\frac{dy}{dx}(L_1^*) > 0$ and $\frac{dy}{dx}(L_2^*) < 0$, the interior equilibrium is HP.

boundary equilibrium $(0, \frac{R}{K})$ is locally asymptotically stable if and only if $\frac{R}{K} < y'$. On the other hand, from Eq. (3), we know also that $\frac{dy}{dx}(L_1^*) > 0$ if $y^* < y_1 (= \frac{a}{2c})$ and $\frac{dy}{dx}(L_1^*) < 0$ if $y^* > y_1$, and that $\frac{dy}{dx}(L_2^*) > 0$ if $x^* < x_2 (= \frac{b}{2d})$ and $\frac{dy}{dx}(L_2^*) < 0$ if $x^* > x_2$. We will show that this result provides a basic relationship between the position of an interior equilibrium (x^*, y^*) and its stability.

In order to determine analytically the existence of an interior equilibrium, let

$$\hat{x} = x - \frac{b}{2d}, \quad \hat{y} = y - \frac{a}{2c}. \tag{4}$$

Then, Eq. (2) can be expressed equivalently as

$$\hat{x}^4 + p\hat{x}^2 + q\hat{x} + \gamma = 0, \tag{5}$$

where

$$\begin{aligned} p &= \frac{2K}{d} \left(\frac{a}{2c} - \frac{R}{K} - \frac{b^2}{4dK} \right), \\ q &= \frac{K^2k}{cd^2} > 0, \\ \gamma &= q \left[\left(\frac{b}{2d} - \frac{r}{k} - \frac{a^2}{4ck} \right) + \frac{c}{k} \left(\frac{a}{2c} - \frac{R}{K} - \frac{b^2}{4dK} \right)^2 \right]. \end{aligned} \tag{6}$$

Let $\hat{x}_1, \hat{x}_2, \hat{x}_3$ and \hat{x}_4 denote the four possible roots of Eq. (5). Then, we must have $\sum_{i=1}^4 \hat{x}_i = 0$ and $\prod_{i=1}^4 \hat{x}_i = \gamma$. Eq. (10) can be factorized as

$$(\hat{x}^2 + a_1\hat{x} + b_1)(\hat{x}^2 + a_2\hat{x} + b_2) = 0, \tag{7}$$

where $a_1 + a_2 = 0$, $a_1a_2 + b_1 + b_2 = p$, $a_1b_2 + a_2b_1 = q$, and $b_1b_2 = \gamma$, i.e.,

$$\begin{aligned} a_2 &= -a_1, \\ b_1 &= \frac{1}{2} \left(p + a_1^2 - \frac{q}{a_1} \right), \\ b_2 &= \frac{1}{2} \left(p + a_1^2 + \frac{q}{a_1} \right) \end{aligned} \tag{8}$$

and

$$a_1^6 + 2pa_1^4 + (p^2 - 4\gamma)a_1^2 - q^2 = 0. \tag{9}$$

It is easy to see that Eq. (9) has at least two real roots about a_1 . Let $\alpha = a_1^2 + \frac{2p}{3}$. Then, Eq. (9) can be rewritten as

$$\alpha^3 + \tilde{p}\alpha + \tilde{q} = 0, \tag{10}$$

where

$$\begin{aligned} \tilde{p} &= -\frac{1}{3}p^2 - 4\gamma, \\ \tilde{q} &= -\frac{2}{27}p^3 + \frac{8}{3}p\gamma - q^2. \end{aligned} \tag{11}$$

Eq. (10) has three roots, denoted by α_1, α_2 and α_3 with

$$\begin{aligned} \alpha_1 &= (\hat{x}_1 + \hat{x}_2)^2 + \frac{2p}{3}, \\ \alpha_2 &= (\hat{x}_1 + \hat{x}_3)^2 + \frac{2p}{3}, \\ \alpha_3 &= (\hat{x}_1 + \hat{x}_4)^2 + \frac{2p}{3}. \end{aligned}$$

Clearly, Eq. (10) has one real root if $\Delta > 0$; it has two different real roots if $\Delta = 0$; and it has three different real roots if $\Delta < 0$, where

$$\Delta = \left(\frac{\tilde{q}}{2} \right)^2 + \left(\frac{\tilde{p}}{3} \right)^3. \tag{12}$$

This implies that Eq. (5) has at most two real roots if $\Delta > 0$; it has one or three real roots if $\Delta = 0$; and it has no real root or four real roots if $\Delta < 0$. Thus, for the existence of interior equilibria in Eq. (1), we have the following result:

Result 1. (i) For $\Delta > 0$, there is one interior equilibrium if both boundary equilibria $(\frac{r}{k}, 0)$ and $(0, \frac{R}{K})$ are unstable (see Fig. 3d–f), or no interior equilibrium can exist if either $(\frac{r}{k}, 0)$ or $(0, \frac{R}{K})$ is stable but the other unstable; (ii) for $\Delta = 0$, there are two interior equilibria if both $(\frac{r}{k}, 0)$ and $(0, \frac{R}{K})$ are unstable (see Fig. 4c, d), or there is one interior equilibrium if either $(\frac{r}{k}, 0)$ or $(0, \frac{R}{K})$ is stable but the other unstable (see Fig. 3b, c), or no interior equilibrium can exist if both $(\frac{r}{k}, 0)$ and $(0, \frac{R}{K})$ are stable; and (iii) for $\Delta < 0$, there are three interior equilibria if both $(\frac{r}{k}, 0)$ and $(0, \frac{R}{K})$ are unstable (see Fig. 5), or there are two interior equilibria if either $(\frac{r}{k}, 0)$ or

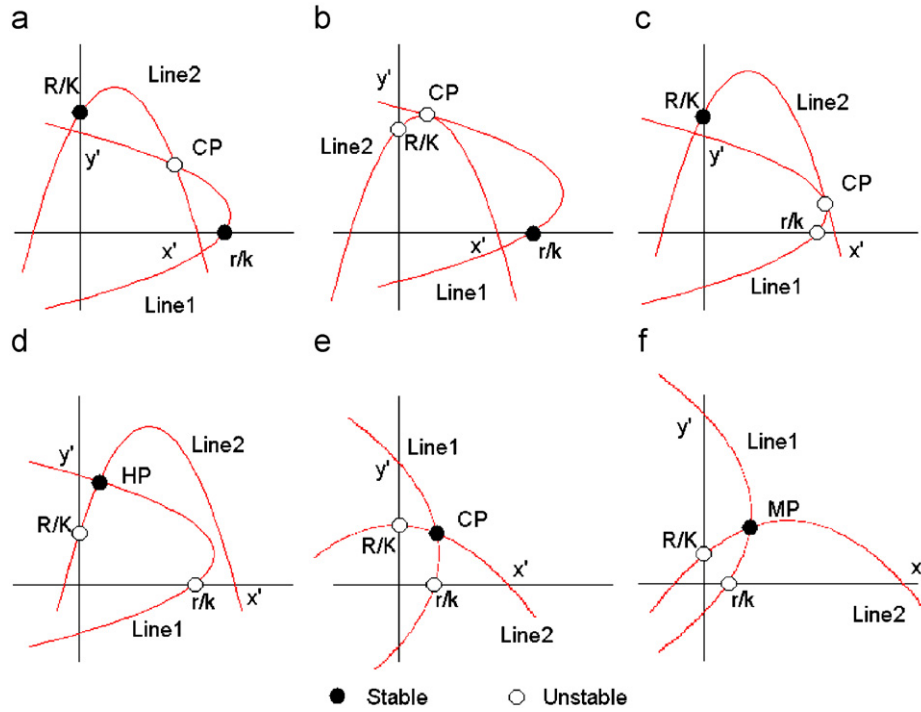


Fig. 3. The situation with only one interior equilibrium: (a)–(c) for $\frac{r}{k} > x'$ and $\frac{R}{K} > y'$, or $\frac{r}{k} > x'$ and $\frac{R}{K} < y'$, or $\frac{r}{k} < x'$ and $\frac{R}{K} > y'$, the interior equilibrium is an unstable CP. (d)–(f); for $\frac{r}{k} < x'$ and $\frac{R}{K} < y'$, the interior equilibrium is a stable HP, or CP, or MP.

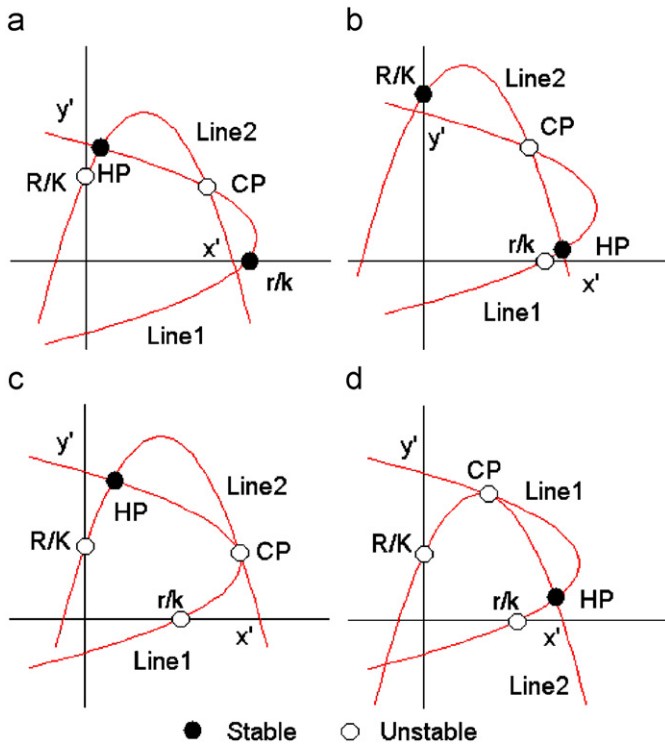


Fig. 4. The situation with two interior equilibria: (a)–(d) for $\frac{r}{k} > x'$ and $\frac{R}{K} < y'$, or $\frac{r}{k} < x'$ and $\frac{R}{K} > y'$, or $\frac{r}{k} < x'$ and $\frac{R}{K} < y'$, one of the two interior equilibria is a stable HP, and other a unstable CP.

$(0, \frac{R}{K})$ is stable but the other unstable (see Fig. 4a, b), or there is one interior equilibrium if both $(\frac{r}{k}, 0)$ and $(0, \frac{R}{K})$ are stable (see Fig. 3a).

For the local asymptotic stability of an interior equilibrium (x^*, y^*) , and the existence of the periodic solutions, we have the following two theorems:

Theorem 2. An interior equilibrium of Eq. (1), (x^*, y^*) , is locally asymptotically stable if and only if

$$\left(\frac{dy}{dx(L_1^*)}\right)^{-1} \frac{dy}{dx(L_2^*)} < 1. \tag{13}$$

Proof. The Jacobian matrix of Eq. (1) about an interior equilibrium (x^*, y^*) , denoted by \mathbf{J} , is given by

$$\mathbf{J} = \begin{pmatrix} -kx^* & x^*(a - 2cy^*) \\ y^*(b - 2dx^*) & -Ky^* \end{pmatrix} = \begin{pmatrix} -kx^* & kx^* \left(\frac{dy}{dx(L_1^*)}\right)^{-1} \\ Ky^* \frac{dy}{dx(L_2^*)} & -Ky^* \end{pmatrix}. \tag{14}$$

Since the eigenvalues of the Jacobian matrix \mathbf{J} are

$$\lambda_{1,2} = \frac{1}{2} \left[-(kx^* + Ky^*) \pm \sqrt{(kx^* + Ky^*)^2 - 4kKx^*y^* \left(1 - \left(\frac{dy}{dx(L_1^*)}\right)^{-1} \frac{dy}{dx(L_2^*)}\right)} \right], \tag{15}$$

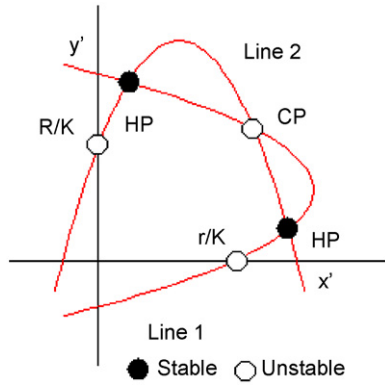


Fig. 5. The situation with three interior equilibria. Two of the interior equilibria are stable HPs, and other one an unstable CP.

the interior equilibrium (x^*, y^*) is locally asymptotically stable if

$$\left(\frac{dy}{dx(L_1^*)}\right)^{-1} \frac{dy}{dx(L_2^*)} < 1. \tag{16}$$

For the situation with

$$\left(\frac{dy}{dx(L_1^*)}\right)^{-1} \frac{dy}{dx(L_2^*)} = 1, \tag{17}$$

i.e., one of the eigenvalues of the Jacobian matrix \mathbf{J} is zero and the other one negative, the interior equilibrium (x^*, y^*) must be unstable (see Appendix B). \square

Theorem 3. For the dynamics given by Eq. (1), the existence of periodic solutions is impossible.

Proof. Let $\psi(x, y) = \frac{1}{xy}$, which is called the Dulac function. Notice that

$$\frac{\partial(\psi P)}{\partial x} + \frac{\partial(\psi Q)}{\partial y} = -\frac{k}{y} - \frac{K}{x} < 0 \tag{18}$$

for all possible $x > 0$ and $y > 0$, where $P = \frac{dx}{dt}$ and $Q = \frac{dy}{dt}$. Thus, from the Bendixson–Dulac theorem, no periodic solutions can exist in Eq. (1). \square

Theorem 3 implies that if there is only one interior equilibrium in Eq. (1) and it is locally asymptotically stable, then it must be globally asymptotically stable. It is necessary to point out that if more than one interior equilibria exist but only one interior equilibrium is locally asymptotically stable, then Theorem 3 does not mean that this locally stable equilibrium must be also globally stable.

According to the definition about the types of interior equilibria, it is easy to see that if an interior equilibrium (x^*, y^*) is a HP, then it must be locally asymptotically stable. In general, three possible situations have to be considered. Firstly, for the situation with only one interior equilibrium, we have the result:

Result 2. (i) For $\frac{r}{k} > x'$ and $\frac{R}{K} > y'$, only one interior equilibrium must exist, and it is unstable since it is a CP

with $(\frac{dy}{dx(L_1^*)})^{-1} \frac{dy}{dx(L_2^*)} > 1$ (see Fig. 3a); (ii) for $\frac{r}{k} > x'$ and $\frac{R}{K} < y'$, or $\frac{r}{k} < x'$ and $\frac{R}{K} > y'$, if there is only one interior equilibrium, then, about this interior equilibrium, we must have $\frac{dy}{dx(L_1^*)} = \frac{dy}{dx(L_2^*)}$, i.e., it must be unstable (see Fig. 3b, 3c); and (iii) for $\frac{r}{k} < x'$ and $\frac{R}{K} < y'$, if only one interior equilibrium exists, then it must be globally asymptotically stable since at this interior equilibrium we must have $(\frac{dy}{dx(L_1^*)})^{-1} \frac{dy}{dx(L_2^*)} < 1$ (see Fig. 3d–f). It is necessary to point out that if a MP exists, then it must be unique and must be asymptotically stable since a MP satisfies $x^* < \frac{b}{2d}$ and $y^* < \frac{a}{2c}$, and the two non-trivial boundaries are unstable if MP exists.

Secondly, for the situation with two interior equilibria, we have the result:

Result 3. (i) For $\frac{r}{k} > x'$ and $\frac{R}{K} < y'$, or $\frac{r}{k} < x'$ and $\frac{R}{K} > y'$, if there are two interior equilibria, then one of the interior equilibria is a HP and the other one a CP, where the HP is locally asymptotically stable, but the CP is unstable since at the CP the inequality $(\frac{dy}{dx(L_1^*)})^{-1} \frac{dy}{dx(L_2^*)} > 1$ holds (see Fig. 4a, b); and (ii) for $\frac{r}{k} < x'$ and $\frac{R}{K} < y'$, if there two interior equilibria, then one of the interior equilibria is a HP and the other one the interior equilibrium with $(\frac{dy}{dx(L_1^*)})^{-1} \frac{dy}{dx(L_2^*)} = 1$, where the HP is globally asymptotically stable, but the later is unstable (see Fig. 4c, 4d).

Finally, for the situation with three interior equilibria, we have the result:

Result 4. For $\frac{r}{k} < x'$ and $\frac{R}{K} < y'$, if there exist three interior equilibria, then two of them are HPs, and another one a CP, where the HPs must be locally asymptotically stable but the CP is unstable since at the CP the inequality $(\frac{dy}{dx(L_1^*)})^{-1} \frac{dy}{dx(L_2^*)} > 1$ holds (see Fig. 5).

The above results show that if an interior equilibrium is a HP or a MP, then it must be locally asymptotically stable; and if an interior equilibrium is a CP, then it can be stable or unstable.

3. Summary

May (1973) pointed out that for population models in deterministic environments, with the environmental parameters all well-defined constants, one is interested in the community equilibria where all the species' populations have time-independent values, that is where all net growth rates are zero. Such an equilibrium may be called stable if, when the populations are perturbed, they in time return to their equilibrium values; the return may be achieved either as damped oscillations or monotonically. In this paper, following Hernandez (1998) and Zhang (2003), the stability of a simple two-species system with transitions between population interactions is investigated. Our main goal is to show the effects of transitions between different population

interactions on the two-species coexistence, and on the stability conditions of the multiple equilibria.

In Eq. (1), the inter-specific interactions are dependent of the system state, and it offers the possibility of a change in the kind of inter-specific interactions due to the variation in population densities, i.e., $a - cy > 0$ ($a - cy < 0$) if $y < \frac{a}{c}$ ($y > \frac{a}{c}$), and $b - dx > 0$ ($b - dx < 0$) if $x < \frac{b}{d}$ ($x > \frac{b}{d}$). Three possible kinds of inter-specific interactions are defined as: (i) competition if $y > \frac{a}{c}$ and $x > \frac{b}{d}$, “(-, -)”; (ii) mutualism if $y < \frac{a}{c}$ and $x < \frac{b}{d}$, “(+, +)”; and (iii) host–parasite (prey–predator) if $y < \frac{a}{c}$ and $x > \frac{b}{d}$, “(+, -)”, or if $y > \frac{a}{c}$ and $x < \frac{b}{d}$, “(-, +)”.

Eq. (1) has three boundary equilibria, which are $(0, 0)$, $(\frac{r}{k}, 0)$ and $(0, \frac{R}{k})$, where $(0, 0)$ is called the trivial boundary equilibrium and it must be unstable. For the non-trivial boundary equilibria $(\frac{r}{k}, 0)$ and $(0, \frac{R}{k})$, Theorem 1 shows that $(\frac{r}{k}, 0)$ is locally asymptotically stable if and only if $R + \frac{r}{k}(b - \frac{rd}{k}) < 0$, and, similarly, $(0, \frac{R}{k})$ is locally asymptotically stable if and only if $r + \frac{R}{k}(a - \frac{Rc}{k}) < 0$. Obviously, if $c \leq (\frac{R}{k})^2 (r + \frac{Rc}{k})$ and $d \leq (\frac{r}{k})^2 (R + \frac{rd}{k})$, then both two non-trivial boundary equilibria must be unstable. As a special case, if $c = 0$ and $d = 0$, then the inter-specific relationship is mutualistic symbiosis, “(+, +)”, for all possible $x > 0$ and $y > 0$. This implies that when one of two populations is at low density but the other at high density, i.e., when the system state is near a non-trivial boundary equilibrium, mutualism will be useful for preventing the exclusion of the rare species. But this does not mean that the stability of a two-species coexistence equilibrium depends only on the stability of the non-trivial boundary equilibria.

For Eq. (1), on the x – y phase plane, L_1 represents the isocline for $dx/dt = 0$, and L_2 the isocline for $dy/dt = 0$. The slopes of the two zero isoclines L_1 and L_2 at an interior equilibrium (x^*, y^*) are denoted by $\frac{dy}{dx}(L_1^*)$ and $\frac{dy}{dx}(L_2^*)$, respectively. According to the signs of $\frac{dy}{dx}(L_1^*)$ and $\frac{dy}{dx}(L_2^*)$, three possible types of the interior equilibria are defined as: (i) CP, if both $\frac{dy}{dx}(L_1^*)$ and $\frac{dy}{dx}(L_2^*)$ are negative; (ii) MP, if both $\frac{dy}{dx}(L_1^*)$ and $\frac{dy}{dx}(L_2^*)$ are positive; and (iii) HP, if $\frac{dy}{dx}(L_1^*) > 0$ and $\frac{dy}{dx}(L_2^*) \leq 0$, or if $\frac{dy}{dx}(L_1^*) < 0$ and $\frac{dy}{dx}(L_2^*) \geq 0$. In Eq. (1), at most three interior equilibria can exist, i.e., the existence of multiple equilibria is possible (see Result 1 in the subsection 2.3). From the Theorem 2, an interior equilibrium is locally asymptotically stable if and only if $(\frac{dy}{dx}(L_1^*))^{-1} \frac{dy}{dx}(L_2^*) < 1$. Notice that $\frac{dy}{dx}(L_1^*) > 0$ ($\frac{dy}{dx}(L_1^*) < 0$) if $y^* < \frac{a}{2c}$ ($y^* > \frac{a}{2c}$), and $\frac{dy}{dx}(L_2^*) > 0$ ($\frac{dy}{dx}(L_2^*) < 0$) if $x^* < \frac{b}{2d}$ ($x^* > \frac{b}{2d}$). Thus, if an interior equilibrium is a HP, or a MP, then it must be locally asymptotically stable, and if it is a CP, then it can be stable or unstable (see Results 2–4 in the subsection 2.3). Finally, for the existence of periodic solutions in Eq. (1), the Theorem 3 shows that it is impossible.

However, the inter-specific relationship is always one of the most important theoretical topics in population and community ecology. In nature, the complexity of the inter-specific relationship should be very important for the coexistence of multiple species. In this paper, we consider only a very simple theoretical model with the possibility of switching from one kind of inter-specific interaction to another, i.e., undergoing transitions between different interactions, due to the variation in population densities. For Eq. (1), the results about the stability of boundary equilibria strongly support Zhang’s (2003) opinion, i.e., mutualism will promote the two-species coexistence. This result implies that the evolution of mutualism may contribute to the multiple species coexistence and stability of ecosystem, and that mutualism may be favored by natural selection.

Appendix A

For the situation with $R + \frac{r}{k}(b - \frac{rd}{k}) = 0$, around $(\frac{r}{k}, 0)$ Eq. (1) can be approximated as

$$\begin{aligned} \frac{d\hat{x}}{dt} &= -r\hat{x} + \Phi(\hat{x}, \hat{y}), \\ \frac{d\hat{y}}{dt} &= \Psi(\hat{x}, \hat{y}), \end{aligned} \tag{19}$$

where $\hat{x} = x - \frac{r}{k} - \frac{ay}{k}$, $\hat{y} = y$, and

$$\begin{aligned} \Phi(\hat{x}, \hat{y}) &= -k\hat{x}^2 - a\hat{x}\hat{y} - \frac{rc}{k}\hat{y}^2 - c\hat{x}\hat{y}^2 - \frac{ac}{k}\hat{y}^3 - \frac{a}{k}\Psi(\hat{x}, \hat{y}), \\ \Psi(\hat{x}, \hat{y}) &= -\left(K + \frac{adr}{R^2} + \frac{Ra}{r}\right)\hat{y}^2 - \left(\frac{dr}{k} + \frac{Rk}{r}\right)\hat{x}\hat{y} \\ &\quad - d\hat{x}^2\hat{y} - 2\frac{da}{k}\hat{x}\hat{y}^2 - \frac{a^2d}{k^2}\hat{y}^3. \end{aligned} \tag{20}$$

From the center manifold theory (Carr, 1981), there exists a local center manifold $\hat{x} = h(\hat{y})$ with $h(0) = 0$ and $h'(0) = 0$, i.e., $h(\hat{y})$ can be expressed as

$$h(\hat{y}) = h_2\hat{y}^2 + h_3\hat{y}^3 + h_4\hat{y}^4 \dots \tag{21}$$

Notice that $\hat{x} = h(\hat{y})$ satisfies

$$\begin{aligned} -r \sum_{j=2}^{\infty} h_j \hat{y}^j + \Phi\left(\sum_{j=2}^{\infty} h_j \hat{y}^j, \hat{y}\right) \\ = \left(\sum_{j=2}^{\infty} j h_j \hat{y}^{j-1}\right) \Psi\left(\sum_{j=2}^{\infty} h_j \hat{y}^j, \hat{y}\right), \end{aligned} \tag{22}$$

i.e., the coefficients h_2, h_3, h_4, \dots can be determined by Eq. (22). From Eqs. (19) and (20), the solution on the local center manifold satisfies the equation

$$\frac{d\hat{y}}{dt} = -\left(K + \frac{adr}{R^2} + \frac{Ra}{r}\right)\hat{y}^2 + \Psi(h(\hat{y}), \hat{y}). \tag{23}$$

Since $K + \frac{adr}{R^2} + \frac{Ra}{r} > 0$, the boundary equilibrium $(\frac{r}{k}, 0)$ is unstable if $R + \frac{r}{k}(b - \frac{rd}{k}) = 0$.

Appendix B

For the situation with

$$\left(\frac{dy}{dx(L_1^*)}\right)^{-1} \frac{dy}{dx(L_2^*)} = 1, \tag{24}$$

i.e., one of the eigenvalues of the Jacobian matrix **J** is zero and the other one negative, notice that about (x^*, y^*) Eq. (1) can be approximated as

$$\begin{aligned} \frac{d\hat{x}}{dt} &= A\hat{x} + B\hat{y} + F(\hat{x}, \hat{y}), \\ \frac{d\hat{y}}{dt} &= C\hat{x} + D\hat{y} + G(\hat{x}, \hat{y}), \end{aligned} \tag{25}$$

with $AD - BC = 0$, where $\hat{x} = x - x^*$, $\hat{y} = y - y^*$, and

$$\begin{aligned} A &= -kx^*, \\ B &= kx^* \left(\frac{dy}{dx(L_1^*)}\right)^{-1}, \\ C &= Ky^* \frac{dy}{dx(L_2^*)}, \\ D &= -Ky^*, \end{aligned} \tag{26}$$

and

$$\begin{aligned} F(\hat{x}, \hat{y}) &= -k\hat{x}^2 + (a - 2cy^*)\hat{x}\hat{y} - cx^*\hat{y}^2 - c\hat{x}\hat{y}^2 \\ &= \frac{A}{x^*} \hat{x}^2 - cx^*\hat{y}^2 + \frac{B}{y^*} \hat{x}\hat{y} - c\hat{x}\hat{y}^2, \\ G(\hat{x}, \hat{y}) &= -dy^*\hat{x}^2 + (b - 2dx^*)\hat{x}\hat{y} - K\hat{y}^2 - d\hat{x}^2\hat{y} \\ &= -dy^*\hat{x}^2 + \frac{D}{y^*} \hat{y}^2 + \frac{C}{y^*} \hat{x}\hat{y} - d\hat{x}^2\hat{y}. \end{aligned} \tag{27}$$

Thus, the transformation

$$\begin{aligned} \tilde{x} &= A\hat{y} - C\hat{x}, \\ \tilde{y} &= (A + D)\hat{y} - \tilde{x}, \\ \tau &= (A + D)t \end{aligned} \tag{28}$$

implies that

$$\begin{aligned} \frac{d\tilde{x}}{d\tau} &= \frac{AG(\hat{x}, \hat{y}) - CF(\hat{x}, \hat{y})}{A + D} \\ &= \tilde{F}(\tilde{x}, \tilde{y}), \\ \frac{d\tilde{y}}{d\tau} &= \tilde{y} + \frac{DG(\hat{x}, \hat{y}) + CF(\hat{x}, \hat{y})}{A + D} \\ &= \tilde{y} + \tilde{G}(\tilde{x}, \tilde{y}), \end{aligned} \tag{29}$$

where $\hat{x} = \frac{A\tilde{y} - D\tilde{x}}{C(A + D)}$ and $\hat{y} = \frac{\tilde{x} + \tilde{y}}{A + D}$. Similarly to the analysis in the proof of Theorem 1, there exists a local center manifold $\tilde{y} = h(\tilde{x}) = \sum_{j=2}^{\infty} h_j \tilde{x}^j$ with $h(0) = 0$ and $h'(0) = 0$, and $h(\tilde{x})$ satisfies

$$h(\tilde{x}) + \tilde{G}(\tilde{x}, h(\tilde{x})) = h'(\tilde{x})\tilde{F}(\tilde{x}, h(\tilde{x})). \tag{30}$$

On this manifold, we have

$$\frac{d\tilde{x}}{d\tau} = \tilde{F}(\tilde{x}, h(\tilde{x})) = \alpha\tilde{x}^2 + o(\tilde{x}^3), \tag{31}$$

where

$$\alpha = (A + D)^{-3} \left(-\frac{AD^2}{C^2} dy^* + Ccx^* \right). \tag{32}$$

If $-\frac{AD^2}{C^2} dy^* + Ccx^* = 0$ holds, then we have

$$-Kd(a - 2cy^*) = c(b - 2dx^*)^2. \tag{33}$$

Notice that $AD - BC = 0$, i.e.,

$$\begin{aligned} (a - 2cy^*)^3 &= \frac{k^2Kc}{d}, \\ (b - 2dx^*)^3 &= \frac{kK^2d}{c}, \end{aligned} \tag{34}$$

and that Eq. (2) can be expressed as

$$\begin{aligned} (a - 2cy^*)^2 &= 4c \left(r - kx^* + \frac{a^2}{4c} \right), \\ (b - 2dx^*)^2 &= 4d \left(R - Ky^* + \frac{b^2}{4d} \right). \end{aligned} \tag{35}$$

Then, we must have

$$\begin{aligned} \frac{3(a - 2cy^*)^2}{4ck} &= \frac{r}{k} + \frac{a^2}{4ck} - \frac{b}{2d}, \\ \frac{3(b - 2dx^*)^2}{4dK} &= \frac{R}{K} + \frac{b^2}{4dK} - \frac{a}{2c}, \end{aligned} \tag{36}$$

i.e., it also implies that

$$\begin{aligned} \frac{r}{k} + \frac{a^2}{4ck} - \frac{b}{2d} &= \frac{3}{4} \left(\frac{kK^2}{cd^2} \right)^{1/3}, \\ \frac{R}{K} + \frac{b^2}{4dK} - \frac{a}{2c} &= \frac{3}{4} \left(\frac{k^2K}{c^2d} \right)^{1/3}, \end{aligned} \tag{37}$$

and

$$\frac{4c}{3k} \left(\frac{R}{K} + \frac{b^2}{4dK} - \frac{a}{2c} \right)^2 = \frac{r}{k} + \frac{a^2}{4ck} - \frac{b}{2d}. \tag{38}$$

Thus, if $-\frac{AD^2}{C^2} dy^* + Ccx^* = 0$ holds, then $\gamma = \frac{K^2}{3d} \left(\frac{R}{K} + \frac{b^2}{4dK} - \frac{a}{2c} \right)^2$ in Eq. (6) that means $\tilde{p} = 0$ and $\tilde{q} = 0$ in Eq. (11), i.e., $\Delta = 0$ in Eq. (13). This implies that Eq. (2) should have a unique real root. But this contradicts that two parabolas L_1 and L_2 have at least two interactions. Thus, we have $\alpha \neq 0$, i.e., an interior equilibrium (x^*, y^*) is unstable if $\left(\frac{dy}{dx(L_1^*)}\right)^{-1} \frac{dy}{dx(L_2^*)} = 1$.

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