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Balance Line in a Lotka-Volterra competition system

静岡大学大学院理工学研究科
中岡慎治 (Shinji Nakaoka)
竹内康博 (Yasuhiro Takeuchi)
Graduate school of Science and Technology, Shizuoka University

1 Introduction

In this paper, let us consider the simplest expression of competing two species, which is called a Lotka-Volterra competition system:

$$\begin{cases} x_1'(t) = x_1(t)[r_1 - ax_1(t) - bx_2(t)], \\ x_2'(t) = x_2(t)[r_2 - cx_1(t) - dx_2(t)], \end{cases} \tag{1.1}$$

Here $x_i(t)$ denotes the i-th population densities of competing two species ($i = 1, 2$). All parameters are assumed to be positive. Let E_0, E_1 and E_2 denote equilibria of system (1.1) which always exist:

$$E_0 = (0,0), \quad E_1 = \left(\frac{r_1}{a}, 0\right), \quad E_2 = \left(0, \frac{r_2}{d}\right).$$

Suppose that

$$\frac{b}{d} < \frac{r_1}{r_2} < \frac{a}{c}. \tag{1.2}$$

Then system (1.1) has a unique positive equilibrium which is a stable node:

$$E^* := (x_1^*, x_2^*) = \left(\frac{dr_1 - br_2}{ad - bc}, \frac{ar_2 - cr_1}{ad - bc}\right).$$

It is well known that the positive equilibrium of system (1.1) is globally asymptotically stable if (1.2) holds. Various approaches are known to show the global attractivity result of the positive equilibrium: The second method of Liapunov can give a global stability result when a suitable Liapunov function is found (see for example, [3] and [6]). On planar systems, Poincaré-Bendixon Theorem is a powerful tool to figure out the behavior of system dynamics. Monotone theory is also a powerful and conceptual tool if one considers competitive (cooperative) system (see [5] and references therein).

Here we take a different approach to show the global attractivity result for the positive equilibrium of system (1.1): By introducing a function with respect to the ratio between densities of two species $P_{ij} = x_i/x_j$, we will show the global attractivity of the positive equilibrium if (1.2) holds. Moreover we will give the explicit form of separatrix if system (1.1) is bistable. In the next section, basic properties for the function P_{ij} are shown. In Section 3, we show that the positive equilibrium is globally attractive if it exists. In Section 4, the graph of the trajectory of the solution of (1.1) are shown. Finally we discuss our results in Section 5.

2 Preliminaries

Consider the following general autonomous planar system:

$$\begin{cases} x_1' = x_1 f_1(x_1, x_2), \\ x_2' = x_2 f_2(x_1, x_2), \end{cases} \tag{G}$$

with the initial condition

$$x_1(0) > 0 \text{ and } x_2(0) > 0, \tag{2.1}$$

where f_1 and f_2 are continuously differentiable. The function π is said to be a continuous dynamical system if π is continuous and has the following properties:

(i) $\pi(x, 0) = x$;

(ii) $\pi(x, t + s) = \pi(\pi(x, t), s)$.

Then (G) generates a continuous dynamical system by defining $\pi(x, t) = x(t)$, where $x(t) = (x_1(t), x_2(t))$ is a solution of (G) satisfying (2.1). Given a point x, the set $\{\pi(x, t) | t \geq 0\}$ is called the *positive trajectory.* A set S is said to be *positively invariant* if all trajectories that begin in S remain in S for all positive time. Let $\{t_n\}_{n=1}^{\infty}$ be a sequence of real numbers which tends to infinity as n tends to infinity. If $P_n = \pi(x, t_n)$ converges to a point P, then P is said to be an omega limit point of x. The set of all such omega limit points is called the *omega limit set* of x, denoted $\omega(x)$. An equilibrium point of (G) (if exists) is said to be *repeller* if it cannot be in the omega limit set of any trajectory other than itself. The dynamical system is said to be *dissipative* if all positive trajectories eventually lie in a bounded set. If the system is dissipative, the omega limit set is a non-empty, compact, connected, invariant set (see also a standard textbook of dynamical systems, e.g. Bhatia and Szegő [1]).

Let $P_{ij} : [0,\infty) \times (0,\infty) \to [0,\infty)$ be a continuously differentiable function $(i, j = 1, 2,\ i \neq j)$. P_{ij} is defined by

$$P_{ij}(x_i, x_j) = x_i/x_j. \tag{2.2}$$

By the definition, it follows that

P-(i): $P_{ij} \cdot P_{ji} = 1$,

P-(ii): $P_{ij} = 0$ iff $x_i = 0$.

The derivative of P_{ij} along the solution of (G) is denoted by $\dot{P}_{ij}(x(t))$. Direct calculation gives

$$\frac{\dot{P}_{ij}(x(t))}{P_{ij}(x(t))} = f_i(x(t)) - f_j(x(t)).$$

Note that this property is stated as the *quotient rule* on replicator dynamics (Excersise 7.1.1 in [3]). Hereafter we simply write $\dot{P}_{ij}(x(t))$ as $\dot{P}_{ij}(t)$ for the convenience.

Competitive Advantage Set, or simply *Advantage Set* $\mathcal{A}_1$ and $\mathcal{A}_2$ are defined by

$$\mathcal{A}_1 := \left\{(x_1, x_2) \in \mathbb{R}^2_+ | f_1(x_1, x_2) > f_2(x_1, x_2)\right\},$$
$$\mathcal{A}_2 := \left\{(x_1, x_2) \in \mathbb{R}^2_+ | f_1(x_1, x_2) < f_2(x_1, x_2)\right\}.$$

Competitive Balance Set, or simply *Balance Set* $\mathcal{B}$ is defined by

$$\mathcal{B} := \left\{(x_1, x_2) \in \mathbb{R}^2_+ | f_1(x_1, x_2) = f_2(x_1, x_2)\right\}.$$

Note that for any $x(t) \in \mathcal{B}$, $\dot{P}_{ij}(t) = 0$. Moreover $\dot{P}_{ij}(t) > 0$ if $x(t) \in \mathcal{A}_i$, while $\dot{P}_{ij}(t) < 0$ if $x(t) \in \mathcal{A}_j$.

Strongly Advantage Set $\mathcal{S} = \mathcal{S}_1 \oplus \mathcal{S}_2$ is defined by

$$\mathcal{S}_1 := \{(x_1, x_2) \in \mathcal{A}_1 | f_1(x_1, x_2) > 0 \text{ and } f_2(x_1, x_2) < 0\},$$
$$\mathcal{S}_2 := \{(x_1, x_2) \in \mathcal{A}_2 | f_1(x_1, x_2) < 0 \text{ and } f_2(x_1, x_2) > 0\}.$$

The null clines of $f_1(x_1, x_2)$ and $f_2(x_1, x_2)$ are denoted by $\mathcal{N}_1$ and $\mathcal{N}_2$, respectively. That is,

$$\mathcal{N}_1 = \{(x_1, x_2) \in \mathbb{R}^2_+ | f_1(x_1, x_2) = 0\},$$
$$\mathcal{N}_2 = \{(x_1, x_2) \in \mathbb{R}^2_+ | f_2(x_1, x_2) = 0\}.$$

Let $x_1^\dagger$ and $x_2^\dagger$ denote roots of $f_1(x_1, 0) = f_2(x_1, 0)$ and $f_1(0, x_2) = f_2(0, x_2)$ (if they exist), respectively. In general, $\mathcal{B}$ is a curve on $\mathbb{R}^2_+$ which is formed by connecting two points $(x_1^\dagger, 0) \in \mathcal{B}$ and $(0, x_2^\dagger) \in \mathcal{B}$. Note that $\mathcal{B}$ is a line for system (1.1). $\mathrm{int}\mathbb{R}_+^2$ denotes the interior of $\mathbb{R}_+^2$. $\mathrm{int}\mathbb{R}_+^2$ is divided by $\mathcal{B}$, that is, $\mathrm{int}\mathbb{R}_+^2 = \mathcal{A}_1 \oplus \mathcal{B} \oplus \mathcal{A}_2$. (see Figs 1 and 2 in Section 4). Finally the *solution ratio line* $\mathcal{L}_t$ is defined by

$$\mathcal{L}_t := \left\{(x_1, x_2) \in \mathbb{R}_+^2 | x_i = P_{ij}(t)x_j\right\}. \tag{2.3}$$

Then $x(t) \in \mathcal{L}_t$.

3 Global attractivity

Let us set $f_1(x_1, x_2) = r_1 - ax_1 - bx_2$ and $f_2(x_1, x_2) = r_2 - cx_1 - dx_2$. First we state some basic properties of system (1.1) without the proof. Throughout the reminder of this section, we assume that (1.2) holds.

Proposition 3.1. *System* (1.1) *is dissipative.* E_0 *is a repeller. Moreover* E_1 *and* E_2 *are also repellers if* (1.2) *holds.*

Proposition 3.2. *Assume that* (1.2) *holds. Then* $E^* \in \mathcal{B}$. $E_0 \in \mathcal{B}$ *if and only if* $r_1 = r_2$. $E_1 \notin \mathcal{B}$ *and* $E_2 \notin \mathcal{B}$.

Proof. The first and the second assertions are clear. By (1.2), $ad - bc > 0$. Then $a \neq c$ or $b \neq d$. Suppose that $a \neq c$. Then $x_1^\dagger = (r_1 - r_2)/(a - c)$ exists. Since (1.2) holds, direct calculation shows that $x_1^\dagger - \frac{r_1}{a} = (cr_1 - ar_2)/a(a - c) \neq 0$. Consequently $E_1 \notin \mathcal{B}$ if $a \neq c$. In the same way, we can show that $E_2 \notin \mathcal{B}$ if $b \neq d$. This completes the proof. □

Let E denote a set of equilibria of system (1.1)

$$E = \{E_0, E_1, E_2, E^*\}.$$

Proposition 3.3. *Assume that* $r_1 = r_2$ *and* (1.2) *holds. Then* $\mathcal{B}$ *is positively invariant.*

Proof. We claim that $x_2 f_2(x_1, x_2) \neq 0$ for any $x = (x_1, x_2) \in \mathcal{B} \setminus E$. In fact, $x_2 f_2(x_1, x_2) = 0$ if and only if $x_2 = 0$ or $f_2(x_1, x_2) = 0$. Note that $x_2 = 0$ iff $x \in E_0$ on $\mathcal{B}$. Moreover $\mathcal{B} \cap \mathcal{N}_2 = E^*$. Hence the implicit function theorem implies that for any $x \in \mathcal{B} \setminus E$,

$$\frac{\partial x_1}{\partial x_2} = -\frac{x_1 f_1(x_1, x_2)}{x_2 f_2(x_1, x_2)} = -\frac{x_1}{x_2}.$$

It follows from (1.2) that $a > c$ and $d > b$ if $r_1 = r_2$. Hence $x \in \mathcal{B} \setminus E$ satisfies $x_1/x_2 = \frac{d-b}{a-c} = x_1^*/x_2^*$. Consequently we obtain that $x_1(t) = x_1^*/x_2^* x_2(t)$ for any $x(t) \in \mathcal{B}$. That is, $\mathcal{L}_t \equiv \mathcal{B}$. This completes the proof. □

Proposition 3.4. *Assume that $r_1 \neq r_2$ and (1.2) holds. Then $\mathcal{B} \setminus E$ is not positively invariant.*

Proof. Assume that there exists $T \geq 0$ such that $x(t) \in \mathcal{B} \setminus E$ for any $t > T$. Hereafter let us fix t arbitrary for $t > T$. Then $\dot{P}_{12}(t) = 0$. Hence $P_{12}(t)$, or equivalently, $x_1(t)x_2^{-1}(t)$ is a positive constant, which is denoted by C. Moreover $\mathcal{L}_t$ is fixed, which is denoted by $\mathcal{L}$. Then $x(t) \in \mathcal{B} \cap \mathcal{L}$. It is clear that $\mathcal{B} \cap \mathcal{L} \neq \emptyset$. Since both of $\mathcal{B}$ and $\mathcal{L}$ are lines on $\mathbb{R}_+^2$, either (i) $\mathcal{B} = \mathcal{L}$ or (ii) $\mathcal{B} \cap \mathcal{L}$ is a point set. Note that $\mathcal{B} = \mathcal{L}$ if and only if $r_1 = r_2$ and $C = \frac{d-b}{a-c} = x_1^*/x_2^*$. Since we assume $r_1 \neq r_2$, only the case (ii) is possible. Then $x(t)$ must be an equilibrium point. More specifically, Proposition 3.2 implies that $x(t) \equiv E^*$. This is a contradiction since $x(t) \in \mathcal{B} \setminus E$. This completes the proof. □

Proposition 3.5. *Assume that (1.2) holds. Then $P_{ij}(t) \not\to 0$ if $t \to \infty$.*

Proof. Assume that $P_{ij}(t) \to 0$ as $t \to \infty$. Then there exists a monotone increasing sequence $\{t_n\}_{n=1}^{\infty}$ such that $\dot{P}_{ij}(t_n) \to 0$ as $n \to \infty$. Note that for any $x(t) \in \mathcal{B}$, $\dot{P}_{ij}(t) = 0$. Hence for any initial point $x^0 \in \mathrm{int}\mathbb{R}_+^2$, $\omega(x^0) \subset \mathcal{B} \cup E$. Since system (1.1) is dissipative, $\omega(x^0)$ is positively invariant. Note that by Proposition 3.1, E_0, E_1 and E_2 are repellers. Moreover Propositions 3.3 and 3.4 imply that $\omega(x^0) \subset \mathcal{B} \setminus E_0$ if $r_1 = r_2$ and $\omega(x^0) \in E^*$ if $r_1 \neq r_2$. This is a contradiction and hence completes the proof. □

In the same way as the proof of Proposition 3.5, we can show the following:

Proposition 3.6. *Assume that (1.2) holds. If there exists a positive constant P_{ij}^* such that $P_{ij}(t) \to P_{ij}^*$ as $t \to \infty$, then $x(t) \to E^*$ as $t \to \infty$.*

Proposition 3.7. *Assume that (1.2) holds. If $x(t)$ eventually remains either in $\mathcal{A}_1$ or $\mathcal{A}_2$, then $x(t) \to E^*$ as $t \to \infty$.*

Proof. Note that if $x(T) \in \mathcal{A}_1$ for some $T \geq 0$, $\dot{P}_{12}(t) > 0$ as long as $x(t) \in \mathcal{A}_1$ for $t \geq T$. Similarly if $x(T) \in \mathcal{A}_2$ for some $T \geq 0$, $\dot{P}_{12}(t) < 0$ as long as $x(t) \in \mathcal{A}_2$ for $t \geq T$. Hereafter we only consider the case where $x(t) \in \mathcal{A}_1$ for $t \geq T$. Then we claim that there exists a positive constant P_{12}^* such that $P_{12}(t) \to P_{12}^*$ as $t \to \infty$. Assume that $P_{12}(t) \to \infty$ as $t \to \infty$. Since system (1.1) is dissipative, $x_2(t) \to 0$ as $t \to \infty$. Then by P-(ii), $P_{21}(t) \to 0$ as $t \to \infty$. However this contradicts to Proposition 3.5. Therefore Proposition 3.6 implies that $x(t) \to E^*$ as $t \to \infty$. This completes the proof. □

Proposition 3.8. *Assume that (1.2) holds. $\mathcal{S} \cup \mathcal{N}_1 \cup \mathcal{N}_2$ is positively invariant.*

Proof. It is sufficient to notice for the solutions on the boundary of $\mathcal{S}$. Note that the boundary of S consists of null clines $\mathcal{N}_1$ and $\mathcal{N}_2$. If there exists $T \geq 0$ such that $x(T) \in \mathcal{A}_1 \cap \mathcal{N}_1$, then $\dot{x}_1(T) = 0$ and $\dot{x}_2(T) < 0$. By the continuity of the solution, there exists $\varepsilon > 0$ such that $x(t) \in \mathcal{S}_1$ for $T < t \leq T + \varepsilon$. The same procedure proves the assertion (see Figure 2). $\square$

Theorem 3.1. *Assume that* (1.2) *holds. Then all solutions tend to the positive equilibrium as* t *tends to infinity.*

Proof. First let us consider the case $r_1 \neq r_2$. If there exists $T \geq 0$ such that $x(T) \in \mathcal{S} \cup \mathcal{N}_1 \cup \mathcal{N}_2$, Proposition 3.7 together with 3.1 implies that $x(t) \to E^*$ as $t \to \infty$ and hence the assertion is true. Otherwise, all solutions remain in $\mathrm{int}\mathbb{R}^2_+ \setminus \mathcal{S}$ for any positive t. We claim that such solutions also eventually remain either in $\mathcal{A}_1$ or $\mathcal{A}_2$. The following two cases are possible: (i) There is no solution which crosses $\mathcal{B}$ or (ii) There is a solution which crosses $\mathcal{B}$. The claim is true for the case (i) by Proposition 3.7. So let us consider the case (ii). If there exists $T_0 \geq 0$ such that $x(T_0) \in \mathcal{B}$, Proposition 3.4 implies that there exists $T_1 > T_0$ such that $x(T_1) \notin \mathcal{B}$. More specifically, if $\dot{x}_1(T_0) > 0$, then $x(T_1) \in \mathcal{A}_2$. Conversely if $\dot{x}_1(T_0) < 0$, then $x(T_1) \in \mathcal{A}_1$. In both cases, we can see that $x(t) \in \mathcal{A}_1$ or $x(t) \in \mathcal{A}_2$ for any $t \geq T_1$. Hence the claim holds true by Proposition 3.7.

Next suppose that $r_1 = r_2$. Since $\mathcal{B}$ is positively invariant, it is sufficient to consider either (iii) $x(t) \notin \mathcal{B}$ for all $t \geq 0$ or (iv) $x(t) \in \mathcal{B}$ for all $t \geq 0$. In the case (iii), $x(t) \in \mathcal{A}_1$ or $x(t) \in \mathcal{A}_2$ for all $t \geq 0$. Hence Proposition 3.7 implies that $x(t) \to E^*$ as $t \to \infty$ and the assertion holds true. Finally let us consider the case (iv). Note that $f_1(x_1, x_2) = f_2(x_1, x_2) = f(x_1, x_2)$ on $\mathcal{B}$. Let $x = x_1 + x_2$. Then

$$\begin{aligned} x' &= x_1' + x_2' \\ &= x_1 f_1(x_1, x_2) + x_2 f_2(x_1, x_2) \\ &= x f(x_1, x_2). \end{aligned}$$

Observe that x is expressed by x_1 and x_2 explicitly if and only if the following system of equations has a unique root:

$$\begin{cases} x_1 + x_2 = x, \\ a x_1 + b x_2 = c x_1 + d x_2 \end{cases}$$

Since $a - c \neq b - d$, direct calculation gives

$$x_1 = \frac{(d-b)x}{a-c-(b-d)} \text{ and } x_2 = \frac{(a-c)x}{a-c-(b-d)}.$$

Then $x(t)$ is a solution of following differential equation

$$x' = rx\left(1 - \frac{x}{K}\right), \quad x \in \mathcal{B} \tag{3.1}$$

where $r = r_1$ and $K = \frac{a-c+(d-b)}{ad-bc}r = x_1^* + x_2^*$. Then (3.1) becomes the Logistic equation and hence $x(t) \to x_1^* + x_2^*$ as $t \to \infty$ on $\mathcal{B}$. This completes the proof. $\square$

4 Trajectories

In this section, let us show some projections onto x_1x_2-phase plane of trajectories for different sets of parameters. Due to the symmetry of system (1.1), we can assume that $r_1 \geq r_2$. Figs 1 and 2 illustrate the null-clines and the balance line, each of which corresponds to dashed lines and the thick line. Figs 3–4 illustrate the trajectories of the solution of (1.1). On these figures, the balance line is drawn by thin line, while the trajectory is drawn by thick line. On Fig.3, the parameters satisfy that $r_1 > r_2$, $\frac{d-b}{a-c} < 0$ and (1.2) holds. The initial point x^0 is taken on $\mathcal{B}$. The trajectory is immediately away from $\mathcal{B}$ and eventually lies in $\mathcal{S}_1$. On Fig.4, the parameters satisfy that $r_1 > r_2$, $\frac{d-b}{a-c} > 0$ and (1.2) holds. The initial point is also taken on $\mathcal{B}$. The trajectory is also away from $\mathcal{B}$ and finally converges to the positive equilibrium. On Fig.5, the parameters satisfy that $r_1 = r_2$. The initial point is taken on $\mathcal{B}$. Note that by Proposition 3.3, $\mathcal{B}$ is positively invariant. The solution converges to the positive equilibrium along the line $x_2 = x_2^*/x_1^* x_1$. Finally Fig. 6 illustrates the trajectory for $r_1 = r_2$. The initial point is taken on $\mathcal{A}_2$. The solution eventually lies on $\mathcal{S}_2$ and converges to the positive equilibrium.

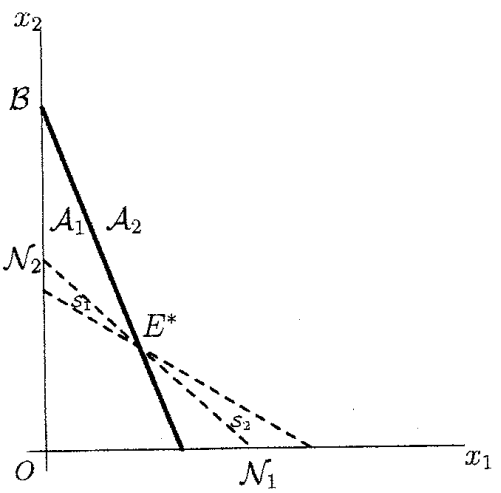

Figure 1: $r_1 > r_2$, $\frac{d-b}{a-c} < 0$ $(a \neq c)$

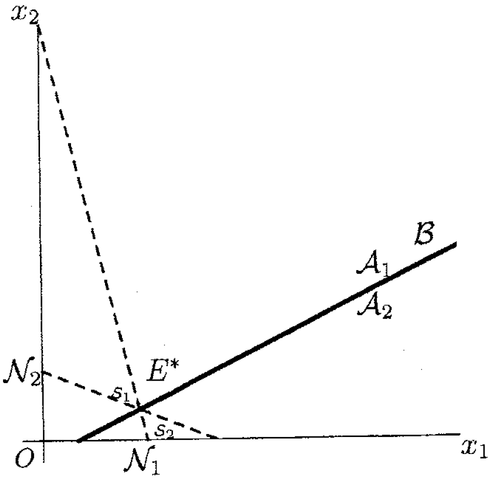

Figure 2: $r_1 > r_2$, $\frac{d-b}{a-c} > 0$ $(a \neq c)$

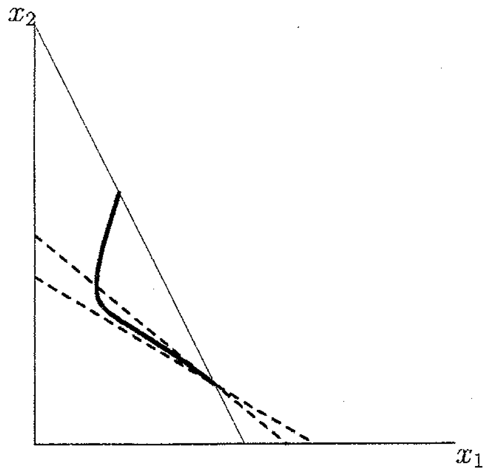

Figure 3: $r_1 > r_2$, $\frac{d-b}{a-c} < 0$, $x^0 \in \mathcal{B}$.

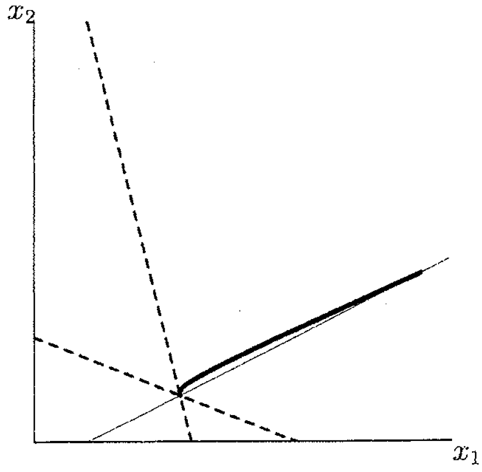

Figure 4: $r_1 > r_2$, $\frac{d-b}{a-c} > 0$, $x^0 \in \mathcal{B}$.

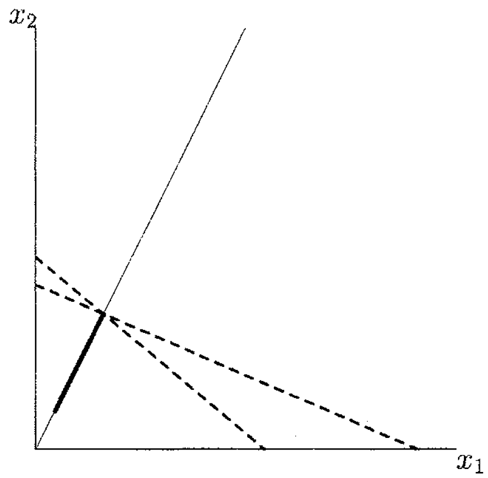

Figure 5: $r_1 = r_2$, $x^0 \in \mathcal{B}$.

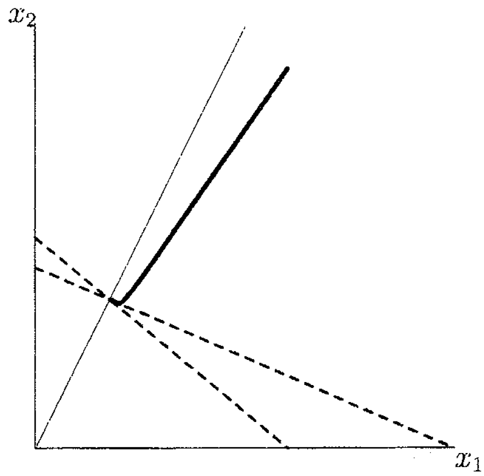

Figure 6: $r_1 = r_2$, $x^0 \in \mathcal{A}_2$.

5 Conclusions

We proved the global attractivity of solutions of system (1.1) by introducing the function in terms of the ratio between x_1 and x_2. It was shown that the balance set $\mathcal{B}$ separates the positive cone. One of separated regions $\mathcal{A}_1$ gives a competitive advantage for x_1, while another region $\mathcal{A}_2$ gives a competitive advantage for x_2. For almost sets of parameters under the situation where the positive equilibrium exists, the balance line $\mathcal{B}$ except for the positive equilibrium is not positively invariant. On the region $\mathcal{A}_1 \cap \{(x_1, x_2) \in \mathbb{R}^2_+ | f_1(x_1, x_2) < 0, f_2(x_1, x_2) < 0\}$, it can happen that the ratio x_1/x_2 increases although x_1 decreases (see Figs 3 and 4). This situation is likely to occur when x_1 has the low density while x_2 has the high density.The density dependence effect highly decreases the density of x_2 even if x_1 is decreasing. If $r_1 = r_2$ and $x^0 \in \mathcal{B}$, as we have shown in Proposition 3.3 and Theorem 3.1, the solution converges to the positive equilibrium along the line. Moreover the total density x_1+x_2 follows the logistic equation (see also Fig.5). This implies that two species are regarded as the same species on $\mathcal{B}$ if $r_1 = r_2$. Geritz *et. al* considered the dynamics of a population of residents that is being invaded by an initially rare mutant [2]. They showed in [2] that under relatively mild conditions *the sum of the mutant and resident population sizes* stays arbitrarily close the initial attractor of the monomorphic resident population whenever the mutant has a strategy sufficiently similar to that of the resident (This is called a Tube Theorem). This result implies that the orbit will stay in *a narrow tube* in the resident-mutant population state space. Schreiber [4] considered a model for apparent competition where two prey share one predator. In [4], it was shown that a model without the positive equilibrium is almost surely permanence. The similar idea of Tube Theorem is exploited in the proof. It would be interesting to study the relationship between the tube set and the balance set. Since system (1.1) is dissipative, there must exist an accumulation set of the ratio function P_{ij} on some compact subset of the positive cone. In this paper, it was shown that the accumulation set corresponds to the positive equilibrium point. If the accumulation set consists of two points, then the solution will be periodic. It is expected that chaotic behaviors is expressed in such a way that the ratio function has infinitely multiple accumulation points. In this paper we only considered the case where the stable positive equilibrium exists. It is well known that there is a separatrix curve if system (1.1) is bistable. Simple consideration shows that the balance set $\mathcal{B}$ corresponds to the separatrix curve if $r_1 = r_2$ and system (1.1) is bistable. It is interesting to give explicit form of the separatrix curve for $r_1 \neq r_2$. This leaves for our future consideration. On the systems where more than three species are interacting with, the chaotic behavior can occur. The method exploited in this paper should be also exploited to higher dimensional systems. This also leaves for our future consideration.

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