

Global Properties of Evolutional Lotka-Volterra System

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ABSTRACT

We will study global properties of evolutional Lotka-Volterra system. We assume that the predatory efficiency is a function of a character of species whose evolution obeys a quantitative genetic model. We will show that the structure of a solution is rather different from that of a non-evolutional system. We will analytically show new ecological features of the dynamics.

Keywords: Lotka-Volterra System; Global Dynamics; Evolution

1. Introduction

In this paper, we study global behavior of an evolutional Lotka-Volterra system for three species

$$\frac{dN_1}{dt} = rN_1(1 - N_1/K) - \frac{a_2 N_1 N_2}{1 + a_2 h_2 N_1}, \quad (1.1)$$

$$\frac{dN_2}{dt} = \frac{c_2 a_2 N_1 N_2}{1 + a_2 h_2 N_1} - d_2 N_2 - \frac{a_3 N_2 N_3}{1 + a_3 h_3 N_2}, \quad (1.2)$$

$$\frac{dN_3}{dt} = \frac{c_3 a_3 N_2 N_3}{1 + a_3 h_3 N_2} - d_3 N_3, \quad (1.3)$$

$$\frac{dz_2}{dt} = -g\delta^{-1}(z_2 - \hat{z}_2) - \frac{gN_3 a_3'}{(1 + a_3 h_3 N_2)^2}, \quad (1.4)$$

for the unknown quantities $N_j(t)$ ($j=1,2,3$) and z_2 which are the population of j th species and the mean character value of the second species, respectively. Here $r > 0, K > 0, h_2 > 0, h_3 > 0, c_2 > 0, c_3 > 0$ are certain constants, and $d_2 > 0$ and $d_3 > 0$ are death rate of the second and the third species, respectively. The quantities $a_2 > 0$ and $a_3 > 0$ are the predatory efficiency of the second and the third species, respectively. The number \hat{z}_2 is the mean character value of the second species with minimal cost. The quantity $g > 0$ is the additive genetic variance and $\delta > 0$ is the cost of evolution, namely, if δ decreases, then the cost increases.

The effect of evolution is expressed in terms of (1.4) and the condition that the predatory efficiency $a_3 \equiv a_3(z_2 - \hat{z}_2)$ is given by

$$a_3 \equiv a_3(z_2 - \hat{z}_2) = a_3^0 - a(z_2 - \hat{z}_2), \quad (1.5)$$

where $a_3^0 > 0$ is a given constant and $0 \leq a(z) \leq a_3^0$ is a function of z . An example of a_3 is given by (C.1) in Section 3. Equation (1.4) follows the quantitative genetical model (cf. [1-5]. See also Section 7). The evolutional Lotka-Volterra system for two species was studied in [3], where rather detailed numerical analysis was made. As for the system for three species, very little is known as to global behavior of solutions even from a numerical point of view. In this paper, we shall make the analytical study of evolutional Lotka-Volterra model for three species and show several new phenomena caused by evolution. We also refer [6] as to non-evolutional case.

Let $\mathbb{R}_+ := \{t \in \mathbb{R}; t \geq 0\}$. Let t_0 and $N_i \in \mathbb{R}_+$ ($i=1,2,3$) and z_2^0 be given. We first prove that (1.1)-(1.4) with the initial condition

$$\begin{aligned} (N_1, N_2, N_3)|_{t=t_0} &= (N_1^0, N_2^0, N_3^0) \in \mathbb{R}_+^3, \\ z_2|_{t=t_0} &= z_2^0, \end{aligned} \quad (1.6)$$

have unique smooth time global solution. (cf. Theorem 2). Then, in terms of estimate of a solution obtained in the proof of Theorem 2, we study behaviors of a solution

related to evolution. Indeed, we will show that the behavior of a solution near the equilibrium point is different from those in the case of tea-cup attractors for a non-evolutional system. Namely, the decay of the predator N_3 starts before the quantity N_2 becomes small because the predatory efficiency a_3 tends to zero, by evolution. We remark that although N_3/N_2 plays an important role in the non-evolutional system near equilibrium point, the quantity $\sqrt{N_3}/N_2$ is crucial in the evolutionary one. This is because the quantity $\sqrt{N_3}/N_2$ is related with the dynamics of evolution. We remark that the effect of evolution in our system is intermittent in the sense that in some subdomain of the phase space fluctuations of prey N_1, N_2 occur as in the case of non-evolutional model, while in other subdomain, evolution stabilizes large fluctuations of N_2 and N_3 . We also discuss the role of γ in (C.1), which is related with the sensitivity of evolution to the character bias $z_2 - \hat{z}_2$. (cf. Lemma 3 and Section 4 for the case of a linear efficiency). In Section 5, we study the uniform convergence of solutions of an evolutional system as the cost of evolution tends to infinity, *i.e.*, δ decreases to zero.

2. Time Global Solution

We shall study the global existence and uniqueness of a solution of the initial value problem. We assume that $0 \leq a(z) \leq a_3^0$ is the twice continuously differentiable function which satisfies

$$a(0) = 0, a'(0) = 0, \tag{2.1}$$

for some $a_3^0 > 0$. Moreover we suppose that there exist $\ell_0 > 0$ and $\ell_1 > 0$ such that

$$a(z) = a_3^0, \forall z \geq \ell_0, z \leq -\ell_1. \tag{2.2}$$

The following local existence and uniqueness theorem is well known.

THEOREM 2.1. *Assume (2.1) and (2.2). Then there exists a $\delta > 0$ such that the system of Equations (1.1)-(1.4) with the initial conditions (1.6) has a unique continuously differentiable solution $(N_1, N_2, N_3), z_2$ in $|t - t_0| < \delta$.*

In the following we study the existence of a global solution. We require the condition

$$0 < N_1^0 < K, N_2^0 > 0, N_3^0 > 0, -\ell_1 < z_2^0 - \hat{z}_2 < \ell_0. \tag{2.3}$$

Remark. If $N_i^0 = 0$ for some j , then, by the uniqueness, any solution of (1.1)-(1.4) satisfies $N_i \equiv 0$. Hence it reduces to a system with less unknown quantities. Note that we avoid this case in (2.3).

We have

THEOREM 2.2. *Suppose that (2.3) is satisfied. Then the system of Equations (1.1)-(1.4) with the initial condition (1.6) has a unique global solution in*

$t_0 \leq t < \infty$.

Proof. First we will show the apriori estimate $N_1(t) < K$ for all t . Suppose that this is not true. Then, by the continuity of $N_1(t)$ and $N_1(t_0) = N_1^0 < K$ in (2.3) we can take the smallest time $t_1 > t_0$ such that $N_1(t_1) = K$. Assume that $N_2(t_1) = 0$. If we set $N_2 = 0$ in (1.1)-(1.4), then we have

$$\begin{aligned} \frac{dN_1}{dt} &= rN_1 \left(1 - \frac{N_1}{K} \right), \frac{dN_3}{dt} = -d_3 N_3, \\ \frac{dz_2}{dt} &= -\delta^{-1} g(z_2 - \hat{z}_2) - gN_3 a_3'. \end{aligned} \tag{2.4}$$

By the local existence and uniqueness theorem, Equations (2.4) with the initial condition

$(N_1, N_3, z_2)|_{t=t_1} = (K, N_3(t_1), z_2^0)$ has a unique solution. We denote the solution by $(\tilde{N}_1, \tilde{N}_3, \tilde{z}_2)$. Then (1.1)-(1.4) with the initial value $(K, 0, N_3(t_1), z_2^0)$ at $t = t_1$ has a solution $(\tilde{N}_1, \tilde{N}_3, \tilde{z}_2)$. By the uniqueness of the solution we obtain $(N_1, N_2, N_3, z_2) = (\tilde{N}_1, 0, \tilde{N}_3, \tilde{z}_2)$. It follows that $N_2(t) \equiv 0$. Because $N_2(t_0) \neq 0$ by (2.3), we have a contradiction. Hence we have $N_2(t_1) > 0$. By the continuity of $N_2(t)$ one may assume that $N_2(t) > 0$ in a sufficiently small neighborhood of t_1 . Then, the second term in the right hand side of (1.1) satisfies $a_2 N_1 N_2 / (1 + a_2 h_2 N_1) > 0$ in a sufficiently small neighborhood of t_1 . On the other hand, since $rN_1(1 - N_1/K_1)$ can be made arbitrarily small by taking a neighborhood of small, it follows that $(dN_1/dt) < 0$ there. Hence N_1 is a decreasing function. This contradicts to $N_1(t_1) = K$. Therefore, there is not t_1 such that $N_1(t) = K$, which shows the desired estimate.

Next we will estimate N_2 from the above. Take $\varepsilon > 0$ that $\varepsilon c_2 \leq 1$, and add ε times (1.2) to (1.1). Then we have

$$\begin{aligned} \frac{dN_1}{dt} + \varepsilon \frac{dN_2}{dt} &= rN_1(1 - N_1 K^{-1}) - \frac{a_2 N_1 N_2}{1 + a_2 h_2 N_1} \\ &+ \varepsilon N_2 \left(\frac{c_2 a_2 N_1}{1 + a_2 h_2 N_1} - d_2 \right) - \varepsilon \frac{a_3 N_3 N_2}{1 + a_3 h_3 N_2} \\ &\leq rN_1(1 - N_1 K^{-1}) - d_2 N_2 \varepsilon = -d_2(N_1 + \varepsilon N_2) + f(t), \end{aligned} \tag{2.5}$$

where $f(t) = rN_1(1 - N_1 K^{-1}) + d_2 N_1 \geq 0$.

Hence, by setting $v(t) = N_1 + N_2$ we obtain

$$\frac{dv}{dt} + d_2 v \leq f(t). \tag{2.6}$$

Multiplying $e^{d_2 t}$ to both sides, and integrating from t_0 to $t, t > t_0$, we obtain

$$\begin{aligned} \int_{t_0}^t \frac{d}{ds} (e^{d_2 s} v) ds &= e^{d_2 t} v(t) - e^{d_2 t_0} v(t_0) \\ &\leq \left| \int_{t_0}^t f(s) e^{d_2 s} ds \right|. \end{aligned} \tag{2.7}$$

By the apriori estimate there exists $M > 0$ depending only on r, K and d_2 such that $f(s) \leq M$. Hence we have

$$\begin{aligned} v(t) &\leq e^{d_2(t_0-t)}v(t_0) + \left| \int_{t_0}^t f(s)e^{d_2(s-t)}ds \right| \\ &\leq e^{d_2(t_0-t)}v(t_0) + M \left| \int_{t_0}^t e^{d_2(s-t)}ds \right|. \end{aligned}$$

Because $\left| \int_{t_0}^t e^{d_2(s-t)}ds \right| \leq d_2^{-1}$, we obtain

$$v(t) \leq e^{d_2(t_0-t)}v(t_0) + Md_2^{-1} \leq v(t_0) + Md_2^{-1}. \quad (2.8)$$

It follows that, for $t > t_0$

$$N_2(t) \leq \varepsilon^{-1} (Md_2^{-1} + N_1(t_0) + \varepsilon N_2(t_0)). \quad (2.9)$$

Note that the right hand side quantity depends on the initial value and the equation and depends neither on $\delta > 0$ nor on $g > 0$.

We make the same argument for $N_3(t)$. Take ε so that $\varepsilon c_3 \leq 1$, and add ε times (1.3) to (1.2). Then we have

$$\begin{aligned} \frac{dN_2}{dt} + \varepsilon \frac{dN_3}{dt} &\leq N_2 \left(\frac{c_2 a_2 N_1}{1 + a_2 h_2 N_1} - d_2 \right) - d_3 \varepsilon N_3 \\ &= -d_3 (N_2 + \varepsilon N_3) + f(t), \end{aligned} \quad (2.10)$$

where

$$f(t) = N_2 \left(\frac{c_2 a_2 N_1}{1 + a_2 h_2 N_1} - d_2 + d_3 \right).$$

By setting $v(t) := N_2 + \varepsilon N_3$ we obtain the equation $dv/dt \leq -d_3 v + f$. Because this equation has a similar form as in the case $N_2(t)$, we can choose a constant $M_1 > 0$ depending only on r, K, d_2, d_3 and the initial values so that $f(t) \leq M_1$. Then we argue in the same way and we obtain

$$v(t) \leq M_1 d_3^{-1} + N_2(t_0) + \varepsilon N_3(t_0) \quad (2.11)$$

In view of the definition of v we have

$$N_3(t) \leq \varepsilon^{-1} (M_1 d_3^{-1} + N_2(t_0) + \varepsilon N_3(t_0)). \quad (2.12)$$

Next we will estimate $N_1(t)$ from the below. By the estimates of N_1 and N_2 from the above there exists L_2 such that $N_1(t) \leq K, N_2 \leq L_2$. It follows that

$$\begin{aligned} \frac{dN_1}{dt} &= rN_1(1 - N_1K^{-1}) - \frac{N_2 a_2 N_1}{1 + a_2 h_2 N_2} \\ &> -\frac{N_2 a_2 N_1}{1 + a_2 h_2 N_2} > -a_2 N_1 N_2 \geq -a_2 N_1 L_2. \end{aligned}$$

By integrating from t_0 to t we obtain

$$N_1(t) \geq N_1(t_0) \exp(-a_2 L_2 |t - t_0|). \quad (2.13)$$

We will estimate N_2 from the below. There exist con-

stants $A_3 > 0, L_3 > 0$ depending on the equation and the initial values such that, $|a_3| \leq A_3, N_3 \leq L_3$. Hence we have

$$\begin{aligned} \frac{dN_2}{dt} &= \frac{c_2 N_2 a_2 N_1}{1 + a_2 h_2 N_1} - d_2 N_2 - \frac{N_2 a_3 N_3}{1 + a_3 h_3 N_2} \\ &> -d_2 N_2 - N_2 a_3 N_3 \geq -d_2 N_2 - N_2 A_3 L_3. \end{aligned}$$

By integrating the inequality from t_0 to t we obtain

$$N_2(t) \geq N_2(t_0) \exp(-(d_2 + A_3 L_3)|t - t_0|). \quad (2.14)$$

The estimate of N_3 from the below can be shown by simple computations.

$$N_3(t) \geq N_3(t_0) \exp(-d_3 |t - t_0|). \quad (2.15)$$

Next we will prove

$$-\ell_1 < z_2(t) - \hat{z}_2 < \ell_0. \quad (2.16)$$

Indeed, we have (2.16) for $t = t_0$ by the initial condition. It follows that if $t - t_0$ is sufficiently small, then (2.16) holds true.

In order to prove (2.16) we assume that there exists t_1 such that either $z_2(t_1) - \hat{z}_2 = \ell_0$ or $z_2(t_1) - \hat{z}_2 = \ell_1$ holds and we show the contradiction. For the sake of simplicity let us assume the former case holds. The latter case can be treated in the same way. By the estimate of $N_3(t)$ from the above we have, for any ε , $0 < \varepsilon < g\ell_0/(2\delta)$ there exists a neighborhood V of ℓ_0 such that if $z_2 - \hat{z}_2 \in V$, then $z_2(t) - \hat{z}_2 > \ell_0/2$ and $g|N_3 a'_3(z_2 - \hat{z}_2)| < \varepsilon$ hold. Hence we have

$$\begin{aligned} \frac{dz_2}{dt} &= -\frac{g}{\delta}(z_2 - \hat{z}_2) - \frac{N_3 a'_3(z_2 - \hat{z}_2)}{(1 + a_3 h_3 N_2)^2} \\ &< -\frac{g}{\delta}(z_2 - \hat{z}_2) + \varepsilon. \end{aligned} \quad (2.17)$$

If $z_2 - \hat{z}_2 \in V$, then the right hand side of (2.17) is negative. Therefore $z_2(t) - \hat{z}_2$ is decreasing near $t = t_1$. This implies that $z_2(t) - \hat{z}_2 < \ell_0$ does not tend to ℓ_0 when $t \rightarrow t_1$. Because $z_2(t)$ is continuous, we have $z_2(t_1) - \hat{z}_2 \neq \ell_0$. This is a contradiction. Hence we have the desired estimate.

We shall prove the existence of a global solution. Set $N(t) = (N_1, N_2, N_3)$ and let $t_0 \leq t < \alpha$ be the maximal interval for which $N(t)$ and $z_2(t)$ are defined. If $\alpha = \infty$, then we are done. Assume that $\alpha < \infty$. We will show that the limits $\lambda_j := \lim_{t \rightarrow \alpha} N_j(t)$ and $\beta := \lim_{t \rightarrow \alpha} z_2(t)$ exist. We set $F(N, z_2) = F = (F_1, F_2, F_3, F_4)$, where F_j is the right hand sides of the Equations (1.1)-(1.4), respectively. We write (1.1)-(1.4) into an equivalent system of integral equations

$$N_j(t) - N_j(t_0) = \int_{t_0}^t F_j(N, z_2) d\sigma. \quad (2.18)$$

By the apriori estimates from the above, $F_j(N(t), z_2(t))$ is bounded on $t_0 \leq t \leq \alpha$. Hence there exists M such that $N_j(t) - N_j(s) \leq M|t - s|$. It follows that the limit $\lambda_j \equiv \lim_{t \rightarrow \alpha} N_j(t)$ exists. If we define $\lambda_j := N_j(\alpha) > 0$, then $N_j(t)$ is continuous up to $t = \alpha$. We will show that it is C^1 . For this purpose it is sufficient to show that $\lim_{t,s \rightarrow \alpha} (N_j'(t) - N_j'(s)) = 0$. We note that $F_j(N, z_2)$ is Lipschitz continuous in each variable because we have apriori estimates of N and z_2 . Namely there exists $C > 0$ independent of N and z_2 such that

$$|F_j(N, z_2) - F_j(\tilde{N}, \tilde{z}_2)| \leq C|N - \tilde{N}| + C|z_2 - \tilde{z}_2|.$$

Hence, by (1.1)-(1.4) we have

$$|N_j'(t) - N_j'(s)| \leq C|N(t) - N(s)| + C|z_2(t) - z_2(s)|.$$

This proves the assertion. We can similarly prove for $z_2(t)$. We can solve (1.1)-(1.4) with the initial values λ_j and $z_2^0, z_2^0 := \lim_{t \rightarrow \alpha} z_2(t)$ at $t = \alpha$. Then by the unique existence of the solution we can extend $N(t)$ and $z_2(t)$ to some neighborhood of $t = \alpha$. This contradicts to the definition of α . Hence we have $\alpha = \infty$. This ends the proof.

Remark. 1) We remark that the apriori estimate of a solution does not depend on the cost of evolution $0 < \delta < \infty$ and the additive genetic variance $g > 0$. This means that the evolution of a character has little effect to the bound of sum of populations of three species.

2) As a corollary to Theorem 2 we see that if there is no effect of evolution, i.e., $a_3(z_2 - \hat{z}_3) \equiv a_3^0$, then (1.1)-(1.3) with the initial condition (1.6) has a unique global solution. Indeed, (1.1)-(1.4) can be split into (1.1)-(1.4), $dz_2/dt = -g\delta^{-1}(z_2 - \hat{z}_2)$. The latter equation can be integrated. In view of the uniqueness of the solution of (1.1)-(1.4) we see that (1.1)-(1.3) has a unique solution.

3. Intermittency of Evolution Effect

We shall study the effect of evolution to dynamics of (1.1)-(1.4). More precisely, we will study how the dynamics of (1.4) is related with that of (1.1)-(1.3). By setting $z = z_2 - \hat{z}_2$ we write (1.4) in the form

$$\frac{dz}{dt} = -\frac{gz}{\delta} - \frac{gN_3 a_3'(z)}{(1 + a_3(z)h_3N_2)^2}. \tag{3.1}$$

Let $\gamma \geq 1$ be an integer and $\ell_0 > 0$ and $0 < \eta \ll 1$ be constants. We assume

$$\begin{aligned} a_3(z) &= a_3^0(\ell_0^{2\gamma} - z^{2\gamma}), \text{ for } |z| < \ell_0 - \eta, \\ a_3(z) &\equiv 0, \text{ for } |z| \geq \ell_0. \end{aligned} \tag{C.1}$$

We also assume that $a_3(z)$ is twice continuously differentiable and nonnegative in the closed intervals $[\ell_0 - \eta, \ell_0]$ and $[-\ell_0, -\ell_0 + \eta]$. If we denote the

right-hand side of (3.1) by $f(z)$, then, by (C.1) we have

$$f(z) = \frac{2\gamma g z N_3 a_3^0 z^{2\gamma-2}}{(1 + a_3^0(\ell_0^{2\gamma} - z^{2\gamma})h_3N_2)^2} - \frac{gz}{\delta}, \tag{3.2}$$

on $|z| \leq \ell_0 - \eta$. We define $\tilde{f}(z)$ on $|z| \leq \ell_0$ by the right-hand side of (3.2). Define, for $\gamma \geq 1$,

$$v := \sqrt{N_3}/N_2, K_\gamma := \sqrt{2\gamma\delta}/\sqrt{a_3^0 h_3 \ell_0^{\gamma+1}}. \tag{3.3}$$

We first study the behavior of $\tilde{f}(z)$.

LEMMA 3.1. 1) Assume $\gamma \geq 2$. Suppose that $N_3 < 1/(2\gamma a_3^0 \ell_0^{2\gamma-2} \delta)$. Then $\tilde{f}(z)$ has a unique zero $z = 0$ in the interval $(-\ell_0, \ell_0)$ and $\tilde{f}(z)/z$ is negative on $(-\ell_0, \ell_0) \setminus \{0\}$.

Assume $N_3 \geq 1/(2\gamma a_3^0 \ell_0^{2\gamma-2} \delta)$. Then $\tilde{f}(z)$ has simple zeros, $\pm z_0$ and 0 on $[-\ell_0, \ell_0]$. The function $\tilde{f}(z)/z$ is negative on the intervals $(-z_0, 0)$ and $(0, z_0)$, while it is positive on $(-\ell_0, -z_0)$ and (z_0, ℓ_0) . (cf. **Figure 1**).

Moreover, there exists $\epsilon_1 > 0$ such that z_0 has an asymptotic behavior

$$z_0/\ell_0 = 1 - K_\gamma v (2\gamma + (\gamma - 1)K_\gamma v)^{-1} + O\left(\left(K_\gamma v\right)^2, N_2^{-1}\right), \tag{3.4}$$

when $K_\gamma v \rightarrow 0, N_2 \geq \epsilon_1$. Similarly we have

$$\begin{aligned} \frac{z_0}{\ell_0} &= \left(1 + 1/a_3^0 \ell_0^{2\gamma} h_3 N_2\right)^{1/(\gamma-1)} \times \left(K_\gamma v\right)^{-1/(\gamma-1)} \\ &+ O\left(\left(K_\gamma v\right)^{-(1+2\gamma)/\gamma-1}\right), \end{aligned} \tag{3.5}$$

when $K_\gamma v \rightarrow \infty$.

2) Assume $\gamma = 1$. If $1 + (a_3^0 \ell_0^2 h_3 N_2)^{-1} > K_1 v$, then $\tilde{f}(z)$ has simple zeros, $\pm z_0$ and 0 on $(-\ell_0, \ell_0)$.

The function $\tilde{f}(z)/z$ is negative on the intervals $(-z_0, 0)$ and $(0, z_0)$, while it is positive on $(-\ell_0, -z_0)$ and (z_0, ℓ_0) . (cf. **Figure 1**).

If $1 + (a_3^0 \ell_0^2 h_3 N_2)^{-1} \leq K_1 v$, then $\tilde{f}(z)$ has a unique zero $z = 0$ in $(-\ell_0, \ell_0)$ and $\tilde{f}(z)/z$ is positive on $(-\ell_0, \ell_0) \setminus \{0\}$. (cf. **Figure 2**).

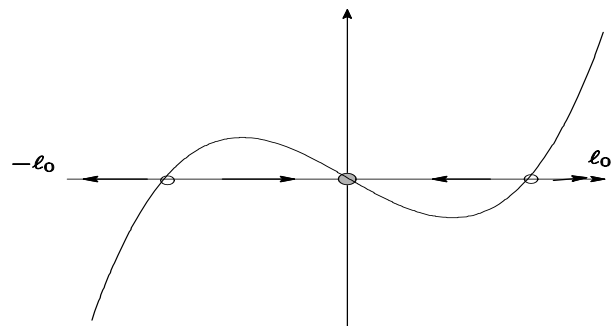


Figure 1. $\gamma \geq 2$.

Proof. We divide the proof into 5 steps.

Step 1. By (C.1) we have

$$\begin{aligned} \delta f / g z &= (1 + a_3 h_3 N_2)^{-2} \left(2\gamma N_3 a_3^0 \delta z^{2\gamma-2} - (1 + a_3 h_3 N_2)^2 \right) \\ &= -\left(a_3^0 \right)^2 h_3^2 N_2^2 (1 + a_3 h_3 N_2)^{-2} \\ &\quad \left(K_\gamma \ell_0^{\gamma+1} \nu z^{\gamma-1} + \left(a_3^0 h_3 N_2 \right)^{-1} + \ell_0^{2\gamma} - z^{2\gamma} \right) \\ &\quad \times \left(-K_\gamma \ell_0^{\gamma+1} \nu z^{\gamma-1} + \left(a_3^0 h_3 N_2 \right)^{-1} + \ell_0^{2\gamma} - z^{2\gamma} \right). \end{aligned} \tag{3.6}$$

Set

$$A_\gamma = 1 / \ell_0^{2\gamma} a_3^0 h_3 N_2, \zeta = z / \ell_0, \tag{3.7}$$

and define

$$g_\pm(\zeta) = \zeta^{2\gamma} \pm \nu K_\gamma \zeta^{\gamma-1} - 1 - A_\gamma. \tag{3.8}$$

We consider the zeros and the sign of $g_\pm(\zeta)$ in the interval $-1 \leq \zeta \leq 1$.

Step 2. First we consider the case $\gamma \geq 2$. Assume that γ is an odd integer. Because $\gamma - 1$ is an even integer, we have $g_-(\zeta) = g_-(-\zeta)$. We have $g_-(1) = -\nu K_\gamma - A_\gamma < 0$ and $g_-(0) \leq -1 - A_\gamma < 0$. Because we easily see that $g_-(\zeta) < 0$ if $0 \leq \zeta \leq 1$, it follows that g_- has no zero point on $[-1, 1]$.

In order to study the zero of g_+ in $(0, 1)$, note $g_+(0) < -1$. One easily see that the assumption $N_3 \geq 1 / (2\gamma a_3^0 \ell_0^{2\gamma-2} \delta)$ is equivalent to $g_+(1) = \nu K_\gamma - A_\gamma \geq 0$. Because $g'_+(\zeta) > 0$ on $(0, 1]$, we see that $g_+(\zeta)$ has only one zero point in the interval $(0, 1]$ if $N_3 \geq 1 / (2\gamma a_3^0 \ell_0^{2\gamma-2} \delta)$. In view of (3.6) we conclude that f has zero points $\pm z_0$ and 0 in the interval $[-1, 1]$ for some $0 < z_0 < 1$. It is also clear that if the opposite inequality $N_3 < 1 / (2\gamma a_3^0 \ell_0^{2\gamma-2} \delta)$ holds, then $f(z)/z < 0$ on $[-1, 1] \setminus \{0\}$.

Next we consider the case γ is even. By the same way as in the odd case, we have $g_+(0) < -1$, $g_+(-1) < -\nu K_\gamma < 0$ and $g_+(1) = \nu K_\gamma - A_\gamma \geq 0$. Since g_+ is strictly increasing on $(0, 1)$, there exists unique ζ_0 , $0 < \zeta_0 \leq 1$ such that $g_+(\zeta_0) = 0$. In order to show that $g_+(\zeta)$ has no zero on $(-1, 0)$, we note

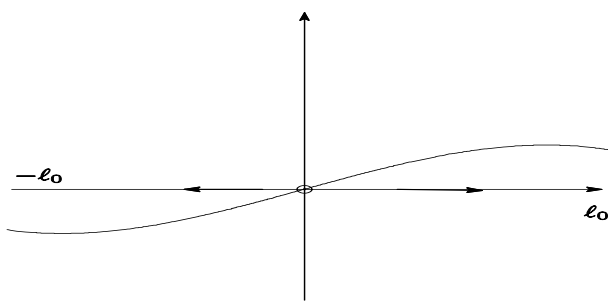


Figure 2. $\gamma = 1$ and $1 + (a_3^0 \ell_0^2 h_3 N_2)^{-1} \leq K_1 \nu$.

$g_+(\zeta) < \zeta^{2\gamma} - 1 + \zeta^{\gamma-1} \nu K_\gamma$. Because $\zeta^{2\gamma} - 1 < 0$ and $\zeta^{\gamma-1} \nu K_\gamma < 0$ on $(-1, 0)$, we see that g_+ has a unique zero point ζ_0 on $(-1, 1)$. Clearly, g_- has only one zero $-\zeta_0$, because $g_+(\zeta) = g_-(-\zeta)$ for all $\zeta, -1 \leq \zeta \leq 1$, which proves the assertion. The sign of $f(z)/z$ is almost clear from the definitions of g_\pm, g_- and the argument in the above.

Step 3. We will show the asymptotic formula of z_0 in (3.4). In view of the argument in Step 2 we may consider $g_+(\zeta) = 0$.

If we set $\zeta = 1 + \xi, (-1 < \xi \leq 0)$, then we have

$$\begin{aligned} A_\gamma &= (1 + \xi)^{2\gamma} - 1 + \nu K_\gamma (1 + \xi)^{\gamma-1} \\ &= 2\gamma \xi + \nu K_\gamma (1 + (\gamma - 1)\xi) + \psi(\xi), \end{aligned} \tag{3.9}$$

where $\psi(\xi) = O(\xi^2)$ is a polynomial of ξ with positive coefficients. Hence we have

$$\begin{aligned} &\xi + (2\gamma + (\gamma - 1)\nu K_\gamma)^{-1} \psi(\xi) \\ &= (A_\gamma - \nu K_\gamma) (2\gamma + (\gamma - 1)\nu K_\gamma)^{-1} \\ &=: \Lambda. \end{aligned} \tag{3.10}$$

Hence, for Λ sufficiently small we can uniquely solve (3.10). By an implicit function theorem we see that $\xi = \xi(\Lambda)$ is a smooth function of Λ such that $\xi(0) = 0, \xi'(0) = 1$. It follows that

$$\begin{aligned} \zeta &= z_0 / \ell_0 = 1 + \xi(\Lambda) + O(\Lambda^2) \\ &= 1 - \nu K_\gamma (2\gamma + (\gamma - 1)\nu K_\gamma)^{-1} + O(\nu^2 K_\gamma^2, N_2^{-1}). \end{aligned}$$

Therefore we have (3.4).

Step 4. Next we will prove (3.5). We will solve $g_\pm(\zeta) = 0$, namely

$$\zeta^{2\gamma} - 1 + \nu K_\gamma \zeta^{\gamma-1} = A_\gamma, \tag{3.11}$$

for $0 < \zeta \leq 1$. Hence we have

$$\nu K_\gamma = \zeta^{1-\gamma} - \zeta^{1+\gamma} + A_\gamma \zeta^{1-\gamma}. \tag{3.12}$$

If ζ does not converges to zero when $\nu K_\gamma \rightarrow \infty$, then there exist $c > 0$ and a sequence $\zeta_n \geq c > 0 (n = 1, 2, \dots)$. Since the right-hand side of (3.12) is bounded for $\zeta = \zeta_n$, this leads to a contradiction. Hence νK_γ is asymptotically equal to $\zeta^{1-\gamma} (1 + A_\gamma)$.

By solving this relation we have

$$\zeta \sim (1 + A_\gamma)^{1/\gamma-1} (\nu K_\gamma)^{-1/\gamma-1}$$

when $\nu K_\gamma \rightarrow \infty$. By (3.11) we have $\zeta^{1-\gamma} = (1 + A_\gamma)^{-1} (\nu K_\gamma + \zeta^{1+\gamma})$. It follows that

$$\begin{aligned} \zeta &= (1 + A_\gamma)^{1/(\gamma-1)} (\nu K_\gamma + \zeta^{1+\gamma})^{1/(1-\gamma)} \\ &= (1 + A_\gamma)^{1/(\gamma-1)} (\nu K_\gamma)^{1/(1-\gamma)} \times \left(1 - \frac{\zeta^{1+\gamma}}{\nu K_\gamma (\gamma - 1)} + \dots \right). \end{aligned}$$

By simple computations we obtain (3.5).

Step5. If $\gamma = 1$, then we have

$g_{\pm}(\zeta) = \zeta^2 \pm \nu K_1 - 1 - A_1$. We can easily see that $g_{-}(\zeta) \neq 0$ on $[-1, 1]$. The solution of $g_{+}(\zeta) = 0$ is given by $\pm\sqrt{1 - \nu K_1 + A_1}$. The rest of the assertion is almost clear from this formula. This completes the proof.

Remark. We will briefly discuss the difference of dynamics of z in (3.1) for f and \tilde{f} . We note that two functions are identical for $|z| \leq \ell_0 - \eta$. For a small number $\eta > 0$, consider the case shown in **Figure 2** for $\gamma = 1$. Then f looks like as in **Figure 3** where new attractive equilibrium points appear near $\pm\ell_0$ because we have made a modification to a_3 so that $\pm f(\pm\ell_0) < 0$. The new equilibrium point corresponds to that of \tilde{f} with modulus larger than ℓ_0 . Because of the new equilibrium points we have an apriori estimate of the solution for f . Namely, the orbit started from a neighborhood of the origin does not go beyond $\pm\ell_0$. This fact is important since, if otherwise, the efficiency $a_3(z)$ becomes negative. Note that the dynamics of f and \tilde{f} is the same outside some neighborhood of the boundary $z = \pm\ell_0$. We also note that a similar situation occurs in the case $\gamma \geq 2$ with $z_0 < \ell_0 - \eta$. (cf. **Figures 1** and **4**). On the other hand, if $z_0 \geq \ell_0 - \eta$, then the dynamics of f and \tilde{f} in $z_0 - z$ may be different, while in other part both are the same.

We also note that the apriori estimate holds for f . Therefore apart from the neighborhood of $z = \pm\ell_0$ the dynamics of f is well approximated by that of \tilde{f} , for which \tilde{f} we can make concrete analysis of the dynamics, although we do not have the apriori estimate.

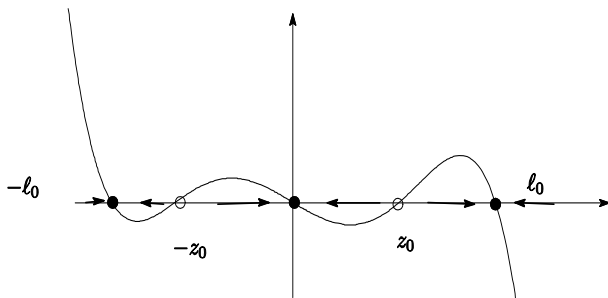


Figure 3. Picture of f . $\gamma = 1$.

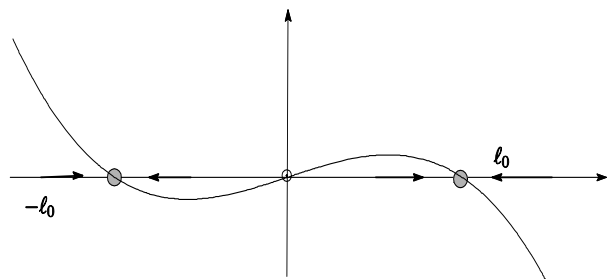


Figure 4. Picture of f . $\gamma \geq 2$.

We will study behaviors of solutions under the effect of evolution.

1) Behaviors near the equilibrium point.

We consider how the dynamics of (1.1)-(1.4) is related to the dynamics (1.1)-(1.3) without evolution. We recall that (1.1)-(1.3) without an evolutionary effect has what is called a tea-cup attractor. The isocline of (1.1)-(1.3), (3.1) is given by the family of equations

$$r(1 - N_1/K) - \frac{a_2 N_2}{1 + a_2 h_2 N_1} = 0, \tag{3.13}$$

$$\frac{c_2 a_2 N_1}{1 + a_2 h_2 N_1} - d_2 - \frac{a_3 N_3}{1 + a_3 h_3 N_2} = 0, \tag{3.14}$$

$$\frac{c_3 a_3 N_2}{1 + a_3 h_3 N_2} - d_3 = 0, \tag{3.15}$$

$$f(z) = 0. \tag{3.16}$$

It follows from (3.15) that

$$a_3 N_2 = \frac{d_3}{c_3 - h_3 d_3} =: A. \tag{3.17}$$

One may assume that A is small since $d_3 \sim 0$ is small. By (3.14) we have

$$a_3 N_3 = (1 + h_3 A) \left(\frac{c_2 a_2 N_1}{1 + a_2 h_2 N_1} - d_2 \right) = 0. \tag{3.18}$$

Let us first consider the non-evolutional case, $z = 0$ or the case where evolution becomes stationary, namely $z \rightarrow 0$. Then there exists $C > 0$ such that $a_3(z) > C$. Hence $N_2 = A/a_3$ is small and N_1 is close to K , by (3.13). It follows that there exists $C_1 > 0$ such that $(c_2 a_2 N_1)/(1 + a_2 h_2 N_1) - d_2 > C_1$ if d_2 is sufficiently small. In terms of (3.17) and (3.18) N_3/N_2 tends to infinity when $A \rightarrow 0$. This implies a typical behavior of N_2 and N_3 around an equilibrium point when there is little effect of evolution. Numerical experiments show that the decrease of N_3 occurs soon after the orbit approaches to the equilibrium point, namely N_3/N_2 becomes sufficiently large.

Let us consider the evolutionary case. Then the main difference from the non-evolutional case is that $a_3(z)$ may tends to zero. For the sake of simplicity, let us consider the case $\gamma = 1$ or $\gamma = 2$. Assume that there exists an orbit such that $N_3 \geq 1$ and N_3/N_2 grows large. Because $\sqrt{N_3}/N_2$ also grows large, it follows from (3.4) that z_0 tends to zero, and we are in the situation that the orbit of $z > z_0$ tends to l_0 . Therefore $a_3(z)$ tends to zero. Hence the boundedness of N_2 implies that $(c_3 a_3 N_2)/(1 + a_3 h_3 N_2) - d_3$ becomes negative. Therefore, by (1.3), N_3 exponentially decreases. Note that the decrease of $a_3(z)$ begins after $\sqrt{N_3}/N_2$ exceeds a certain constant independent of N_2 and N_3 when

$\gamma = 1$. This exhibits a strong contrast to the non evolutionary case where the collapse of N_3 occurs after N_3/N_2 becomes sufficiently large.

2) *Effect of the parameter γ to evolution.*

In the predatory efficiency $a_3(z)$ in (C.1) γ represents sensitivity to z . Namely, as γ increases, $a_3(z)$ for small z approaches to a constant function. The dynamics of z is quite different in the cases $\gamma = 1$ and $\gamma \geq 2$. Indeed, if $\gamma = 1$ and

$$1 + (l_0^2 a_3^0 h_3 N_2)^{-1} \leq K_1 v = \frac{\sqrt{2\delta}}{l_0^2 h_3 \sqrt{a_3^0}} \frac{\sqrt{N_3}}{N_2},$$

then evolution progresses. (cf. **Figure 2** and **Figure 3**). The latter condition means either the cost of evolution is small, $\delta \gg 1$ or $\sqrt{N_3}/N_2 \gg 1$. We note that the attractive equilibrium points near $z = \pm \ell_0$ have the effect to hold the orbits around $z = \pm \ell_0$. Conversely, if $1 + (l_0^2 a_3^0 h_3 N_2)^{-1} \geq K_1 v$, then we see that fluctuations in progress and rest of evolution takes place.

In the case $\gamma \geq 2$ we have a different situation. Indeed, if $N_3 < 1/(2\gamma a_3^0 \delta \ell_0^{2\gamma-2})$, then the evolution becomes stationary. If otherwise, then similar fluctuations in progress and rest of evolution as in the case $\gamma = 1$ takes place. We will show in the next section that in the linear case $a_3(z) = \alpha z + \beta$ we have a sharp contrast to the case $\gamma \geq 2$.

3) *Fluctuations of N_1 and N_2 .*

The rhythm of N_1 and N_2 is also observed in a non- evolutionary system and it is related with the structure of a tea-cup attractor. We have a similar phenomenon for an evolutionary system.

Let $\tilde{N}_1, \tilde{N}_2, \tilde{N}_3 = 0$ and \tilde{z} be a solution of (1.1)-(1.4). One can show by Poincaré –Bendixon theorem that \tilde{N}_1 and \tilde{N}_2 are an oscillating solution of two species under appropriate choice of parameters. Note that \tilde{z} tends to zero exponentially. By the continuity of solutions of the initial value problem with respect to an initial value and the apriori estimate of a solution, one can see that for every $T > 0$ and $\varepsilon > 0$ there exists $\delta > 0$ such that if

$$\begin{aligned} |N_1(0) - \tilde{N}_1(0)| < \delta, |N_2(0) - \tilde{N}_2(0)| < \delta, \\ N_3(0) < \delta, |z(0) - \tilde{z}(0)| < \delta, \end{aligned}$$

then

$$\begin{aligned} |N_1(t) - \tilde{N}_1(t)| < \varepsilon, |N_2(t) - \tilde{N}_2(t)| < \varepsilon, \\ N_3(t) < \varepsilon, |z(t) - \tilde{z}(t)| < \varepsilon, \end{aligned}$$

for all $0 \leq t \leq T$. Here, without loss of generality we may assume that the initial time is 0. Especially, this shows that there appears a rhythm of N_1 and N_2 for some interval of time. Note that N_3 is small and the evolution becomes stationary, i.e., $a_3 \rightarrow a_3^0$.

In order to estimate T , we take $N_1(0) = \tilde{N}_1(0)$, $N_2(0) = \tilde{N}_2(0)$, and $z(0) = \tilde{z}(0)$. By integrating the equation of N_3 , one has

$$N_3(t) = N_3(0) \exp\left(-d_3 t + \int_0^t \frac{c_3 a_3 N_2(s)}{1 + h_3 a_3 N_2(s)} ds\right).$$

Hence, if we have

$$\left| -d_3 t + \int_0^t \frac{c_3 a_3 N_2(s)}{1 + h_3 a_3 N_2(s)} ds \right| \leq \eta t, \quad 0 \leq t \leq T \quad (3.19)$$

for sufficiently small η , then we have

$N_3(t) \leq N_3(0) e^{\eta t} < \varepsilon$, from which we have the estimate of time length T , $T < \eta^{-1} \ln(\varepsilon/N_3(0))$. We have a similar condition like (3.19) in the general case $t_0 \leq t \leq t_0 + T$ by replacing 0 and T , respectively, by t_0 and $T_0 + T$. A similar condition like (3.19) holds for some t_0 and T if we have an averaging property:

$$\lim_{t \rightarrow \infty} \frac{1}{t} \int_0^t \frac{c_3 a_3 N_2(s)}{1 + h_3 a_3 N_2(s)} ds = d_3.$$

4) *The limit case when evolution cost tends to zero.*

We assume $N_3 > 0$. If the evolution cost tends to zero, namely δ grows from zero to ∞ , then, by (3.4) and the definition of K_γ , z_0 approaches to the origin.

Therefore, the evolution progresses, namely z approaches either of the points $\pm \ell_0$. It follows that the predatory efficiency $a_3 \rightarrow 0$. By the same reasoning as in 1) N_3 tends to zero. We note that in the limit case $\delta \rightarrow \infty$ the third species dies out. This agrees with an ecological observation.

4. Evolution for a Linear Predatory Efficiency

We will discuss the evolution in the case

$$a_3(z) = \begin{cases} \alpha z + \beta, & \text{if } \alpha z + \beta \geq 0 \\ 0, & \text{if otherwise,} \end{cases} \quad (4.1)$$

where $\alpha \neq 0$ is a real constant and $\beta > 0$. As in the previous case we make modifications of $a_3(z)$ in some small neighborhood of the zero point $\ell_0 = -\beta/\alpha$ such that $a_3 \in C^1(\mathbb{R})$.

For the sake of simplicity, we assume that $\alpha > 0$. By repeating the same arguments as in Section 2 we see that the system of Equations (1.1)-(1.4) with the initial condition (1.6) has a unique global solution in $t_0 \leq t < \infty$.

We will study the dynamics of the evolution in relation with the populations N_2 and N_3 . We now define

$$f(z) := -z/\delta - \alpha N_3 (1 + h_3 N_2 (\alpha z + \beta))^{-2}. \quad (4.2)$$

The condition $f(z) \geq 0$ is equivalent to

$$z(1+h_3N_2(\alpha z+\beta))^2+\alpha\delta N_3\leq 0.$$

By definition we may consider (4.3) in the set $I:=\{z;\alpha z+\beta\geq 0\}$ because, if otherwise, $f(z)=-z/\delta>0$. Set

$$\phi(z):=z(1+h_3N_2(\alpha z+\beta))^2$$

and calculate the minimum of $\phi(z)$ in I . It is taken at $z=-(1+h_3N_2\beta)/3\alpha h_3N_2$ with the minimum value given by

$$-4\frac{(1+h_3N_2\beta)^3}{27\alpha h_3N_2}\sim -4\frac{\beta^3N_2^2h_3^2}{27\alpha}+O(N_2).$$

We recall that $f(z)\geq 0$ is equivalent to $\phi(z)+\alpha\delta N_3\leq 0$. Therefore, if $-\alpha\delta N_3>-4\beta^3N_2^2h_3^2/(27\alpha)$ modulo terms of $O(N_2)$, namely

$$\sqrt{N_3}/N_2<c_0/\sqrt{\delta}, c_0=2\beta\sqrt{\beta}h_3/(3\alpha\sqrt{3}), \tag{4.4}$$

then there appear an attractive equilibrium point z_0 near the origin $z=0$. This means that the predatory efficiency a_3 is close to a constant function if $\sqrt{N_3}/N_2$ is sufficiently small. Indeed, the equilibrium point z_0 can be estimated as

$$z_0=-\frac{\alpha\delta}{\beta^2h_3^2}\left(\sqrt{N_3}/N_2\right)^2+O\left(\left(\sqrt{N_3}/N_2\right)^3\right).$$

In view of the linearity of $a_3(z)$ and the smallness of $\sqrt{N_3}/N_2$ near the equilibrium point we see that $a_3(z)$ is almost constant for small changes of $\sqrt{N_3}/N_2$.

Suppose now that (4.4) does not hold. Then the attractive equilibrium point near $z=0$ disappears, and there remains an attractive equilibrium point near the zero of a_3 . Hence the evolution progresses and $a_3(z)$ tends to zero. This alternative between the rest and the progress of evolution shows a high contrast to the case of a convex predatory efficiency function discussed in the previous section.

5. Behaviors of Solutions as Cost Increases

In this section we study the convergence of a solution of an evolutionary system to that of a non-evolutional one when the evolutionary cost increases, namely δ decreases to zero. Let $N_j(t)\equiv N_j(t,\delta)$ and $z_2(t)\equiv z_2(t,\delta)$ be the solution of (1.1)-(1.4). Let $\tilde{N}_j(t)$ be the solution of the non-evolutional system (1.1)-(1.3), namely $a_3(z_2-\hat{z}_2)\equiv a_3^0$. Then we have

THEOREM 5.1. *Assume (2.3). Let $T>0$ be arbitrarily given. Then we have*

$$\lim_{\delta\rightarrow 0}N(t,\delta)=\tilde{N}(t)$$

uniformly in t on $t_0\leq t\leq T+t_0$.

Proof. By integrating (1.4) we have

$$z_2-\hat{z}_2=-g\int_{t_0}^t\exp\left(-\frac{g}{\delta}(t-s)\right)\frac{N_3(s)a_3'}{(1+a_3h_3N_2(s))^2}ds. \tag{5.1}$$

If we make the change of variables, $\sigma=g(t-s)/\delta$, then we have

$$z_2-\hat{z}_2=-\delta\int_0^{t_1}e^{-\sigma}w(\sigma)d\sigma, \tag{5.2}$$

where $t_1=g(t-t_0)/\delta$ and

$$w(\sigma)=\frac{N_3(t-\delta g^{-1}\sigma)a_3'}{(1+a_3h_3N_2(t-\delta g^{-1}\sigma))^2}.$$

Because $N_3(t-\delta g^{-1}\sigma)$ is uniformly bounded in δ by the apriori estimate, it follows that e^σ times the integrand is uniformly bounded in $t\geq t_0$ when $\delta\rightarrow 0$. Hence, the modulus of the integral can be bounded by a constant times $\int_0^\infty e^{-\sigma}d\sigma$. It follows that $z_2-\hat{z}_2\rightarrow 0$

uniformly in $t\geq t_0$ when $\delta\rightarrow 0$. This entails that $a_3(z_2-\hat{z}_2)\rightarrow a_3^0$ ($\delta\rightarrow 0$) uniformly in $t\geq t_0$.

For the sake of simplicity we write (1.1)-(1.3) in

$$N(t)\equiv N(t,\delta)=N^0+\int_{t_0}^tF(N(s,\delta))ds,$$

where we use the same notation F as in (2.18). Since

$$N(t,\delta)-\tilde{N}(t)=\int_{t_0}^tF(N(s,\delta))-F(\tilde{N}(s))ds,$$

we have

$$\left|N(t,\delta)-\tilde{N}(t)\right|\leq\int_{t_0}^t\left|F(N(s,\delta))-F(\tilde{N}(s))\right|ds, \tag{5.3}$$

where the absolute value of a vector means the norm of a vector. Because we have the uniform estimate of $N(s,\delta)$ in δ by (1) of Remark in Section 2, we have

$$\begin{aligned} &\left|F(N(s,\delta))-F(\tilde{N}(s))\right| \\ &\leq K_1\left(\left|N(s,\delta)-\tilde{N}(s)\right|+|a_3-a_3^0|\right), \end{aligned}$$

for some $K_1>0$ independent of δ .

By (1.5) and (5.2) we have

$$a_3(z_2-\hat{z}_2)-a_3^0=-a\left(-\delta\int_0^{t_1}e^{-\sigma}w(\sigma)d\sigma\right). \tag{5.4}$$

Because $a(0)=0$, there exists a constant $K_2>0$ independent of δ such that the right hand side of (5.4) can be estimated by $K_2\delta$. It follows that for any $\varepsilon>0$ there exist $\delta_0>0$ and $A>0$ such that, for $0<\delta<\delta_0$

$$\left|F(N(s,\delta))-F(\tilde{N}(s))\right|\leq A\left|N(s,\delta)-\tilde{N}(s)\right|+\varepsilon.$$

Therefore we have

$$\left|N(t,\delta)-\tilde{N}(t)\right|\leq\varepsilon T+A\left|\int_{t_0}^t\left|N(\sigma,\delta)-\tilde{N}(\sigma)\right|d\sigma\right|.$$

By Gronwall's inequality we obtain, for $0 < \delta < \delta_0$

$$|N(t, \delta) - \tilde{N}(t)| \leq \varepsilon T \exp(A|t - t_0|)$$

Because $\varepsilon > 0$ is arbitrary, we have the desired estimate.

6. Discussion

Evolutional Lotka-Volterra system does not seem to be well understood analytically except for the case of two species. In this paper, we have studied how the evolutionary change of a character influences global behaviors of a Lotka-Volterra system for three species. We introduced an evolutionary equation based on a quantitative genetic model into a Lotka-Volterra system of equations and we proved the existence and the uniqueness of a global solution as well as apriori estimates of a solution. By virtue of these properties, we have given analytical proofs of properties which are different from the non-evolutional system. We hope that some of the properties shown in this paper hold for more general food web settings. It is also interesting to make numerical analysis of our theory in order to understand the effect of evolution. The study of these problems will be left for the future study.

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Appendix

(A) The following lemma is used in Section 5.

LEMMA. (Gronwall) *Let $I = [a, b] \subseteq \mathbb{R}$ be a closed interval and let $s \in I$. Let u be continuously differentiable in I such that, for some constants $c \geq 0$ and $A \geq 0$ the inequality*

$$0 \leq u(t) \leq c + A \left| \int_s^t u(\sigma) d\sigma \right|$$

holds true for $t \in I$. Then we have $u(t) \leq c \exp(A|t-s|)$ on I .

Proof. For the sake of simplicity, we consider the case $t \geq s$. Denoting the right hand side of the inequality by $v(t)$ we have the relations, $u(t) \leq v(t)$, $v(s) = c$ and $\dot{v}(t) = Au(t) \leq Av(t)$. Multiplying the last inequality with $e^{-A(t-s)}$, we have $(d/dt)(e^{-A(t-s)}v(t)) \leq 0$. By integration we get $u(t) \leq v(t) \leq ce^{A|t-s|}$.

(B) We will briefly show how to deduce (1.4) from the theory of quantitative genetics. Let $z = z_2 - \bar{z}_2$, g and w be the average character value, the additive genetic variance and the average adaptability of the character value z , respectively. Following the quantitative genetical model we have (cf. [1] and [2]).

$$dz/dt = g(\partial/\partial z) \log W(z).$$

The left-hand side is the speed of evolution of a character value. Following Fisher, [7] we have $W = e^r$. We assume that (cf. [3-5])

$$r(z) = N_2^{-1} (dN_2/dt) + \log W_2,$$

$$W_2 = \exp(-z^2/2\delta),$$

where δ is the cost of evolution. By definition we have

$$\frac{\partial}{\partial z} \left(\frac{1}{N_2} \frac{dN_2}{dt} \right) = \frac{\partial}{\partial z} \left(\frac{c_2 a_2 N_1}{1 + h_2 a_2 N_1} - d_2 - \frac{a_3 N_3}{1 + a_3 h_3 N_2} \right). \tag{7.1}$$

Here a_2 , h_2 and d_2 are certain constants. We have

$$\frac{a_3 N_3}{1 + a_3 h_3 N_2} = \frac{N_3}{N_2} - \frac{N_3}{N_2} \frac{1}{1 + a_3 h_3 N_2}.$$

Because one may regards N_j as a constant function when z varies, the right-hand side of (7.1) can be replaced by

$$\frac{N_3}{N_2} \frac{a'_3 N_2}{(1 + a_3 h_3 N_2)^2} = - \frac{N_3 a'_3}{(1 + a_3 h_3 N_2)^2}.$$

Hence we obtain (1.4). ■