

Global stability in a class of competitive cubic systems

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Abstract

We consider an alternative Lotka-Volterra competition model in which two species co-exist stably in interspecific competition. This model consists of a pair of autonomous differential equations and assumes that competitive interactions, both intra-and interspecific, are non-linear. By means of an appropriately constructed Lyapunov function, sufficient conditions are derived for the global stability of the unique positive steady state. © 1997 Elsevier Science B.V.

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1. Introduction

The main purpose of this paper is to establish conditions for the global asymptotic stability of the unique equilibrium point of the system:

$$\begin{aligned}\frac{dN_1}{dt} &= \frac{r_1 N_1}{K_1} (K_1 - N_1 - \alpha_{12} N_2 - \beta_{12} N_1 N_2 - \delta_1 N_1^2), \\ \frac{dN_2}{dt} &= \frac{r_2 N_2}{K_2} (K_2 - \alpha_{21} N_1 - N_2 - \beta_{21} N_1 N_2 - \delta_2 N_2^2), \\ N_1(0) &= N_1^0 > 0, \quad N_2(0) = N_2^0 > 0\end{aligned}\quad (1.1)$$

The variables $N_1(t)$ and $N_2(t)$ represent the densities (numbers, mass, or even energy) of two competing species at time t for a common food supply, with r_i and α_{ij} representing the intrinsic growth rates and interspecific competition coefficients, respectively. The terms in $N_1 N_2$ suggest that there is an inhibiting effect on the growth of both species and the second order terms $-\delta_1 N_1^2$ and $-\delta_2 N_2^2$ mean self-interactions among members of the same species, other than sharing resources. An additional feature of this model is that the K 's do not represent the carrying capacities of the environment if $\delta_i > 0$. For instance, K_i are certain parameters whose values are independent of time. The prediction of the carrying ca-

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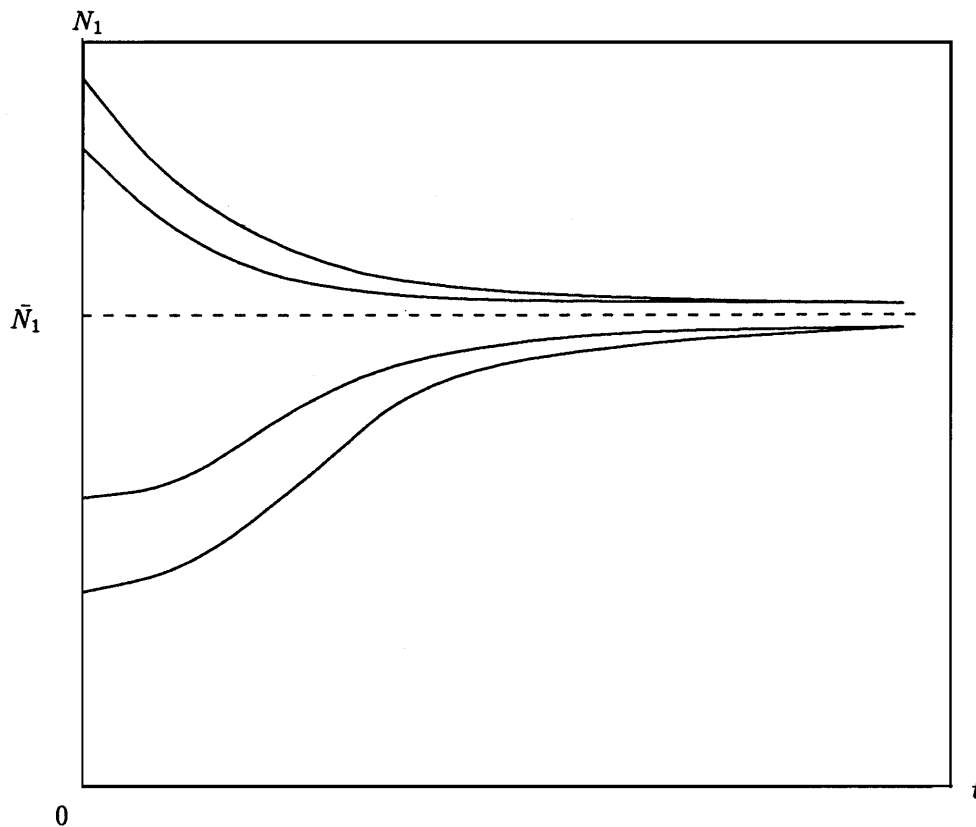


Fig. 1. Solution to generalized logistic differential equation for four values of initial population size.

capacities of system Eq. (1.1) will be discussed in the next section.

The system Eq. (1.1) represents one of many possible generalizations of the classical Gause-Lotka-Volterra model for two competing species, and was proposed by (Ayala et al., 1973) in experimental studies of interspecific competition with *Drosophila* species. For this system, (Ayala et al., 1973) showed by numerical analysis that two-species stable equilibria can also occur below the diagonal joining the carrying capacities of the two species; that is, when the competition between the species is unconditional. However, the global dynamical behavior of solutions to Eq. (1.1) in R_+^2 has not been proved.

For each species modelled in Eq. (1.1) for which $K_i > 0$ and $\delta_i > 0$, it follows that, in the absence of interspecific interactions, these species satisfy a generalized logistic growth equation of

the form

$$\frac{dN_i}{dt} = \frac{r_i N_i}{K_i} (K_i - N_i - \delta_i N_i^2), \quad i = 1, 2$$

In the Appendix we have shown that the solutions must look approximately like Fig. 1. On the other hand, if $\beta_{ij} = \delta_i = 0$, Eq. (1.1) becomes the classical Gause-Lotka-Volterra model of two competing species and it has long been known that the conditions $K_1/\alpha_{12} > K_2$ and $K_2/\alpha_{21} > K_1$ are necessary and sufficient for the existence of a stable equilibrium point of the system Eq. (1.1) such that both components are positive, and it attracts all solutions with initial values in the open first quadrant of the N_1, N_2 -plane (see, for example, Hofbauer and Sigmund, 1991). By using a suitable Lyapunov function (Chattopadhyay, 1996) investigated the local and global behavior of the competitive model (Eq. (1.1)) for $\delta_1 = \delta_2 = 0$.

In this paper we suggest a new way to approach the cubic system (Eq. (1.1)) based on the Liénard theory of ordinary differential equations. Our main result is a sufficient condition for the global asymptotic stability of the unique positive steady state. The significance of this result can be interpreted as a disproof of the principle of competitive exclusion (McGehee and Armstrong, 1977) or the inadequacy of the logistic equation formulation to analyse all cases of competition.

To prove the above claim, we transform (Eq. (1.1)) into a Liénard equation

$$\frac{d^2 X}{d\tau^2} + f(X) \frac{dX}{d\tau} + g(X) = 0 \quad (1.2)$$

or the equivalent planar system

$$\begin{aligned} \frac{dX}{d\tau} &= -V - F(X), \\ \frac{dV}{d\tau} &= g(X) \end{aligned} \quad (1.3)$$

where $F(X) = \int_0^X f(\xi) d\xi$; and we consider the Energy Function

$$E(X, V) = \frac{1}{2}V^2 + \int_0^X g(\mu) d\mu \quad (1.4)$$

as a natural Lyapunov function for Eq. (1.3).

Following the publication of (Ayala et al., 1973), a number of new competition models were suggested each of which differed from the Gause-Lotka-Volterra model in the important feature of isocline shape; and specially with regard to questions on coexistence or theoretical invalidation of the principle of competitive exclusion (see, for example, models 2, 3, 5, 6, 13, 16 and 17 in Table 1).

2. Phase plane analysis

In this section, we give the equilibria and isocline analysis of the system Eq. (1.1).

First, we note that there is a carrying capacity for each population, i.e. there are unique positive constants \bar{N}_1, \bar{N}_2 such that

$$K_1 = \bar{N}_1 + \delta_1 \bar{N}_1^2 \quad \text{and} \quad K_2 = \bar{N}_2 + \delta_2 \bar{N}_2^2 \quad (2.1)$$

that is, the number of N_i individuals that satisfies $dN_i/dt = 0$, $i = 1, 2$. Thus, in the absence of the second species, we would have $\lim_{t \rightarrow +\infty} N_1(t) = \bar{N}_1$. Similarly, in the absence of the first species, we should have $\lim_{t \rightarrow +\infty} N_2(t) = \bar{N}_2$ (see Appendix). The parameter \bar{N}_i is called the ‘carrying capacity’ of the environment for N_i , $i = 1, 2$.

In the remainder of this paper we will consider

$$\bar{N}_1 < K_2/\alpha_{21} \quad \text{and} \quad \bar{N}_2 < K_1/\alpha_{12} \quad (2.2)$$

The competitor isocline

$$K_1 - N_1 - \alpha_{12}N_2 - \beta_{12}N_1N_2 - \delta_1N_1^2 = 0 \quad (2.3)$$

defines a strictly decreasing continuous function $N_2 = \phi_1(N_1)$ on $[0, \bar{N}_1]$, such that $\phi_1(0) = K_1/\alpha_{12}$ and $\phi_1(\bar{N}_1) = 0$. Analogously, the isocline

$$K_2 - \alpha_{21}N_1 - N_2 - \beta_{21}N_1N_2 - \delta_2N_2^2 = 0 \quad (2.4)$$

defines a strictly decreasing continuous function $N_1 = \phi_2(N_2)$ on $[0, \bar{N}_2]$, such that $\phi_2(0) = K_2/\alpha_{21}$ and $\phi_2(\bar{N}_2) = 0$.

For instance, the function $N_2 = \phi_1(N_1)$ is a concave up on $[0, \bar{N}_1]$ if and only if

$$K_1\beta_{12}^2 + \alpha_{12}\beta_{12} - \delta_1\alpha_{12}^2 > 0 \quad (2.5)$$

with a similar condition for $N_1 = \phi_2(N_2)$:

$$K_2\beta_{21}^2 + \alpha_{21}\beta_{21} - \delta_2\alpha_{21}^2 > 0 \quad (2.6)$$

It is also easy to see that if Eq. (2.2) occurs, the isoclines $N_2 = \phi_1(N_1)$ and $N_1 = \phi_2(N_2)$ intersect in a point $E_4 := (N_1^*, N_2^*)$ in the first quadrant, i.e. the system Eq. (1.1) has at least one positive equilibrium. On the boundary of the positive quadrant the system has three equilibrium points: $E_1 := (0, 0)$, $E_2 := (\bar{N}_1, 0)$ and $E_3 := (0, \bar{N}_2)$. A simple linear stability analysis shows that E_1 is an unstable node, E_2 and E_3 are saddle points, attracting on the axes and repelling away from the axes, while E_4 is locally asymptotically stable if $\alpha_{12} < \beta_{12}/\beta_{21} < 1/\alpha_{21}$ holds.

In order to ensure the uniqueness of the positive equilibrium point $E_4 := (N_1^*, N_2^*)$, we define

$$C = \frac{1}{2}A\omega, \quad D = \frac{1}{4}\omega^2, \quad \text{and} \quad \omega = B - \frac{1}{4}A^2 \quad (2.7)$$

where

$$\begin{aligned} \gamma A &= \beta_{12}\beta_{21} - \delta_1\delta_2 + \beta_{12}(\delta_1 - \alpha_{21}\beta_{12}) \\ &\quad + \delta_1(\alpha_{12}\beta_{21} - \delta_2), \end{aligned}$$

Table 1
Models of interspecific competition

Model number	Autonomous systems	References
1	$N'_1 = N_1(b_1 - \alpha_{11}N_1 - \alpha_{12}N_2 - \alpha_{13}N_1N_2 - \alpha_{14}N_1^2 - \alpha_{15}N_2^2)$ $N'_2 = N_2(b_2 - a_{21}N_1 - a_{22}N_2 - a_{23}N_1N_2 - a_{24}N_1^2 - a_{25}N_2^2)$	Abdelkader, 1974 Abdelkader, 1982 Ayala et al., 1973 Chattopadhyay, 1996 Freedman, 1980 Gause, 1934 Lotka, 1925 Maynard Smith, 1974 Volterra, 1931
2	$N'_1 = N_1(b_1 - a_{11}\log N_1 - a_{12}\log N_2)$ $N'_2 = N_2(b_2 - a_{21}\log N_1 - a_{22}\log N_2)$	Gomatam, 1974
3	$N'_1 = \sqrt{N_1}(b_1 - a_{11}\sqrt{N_1} - a_{12}\sqrt{N_2})$ $N'_2 = \sqrt{N_2}(b_2 - a_{21}\sqrt{N_1} - a_{22}\sqrt{N_2})$	Arrigoni and Steiner, 1983
4	$N'_1 = N_1[b_1 - a_{11}N_1 - f(N_2)]$ $N'_2 = N_2[b_2 - g(N_1) - g_{21}N_2]$	Cunningham, 1955 Hutchinson, 1947
5	$N'_1 = N_1[b_1 - a_{11}N_1 - a_{12}N_2 - a_{13}((N_1N_2^2)^{2/3}/N_1)]$ $N'_2 = N_2[b_2 - a_{21}N_1 - a_{22}N_2 - a_{23}((N_2N_1^2)^{2/3}/N_2)]$	Utz and Waltman, 1963 Antonelli et al., 1992
6	$N'_1 = N_1(b_1 - a_{11}N_1^{\theta_1} - a_{12}N_2)$ $N'_2 = N_2(b_2 - a_{21}N_1 - a_{22}N_2^{\theta_2})$	Gilpin and Ayala, 1973 Goh, 1980
7	$N'_1 = N_1[b_1 - a_{11}N_1 - a_{12}N_2 - a_{13}(1 - e^{-a_{14}N_2})]$ $N'_2 = N_2[b_2 - a_{21}N_1 - a_{22}N_2 - a_{23}(1 - e^{-a_{24}N_2})]$	Wang Yuquan, 1989 Ayala et al., 1973
8	$N'_1 = N_1(b_1 - a_{11}N_1 - a_{12}N_2) - E$ $N'_2 = N_2(b_2 - a_{21}N_1 - a_{22}N_2) - F$	Brauer and Sanchez, 1975
9	$N'_1 = N_1(b_1 - a_{11}N_1 - a_{12}N_2) - b_2N_1$ $N'_2 = N_2(b_2 - a_{21}N_1 - a_{22}N_2) - b_4N_2$	Griffel, 1979 Chaudhuri, 1986
10	$N'_1 = N_1((b_1/N_1) - a_{11} - a_{12}N_1 - a_{13}N_2)$ $N'_2 = N_2(-a_{21} - (b_2/N_2) - a_{22}N_1 - a_{23}N_2)$	Kapur, 1980 Gilpin and Ayala, 1976
11	$N'_1 = N_1[b_1(N_1/N_1 + a_{11}N_2) - a_{12} - a_{13}N_1]$ $N'_2 = N_2[b_2(N_2/N_2 + a_{21}N_1) - a_{22} - a_{23}N_2]$	Kuno, 1992
12	$N'_1 = N_1[(1 - (N_1 + a_{12}N_2)/a_{13})/(1 - (N_1 + a_{12}N_2)/a_{14})]$ $N'_2 = N_2[(1 - (N_1 + a_{21}N_2)/a_{15})/(1 - (N_1 + a_{21}N_2)/a_{16})]$	Sun et al., 1991
13	$N'_1 = N_1(-a_{11} - a_{12}N_1 - a_{13}N_2 + (b_1/N_1 + b_2N_2))$ $N'_2 = N_2(-a_{21} - a_{22}N_1 - a_{23}N_2 + (b_3/N_1 + b_2N_2))$	Schoener, 1976
14	$N'_1 = N_1(b_1 - a_{11}N_1 - a_{12}N_2) - a_{13}((N_1 - N_2/N_1 + N_2))$ $N'_2 = N_2(b_2 - a_{21}N_1 - a_{22}N_2) - a_{23}((N_1 - N_2/N_1 + N_2))$	Messia et al., 1985
15	$N'_1 = N_1[(k - N_1 - N_2 - a_{12}N_2) - a_{13} - a_{14}N_2]$ $N'_2 = N_2[(k - N_1 - N_2 - a_{21}N_2) - a_{15} - a_{16}N_1]$	Sebens, 1987
16	$N'_1 = N_1[f_1(N_1) - f_2(N_2)]$ $N'_2 = N_2[-g_1(N_1) + g_2(N_2)]$	Brauer, 1974
17	$N'_1 = N_1f(N_1, N_2)$ $N'_2 = N_2g(N_1, N_2)$	Albrecht et al., 1974 Hirsch, 1982 Hirsch, 1985 Hirsch and Smale, 1974 Kigami, 1984 McGehee and Armstrong, 1977

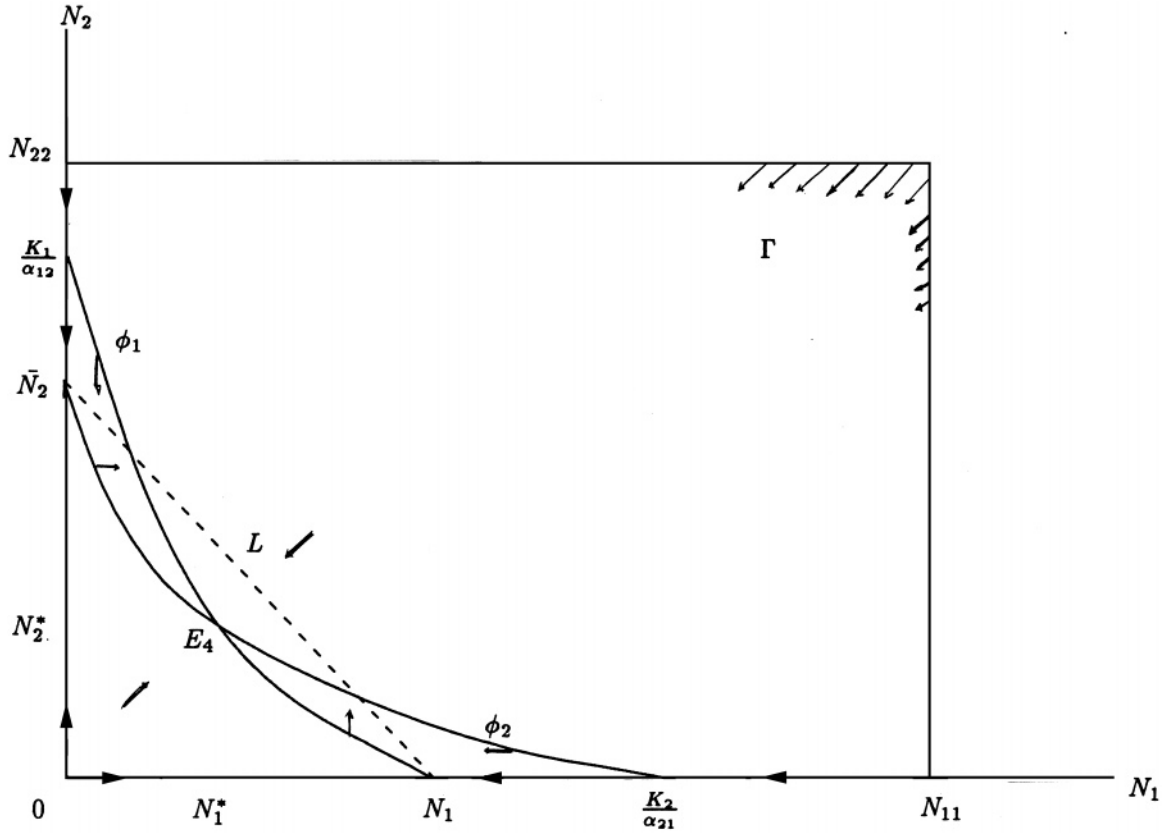


Fig. 2. Stable coexistence in unqualified competition, i.e. $N_1^*/N_1 + N_2^*/N_2 \leq 1$. The rectangle is compact and positively invariant. All trajectories approach $E_4 := (N_1^*, N_2^*)$ asymptotically as $t \rightarrow \infty$.

$$\begin{aligned} \gamma B &= \beta_{12} + 2K_1 - \delta_2 + \alpha_{12}(\beta_{21} + \delta_1 - 2\alpha_{21}\beta_{12}) \\ &\quad + \beta_{12}(K_2\beta_{12} - K_1\beta_{21}), \end{aligned}$$

$$\begin{aligned} \gamma C &= K_2\alpha_{12} + 2K_1\delta_2 - K_1 \\ &\quad + \alpha_{12}(1 + K_2\beta_{12} - \alpha_{12}\alpha_{21} - K_1\beta_{21}), \end{aligned}$$

$$\gamma D = \alpha_{12}(K_2\alpha_{12} - K_1) - K_1^2\delta_2,$$

$$\gamma = \delta_1(\beta_{12}\beta_{21} - \delta_1\delta_2) \quad (2.8)$$

The following algebraic result is fundamental in our analysis (see Fig. 2).

Theorem 2.1. Consider system Eq. (1.1) and let Eqs. (2.2), (2.3), (2.4), (2.5), (2.6), (2.7) and (2.8) hold. Further assume that $\omega > 0$ and $\gamma \neq 0$. Then system Eq. (1.1) has exactly one positive equilibrium point $E_4 := (N_1^*, N_2^*)$ with

$$N_1^* = \frac{-A + \sqrt{A^2 - 8\omega}}{4} \quad (2.9)$$

$$N_2^* = \frac{K_1 - N_1^* - \delta_1(N_1^*)^2}{\alpha_{12} + \beta_{12}N_1^*} \quad (2.10)$$

Proof. The existence of $E_4 := (N_1^*, N_2^*)$ in $\text{Int } \mathbb{R}_+^2$ follows from hypothesis Eq. (2.2). For E_4 to be unique, we note that N_1^* and N_2^* are the positive solution of the system of following algebraic equations:

$$K_1 - N_1 - \alpha_{12}N_2 - \beta_{12}N_1N_2 - \delta_1N_1^2 = 0,$$

$$K_2 - \alpha_{21}N_1 - N_2 - \beta_{21}N_1N_2 - \delta_2N_2^2 = 0$$

The first of these gives Eq. (2.10) which on substituting into the second gives N_1^* as roots of the quartic polynomial

$$P(N_1) = N_1^4 + AN_1^3 + BN_1^2 + CN_1 + D$$

where A , B , C and D are defined in Eq. (2.8). A little algebra shows that

$$P(N_1) = (N_1^2 + \frac{1}{2}AN_1 + \frac{1}{2}\omega)^2 + (C - \frac{1}{2}A\omega)N_1 + (D - \frac{1}{4}\omega^2)$$

From the hypothesis Eq. (2.7), we obtain

$$P(N_1) = (N_1^2 + \frac{1}{2}AN_1 + \frac{1}{2}\omega)^2$$

and this leads to N_1 , as indicated in Eq. (2.9). This completes the proof of the second assertion.

Remark 2.1. For general phase-plane analysis in mathematical models of competition between species, we refer to (Albrecht et al., 1974; Hirsch and Smale, 1974; Nunney, 1981; Rescigno and Richardson, 1967; Schoener, 1976; Vance, 1985 and Waltman, 1983).

3. Preliminary lemmas

In order to prove our main result we need the following lemmas:

Lemma 3.1. The closed rectangle $\Gamma \subset R_+^2$ with vertices $(0, 0)$, $(N_{11}, 0)$, $(0, N_{22})$, (N_{11}, N_{22}) is a positive invariant set of the system Eq. (1.1) for $N_{11} > \bar{N}_1$, $N_{22} > \bar{N}_2$.

Proof. For details and a proof, see (Hirsch and Smale, 1974) (pp. 270).

Lemma 3.2. Assume that Eq. (2.2) holds. Then Eq. (1.1) has no limit cycles in $\text{Int } \Gamma$.

Proof. Consider the function $M = 1/N_1N_2$ and calculate:

$$\begin{aligned} L &= \frac{\partial}{\partial N_1} \left(M \frac{dN_1}{dt} \right) + \frac{\partial}{\partial N_2} \left(M \frac{dN_2}{dt} \right) \\ &= -\frac{r_1}{K_1} \frac{1}{N_1} (1 + 2\delta_1 N_1 + \beta_{12} N_2) \\ &\quad - \frac{r_2}{K_2} \frac{1}{N_2} (1 + \beta_{21} N_1 + 2\delta_2 N_2) \end{aligned}$$

Since the parameters are positive, $L < 0$ over the domain of interest and the Dulac-Bendixson crite-

rion is satisfied. It follows then that there are no limit cycles in $\text{Int } \Gamma$ (see Zhang Zhi-fen et al., 1992, p. 195).

Remark 3.1. This result can also be obtained by using a monotonicity condition (for details, see Hirsch, 1982, 1985).

Lemma 3.3. Suppose the inequalities Eq. (2.2) hold. Then the system Eq. (1.1) can be transformed into an equation of Liénard type (Eq. 1.2) or the equivalent planar system Eq. (1.3).

Proof. First, we introduce the coordinates $X = N_1 - N_1^*$, $Y = N_2 - N_2^*$, in order to put the equilibrium point $E_4 := (N_1^*, N_2^*)$ in the origin. System Eq. (1.1) transforms into

$$\begin{aligned} \frac{dX}{dt} &= \frac{r_1(X + N_1^*)}{K_1} [K_1 - (X + N_1^*) - \alpha_{12}(Y + N_2^*) \\ &\quad - \beta_{12}(X + N_1^*)(Y + N_2^*) - \delta_1(X + N_1^*)^2], \\ \frac{dY}{dt} &= \frac{r_2(Y + N_2^*)}{K_2} [K_2 - \alpha_{21}(X + N_1^*) - (Y + N_2^*) \\ &\quad - \beta_{21}(X + N_1^*)(Y + N_2^*) - \delta_2(Y + N_2^*)^2] \end{aligned} \quad (3.1)$$

Now let

$$\begin{aligned} Z &= \frac{r_1(X + N_1^*)}{K_1} [K_1 - (X + N_1^*) - \alpha_{12}(Y + N_2^*) \\ &\quad - \beta_{12}(X + N_1^*)(Y + N_2^*) - \delta_1(X + N_1^*)^2] \end{aligned}$$

Then Eq. (3.1) becomes

$$\begin{aligned} \frac{dX}{dt} &= Z, \\ \frac{dZ}{dt} &= G_0(X) + G_1(X)Z + G_2(X)Z^2 + G_3(X)Z^3 \end{aligned} \quad (3.2)$$

where

$$\begin{aligned} G_0(X) &= -\frac{r_1 r_2}{K_1 K_2} (X + N_1^*) [K_1 - (X + N_1^*) - \delta_1(X + N_1^*)^2] \\ &\quad \times [K_2 - \alpha_{21}(X + N_1^*) - \phi_1(X + N_1^*) \\ &\quad - \beta_{21}(X + N_1^*)\phi_1(X + N_1^*) - \delta_2\phi_1^2(X + N_1^*)]; \end{aligned}$$

$$\begin{aligned}
G_1(X) &= \frac{r_2}{K_2} [K_2 - \alpha_{21}(X + N_1^*) - \phi_1(X + N_1^*) \\
&\quad - \beta_{21}(X + N_1^*)\phi_1(X + N_1^*) - \delta_2\phi_1^2(X + N_1^*)] \\
&\quad + \frac{r_1}{K_1} (X + N_1^*)[\alpha_{12} + \beta_{12}(X + N_1^*)]\phi_1'(X + N_1^*) \\
&\quad - \frac{r_2}{K_2} [1 + \beta_{21}(X + N_1^*)]\phi_1(X + N_1^*) \\
&\quad - \frac{2r_2\delta_2}{K_2} \phi_1^2(X + N_1^*); \quad (3.3)
\end{aligned}$$

$$\begin{aligned}
\frac{dX}{ds} &= U \\
\frac{dU}{ds} &= -H_0(X) - H_1(X)U - H_2(X)U^2 \quad (3.6)
\end{aligned}$$

where

$$\begin{aligned}
H_0(X) &= -\frac{G_0(X)}{\psi^2(X)}; \\
H_1(X) &= -\frac{G_1(X)\psi(X) + 3G_0(X)}{\psi^2(X)}; \\
H_2(X) &= \frac{G_3(X)\psi^3(X) - G_1(X)\psi(X) - 2G_0(X)}{\psi^2(X)} \quad (3.7)
\end{aligned}$$

$$G_2(X) = \frac{(r_1\alpha_{12}/K_1 + r_2/K_2) + (2r_1\beta_{12}/K_1 + r_2\beta_{21}/K_2)(X + N_1^*) + 3r_2\delta_2\phi_1(X + N_1^*)/K_2}{[r_1(X + N_1^*)/K_1][\alpha_{12} + \beta_{12}(X + N_1^*)]};$$

$$G_3(X) = -\frac{r_2\delta_2/K_2}{[r_1^2(X + N_1^*)^2/K_1^2][\alpha_{12} + \beta_{12}(X + N_1^*)]^2};$$

and $\phi_1(N_1)$ is the isocline obtained from (Eq. (2.3)), that is,

$$\phi_1(N_1) = \frac{K_1 - N_1 - \delta_1 N_1^2}{\alpha_{12} + \beta_{12} N_1}$$

Now we introduce the new transformation

$$U = \frac{Z}{\psi(X) - Z},$$

where

$$\begin{aligned}
\psi(X)\psi'(X) &= \sum_{i=0}^3 G_i(X)\psi^i(X), \quad \psi(X) \neq 0, \\
\psi(0) &> 0; \quad (3.4)
\end{aligned}$$

which when substituted into Eq. (3.2) gives

$$\begin{aligned}
\frac{dX}{dt} &= \frac{\psi(X)U}{1+U} \\
\frac{dU}{dt} &= \frac{1+2U}{\psi(X)} G_0(X) + G_1(X)U - \frac{\psi^2(X)}{1+U} G_3(X)U^2 \quad (3.5)
\end{aligned}$$

If now we introduce a new independent variable s by setting

$$\frac{dt}{ds} = \frac{1+U}{\psi(X)} > 0,$$

then from Eq. (3.5) we obtain

Finally, the substitution

$$\frac{ds}{d\tau} = \phi(X) = \exp\left[\int_0^X H_2(\eta)d\eta\right],$$

transforms Eq. (3.6) into the Liénard equation Eq. (1.2), where

$$f(X) = H_1(X)\phi(X) \quad \text{and} \quad g(X) = H_0(X)\phi^2(X) \quad (3.8)$$

This proves the lemma.

Remark 3.2. The change of variables used in this lemma can be found in Cherkas (1976, 1978) and Ye Yan-qian et al. (1986).

Remark 3.3. A survey of results and methods for planar Liénard-system (Eq. (1.3)) can be found in the books of Ye Yan-qian et al. (1986) and Zhang Zhi-fen et al. (1992); see also Cherkas (1977).

Lemma 3.4. Consider the Liénard-system Eq. (1.3). Assume that $f(X)$ and $g(X)$ are continuous functions satisfying

$$Xg(X) > 0 \text{ if } X \neq 0 \quad (3.9)$$

and

$$f(X) > 0 \text{ if } |X| \text{ is small enough} \quad (3.10)$$

Then the equilibrium $0 := (0, 0)$ of (Eq. (1.3)) is locally asymptotically stable.

Proof. Consider the positive definite function (Eq. (1.4)). From condition (Eq. (3.10)) we have

$$E'(X, V) = -g(X)F(X) < 0$$

Thus E is a strong Lyapunov function for (Eq. (1.3)); and the lemma follows by means of Lyapunov's direct method (e.g. see Hirsch and Smale, 1974).

4. Main result

We are now ready to prove our main result.

Theorem 4.1. Assume that (Eqs. (2.2)–(2.8)) hold. Then system (Eq. (1.1)) has a unique positive equilibrium $E_4 := (N_1^*, N_2^*)$ which is globally asymptotically stable with respect to all solutions initiating in $\text{Int } R_+^2$.

Proof. The existence and uniqueness of $E_4 := (N_1^*, N_2^*)$ follows directly from hypothesis (Eq. (2.2)) and Theorem 2.1. By Lemma 3.3, we know that the competitive model (Eq. (1.1)) can be transformed into Liénard's system (Eq. (1.3)) for which we have a local stability result of the equilibrium point $0 := (0, 0)$ given by Lemma 3.4. Thus, using the Poincaré-Bendixson theorem (Hirsch and Smale, 1974), Lemma 3.1 and 3.2, we need only to verify that the conditions (Eq. (3.9)) and (Eq. (3.10)) of Lemma 3.4 hold for the Liénard-system (Eq. (1.3)), when f and g are given as in (Eq. (3.8)).

First, we observe that (Eq. (3.9)) is equivalent to

$$\begin{aligned} & (N_1 - N_1^*)H_0(N_1 - N_1^*) \\ &= -\frac{(N_1 - N_1^*)G_0(N_1 - N_1^*)}{\psi^2(N_1 - N_1^*)} > 0, \quad N_1 \neq N_1^*, \end{aligned} \quad (4.1)$$

where

$$\begin{aligned} & G_0(N_1 - N_1^*) \\ &= -\frac{r_1 r_2}{K_1 K_2} N_1 [K_1 - N_1 - \delta_1 N_1^2] \\ & \quad \times [K_2 - \alpha_{21} N_1 - \phi_1(N_1) - \beta_{21} N_1 \phi_1(N_1) \\ & \quad - \delta_2 \phi_1^2(N_1)] \end{aligned}$$

By the usual isocline analysis in Section 2 and the uniqueness of $E_4 := (N_1^*, N_2^*)$, we have

$$G_0(N_1 - N_1^*) > 0 \quad \text{for} \quad 0 < N_1 < N_1^*$$

and

$$G_0(N_1 - N_1^*) < 0 \quad \text{for} \quad N_1^* < N_1 < \bar{N}_1$$

which implies Eq. (4.1); and respectively, Eq. (3.9).

We now note that Eq. (3.10) is equivalent to

$$H_1(0) > 0 \quad (4.2)$$

where

$$\begin{aligned} & \psi(0)H_1(0) = -G_1(0) \\ &= -\frac{r_1}{K_1} N_1^* (\alpha_{12} + \beta_{12} N_1^*) \phi_1'(N_1) \Big|_{N_1 = N_1^*} \\ & \quad + \frac{r_2}{K_2} (1 + \beta_{21} N_1^*) \phi_1(N_1^*) + \frac{2r_2}{K_2} \phi_1^2(N_1^*) \end{aligned}$$

Clearly, the right side of the equality is positive and using the fact that $\psi(0) > 0$, we obtain (Eq. (4.2)); and consequently (Eq. (3.10)). Thus the conditions of lemma 3.4 are satisfied and, our theorem is proved.

Remark 4.1. (Hirsch and Smale, 1974) (pp. 265–273) have proved this result only in the generic case without using Lyapunov function.

Remark 4.2. In the special case $\beta_{12} = \beta_{21} = 0$ the competitor isoclines are convex, and the equilibrium must occur above the straight line connecting the phase plane points $(\bar{N}_1, 0)$ and $(0, \bar{N}_2)$. That is, the stable equilibrium only occurs if the competition is 'qualified' (see Fig. 3).

5. The logistic case

In this section, we consider the system (Eq. (1.1)) when $\delta_1 = \delta_2 = 0$, namely

$$\begin{aligned} \frac{dN_1}{dt} &= \frac{r_1 N_1}{K_1} (K_1 - N_1 - \alpha_{12} N_2 - \beta_{12} N_1 N_2) \\ \frac{dN_2}{dt} &= \frac{r_2 N_2}{K_2} (K_2 - \alpha_{21} N_1 - N_2 - \beta_{21} N_1 N_2) \end{aligned} \quad (5.1)$$

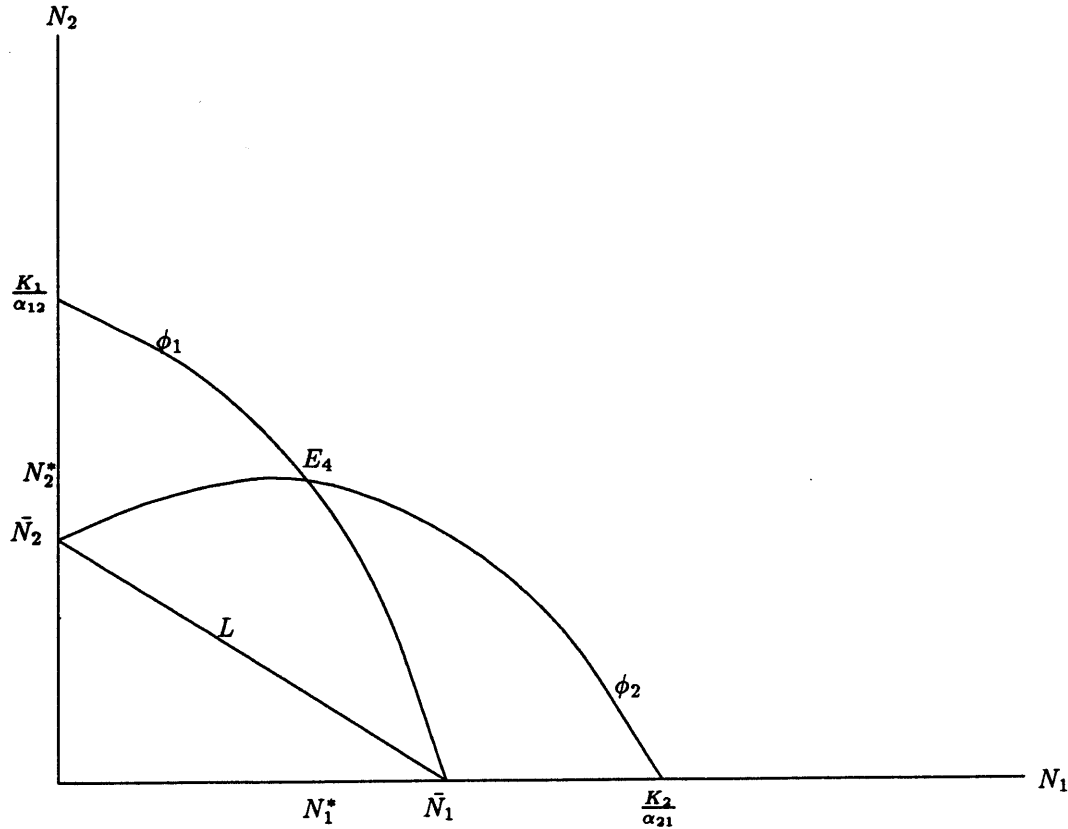


Fig. 3. The competitor isoclines are convex. The curves ϕ_1 and ϕ_2 cross at a stable equilibrium located above the straight line L connecting $(\bar{N}_1, 0)$ and $(0, \bar{N}_2)$.

We shall study (Eq. (5.1)) together with the following assumption

$$\alpha_{21} < K_2/K_1 < \beta_{21}/\beta_{12} < 1/\alpha_{12} \quad (5.2)$$

Under the preceding assumption one can show the existence of a unique interior equilibrium $E_4 := (N_1^*, N_2^*)$, where the isoclines

$$\phi_1(N_1) = \frac{K_1 - N_1}{\alpha_{12} + \beta_{12}N_1} \quad \text{and} \quad \phi_2(N_1) = \frac{K_2 - \alpha_{21}N_1}{1 + \beta_{21}N_1}$$

do intersect; or equivalently, there exists $N_1^*, N_2^* > 0$, such that

$$\begin{aligned} &(\alpha_{21}\beta_{12} - \beta_{21})(N_1^*)^2 \\ &+ (K_1\beta_{21} + \alpha_{12}\alpha_{21} - K_2\beta_{12} - 1)N_1^* + (K_1 - K_2\alpha_{12}) \\ &= 0 \end{aligned}$$

and

$$N_2^* = \frac{K_1 - N_1^*}{\alpha_{12} + \beta_{12}N_1^*}$$

Further, there are three other equilibria in the first quadrant, $E_1 := (0, 0)$; $E_2 := (K_1, 0)$; $E_3 := (0, K_2)$. E_1 is unstable, E_2 and E_3 are hyperbolic, attracting on the axis and repelling away from the axes (see Fig. 4).

We obtain the following result:

Theorem 5.1. Assume that (Eq. (5.2)) holds. Then $E_4 := (N_1^*, N_2^*)$ is a globally asymptotically stable equilibrium of (Eq. (5.1)).

Proof. We can rewrite (Eq. (3.2)) as

$$\begin{aligned} \frac{dX}{dt} &= Z \\ \frac{dZ}{dt} &= -G_0(X) - G_1(X)Z - G_2(X)Z^2 \end{aligned} \quad (5.3)$$

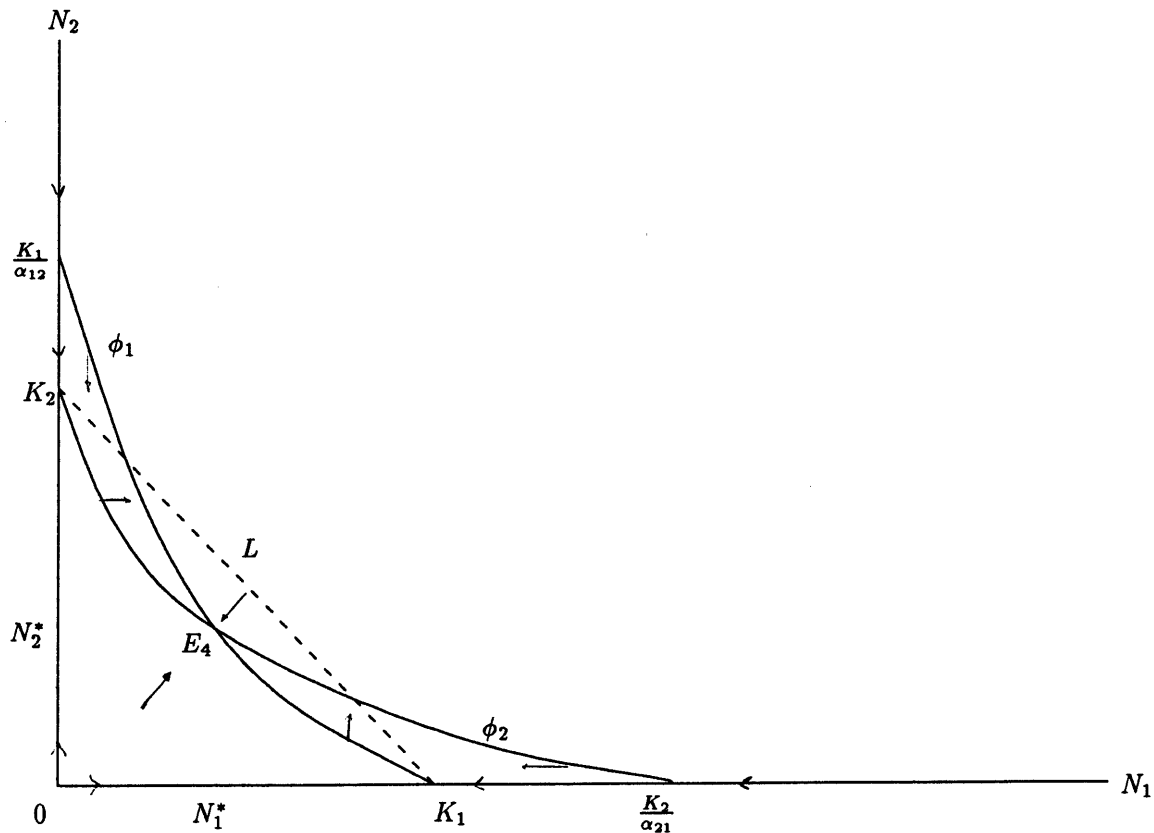


Fig. 4. Stable coexistence in unqualified competition, i.e. $N_1^*/K_1 + N_2^*/K_2 \leq 1$. All trajectories approach $E_4 = (N_1^*, N_2^*)$ asymptotically as $t \rightarrow \infty$.

where

$$G_0(X) = \frac{r_1 r_2}{K_1 K_2} (X + N_1^*) [K_1 - (X + N_1^*)] \\ \times [1 + \beta_{21}(X + N_1^*)] \\ \times [\phi_2(X + N_1^*) - \phi_1(X + N_1^*)];$$

$$G_1(X) \\ = -\frac{r_2}{K_2} [K_2 - \alpha_{21}(X + N_1^*) - \phi_1(X + N_1^*) \\ - \beta_{21}(X + N_1^*) \phi_1(X + N_1^*)] \\ - \frac{r_1}{K_1} (X + N_1^*) [\alpha_{12} + \beta_{12}(X + N_1^*)] \phi_1'(X + N_1^*) \\ + \frac{r_2}{K_2} [1 + \beta_{21}(X + N_1^*)] \phi_1(X + N_1^*);$$

$$G_2(X)$$

$$= -\frac{r_1 [\alpha_{12} + 2\beta_{12}(X + N_1^*)]/K_1 + r_2 [1 + \beta_{21}(X + N_1^*)]/K_2}{r_1 (X + N_1^*) [\alpha_{12} + \beta_{12}(X + N_1^*)]/K_1}$$

Introducing a new independent variable τ by setting

$$\frac{dt}{d\tau} = \pi(X) = \exp \left[\int_0^X G_2(\zeta) d\zeta \right],$$

i.e.

$$\frac{dt}{d\tau} = \pi(X) = \left[\frac{N_1^*}{X + N_1^*} \right]^{K_1 r_2 / K_2 r_1 \alpha_{12} + 1} \\ \left[\frac{\alpha_{12} + \beta_{12} N_1^*}{\alpha_{12} + \beta_{12}(X + N_1^*)} \right]^{K_1 r_2 (\alpha_{12} \beta_{21} - \beta_{12}) / K_2 r_1 + 1}$$

we obtain a Liénard-type system (Eq. (1.3)), where

$$f(X) = G_1(X)\pi(X)$$

$$g(X) = G_0(X)\pi^2(X)$$

From $(N_1 - N_1^*)G_0(N_1 - N_1^*) > 0$, $N_1 \neq N_1^*$, it is evident that

$$Xg(X) > 0, X \neq 0;$$

and from

$$\phi'_1(N_1)|_{N_1=N_1^*} < 0$$

it follows immediately that $G_1(0) > 0$ or $f(0) > 0$.

Thus the conditions (Eqs. (3.9) and (3.10)) are satisfied, and the theorem is proved.

Remark 5.1. Using a completely different method, Chattopadhyay (1996) was able to show the global stability of the interior equilibrium point $E_4 := (N_1^*, N_2^*)$.

6. Concluding remarks

The purpose of this article has been to introduce the elementary technique of Liénard's equation to establish conditions for the global asymptotic stability of the unique positive equilibrium point in the alternative Gause-Lotka-Volterra competitive system (Eq. (1.1)). Attempts to introduce second order differential equations in population dynamics modelling have been made in the past (see, for example, Bojadziev, 1983; Clark, 1971; Freedman, 1980; Ginzburgh, 1986; Innis, 1972). See also (Moreira, 1992) for an exhaustive survey of these results up to 1970.

Our main result says that two-species stable equilibria can also occur below the line L joining the carrying capacities of the two species, known as the region of 'strong mutual depression', whereas the Gause-Lotka-Volterra model does not; that is, coexistence is possible only above the line L . These analytical results point to the need for constructing theoretical models which will clarify the role of conditions for competitive coexistence in ecology and the controversial Gause's Principle or Principle of Competitive Exclusion (Armstrong and McGehee, 1980; McGehee and

Armstrong, 1977; Rescigno and Richardson, 1965). (Hutchinson, 1947), in reviewing the theory of competition between two species, summarized it with the statement: The mathematical difficulties encountered in such an elaboration of the theory are considerable. He then concluded that "... but it is hoped that they may be overcome at some future time".

To conclude this paper, by essentially the same argument as in the proof of Theorem 4.1, one can show global stability results for the more general competitive system:

$$\begin{aligned} \frac{dN_1}{dt} &= N_1g(N_1) - N_2p(N_1) \\ \frac{dN_2}{dt} &= N_2[K_2 - \alpha_{21}N_1 - \alpha_{22}N_2 - N_1h(N_2)] \end{aligned} \quad (6.1)$$

where

$$\begin{aligned} g(N_1) &= K_1 - \sum_{j=1}^n \alpha_{1j} N_1^j, \\ p(N_1) &= N_1 \sum_{k=0}^m \beta_{1k} N_1^k \\ h(N_2) &= \sum_{s=0}^2 \gamma_{1s} N_2^s \end{aligned} \quad (6.2)$$

We omit the proof to avoid repetition.

Appendix A

Consider the generalized logistic differential equation governing population growth:

$$\frac{dN_1}{dt} = \frac{r_1 N_1}{K_1} (K_1 - N_1 - \delta_1 N_1^2)$$

We can see that dN_1/dt is zero (horizontal) for $N_1 = 0$ and for $N_1 = \bar{N}_1 > 0$ where $K_1 = \bar{N}_1 + \delta_1 \bar{N}_1^2$.

We can also show that dN_1/dt is positive for $0 < N_1 < \bar{N}_1$ and negative for $N_1 > \bar{N}_1$.

To look at the solutions graphically, we want to consider the concavity which depends on the second derivatives. This we can get:

$$\frac{d^2 N_1}{dt^2} = \frac{r_1}{K_1} (K_1 - 2N_1 - 3\delta_1 N_1^2) \frac{dN_1}{dt}$$

We can show that d^2N_1/dt^2 is positive (concave upward) for $N_1 < N_1^0$, and that $\frac{d^2N_1}{dt^2}$ is negative (concave downward) for $N_1^0 < N_1 < \bar{N}_1$, where $K_1 = 2N_1^0 + 3\delta_1(N_1^0)^2$. The most important thing to notice is that $N_1(t) \rightarrow \bar{N}_1$ as $t \rightarrow +\infty$ (\bar{N}_1 is called the ‘carrying capacity’ of the environment). All this information fits together as illustrated in Fig. 1.

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