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Global Properties Of Selection Dynamics Model For N-Subspecies With Nonlinear Rate*

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Abstract

In this paper, we study the dynamics of n-subspecies selection function with nonlinear growth rate. Lyapunov functions for selection function are introduced, and global properties of the model are thereby established. We find that the conclusion "survival of the first, survival of all" still holds for the population with n-subspecies.

1 Introduction

It is well known that replication, selection, and mutation are the fundamental and defining principles of biological systems. Also these are the three basic building blocks of evolutionary dynamics. One type may reproduce faster and thereby outcompete the others [1]. Assume that there are n different types of subspecies in a population, and we label them $i = 1, 2, \dots, n$. Denote by $x_i(t)$ the frequency of type i, and by a_i the fitness of type i. Here, fitness is a non-negative real number and describes the rate of reproduction. Assume that their growth rates are non-linear functions of their frequencies. Thus the dynamics can be described by the following model

$$\dot{x_i} = a_i x_i^c - \phi x_i, \quad i = 1, 2, \dots, n, \tag{1}$$

where $c > 0$, and ϕ is the average fitness of the population given by

$$\phi = \sum_{i=1}^{n} a_i x_i^c. \tag{2}$$

Note that the total population size remains constant: $\sum_{i=1}^{n} x_i = 1$ and $\sum_{i=1}^{n} \dot{x_i} = 0$. First, we give the definition which satisfies this property.

DEFINITION 1. [2] The standard n-simplex is

$$\left\{ y \in \mathbf{R}^{n+1} : y_i > 0, i = 1, \dots, n; \sum_{i=0}^{n} y_i = 1 \right\}.$$

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Let Δ_n denote the closure of the standard n-simplex, called the standard closed n-simplex.

To bring the definition into correspondence with [1]. Let

$$S_n = \left\{ x = (x_1, \ldots, x_n) \in \mathbf{R}^n : x_i \geq 0, \sum x_i = 1 \right\}, \tag{3}$$

which means S_n is the standard closed $(n-1)$-simplex.

If $c = 1$, equation (1) contains a single globally stable equilibrium. Starting from any initial condition in the standard $(n-1)$-simplex, the population will converge to a corner point where but one type have become extinct. The winner k satisfies that $a_k > a_i$ for all $i \neq k$. The system shows competitive exclusion: the fittest type will outcompete all others, which is called "survival of the fittest". See [1].

In the case $c \neq 1$, if $c < 1$, then growth is subexponential. In the absence of the density limitation ϕ, the growth curve of each type would be slower than exponential. In contrast, if $c > 1$, then growth is superexponential. The growth curve of each type would be faster than exponential in the absence of the density limitation ϕ. For $n = 2$, Nowak [1] shows that the superexponential growth favors whoever was there first (survival of the first) whereas subexponential growth leads to the survival of all.

We do not know the dynamics of equation (1) if $c \neq 1$ and $n > 2$. Volterra-type Lyapunov function is widely used to consider the global dynamics of population models [8, 9, 10, 11, 12]. Motivated by the methods used in [3, 4, 5], in this article, we investigate this case using Lyapunov direct method. First of all, there is only one inner equilibrium $X_0 = (x_1^0, x_2^0, \ldots, x_n^0)$ which satisfies

$$a_1(x_1^0)^{c-1} = a_2(x_2^0)^{c-1} = \cdots = a_n(x_n^0)^{c-1}. \tag{4}$$

We only consider the inner points of S_n, and other points can be investigated in some lower dimensional simplex.

2 Case 1. $c < 1$

In the case $c < 1$, there is a global Lyapunov function which allows a straightforward investigating of global properties of the system (1). The following theorem holds for the system.

THEOREM 1. If $c < 1$, then every vertex is unstable; and the inner equilibrium X_0 is globally asymptotically stable.

PROOF. It is easy to check that the vertex is unstable. We then prove the second part. A Lyapunov function

$$V(x_1, x_2, \ldots, x_n) = \left(x_1 - x_1^0 \ln \frac{x_1}{x_1^0}\right) + \left(x_2 - x_2^0 \ln \frac{x_2}{x_2^0}\right) + \cdots + \left(x_n - x_n^0 \ln \frac{x_n}{x_n^0}\right) \tag{5}$$

satisfies

$$\begin{aligned}
\frac{dV}{dt} &= \left(\dot{x_1} - \frac{x_1^0}{x_1}\dot{x_1}\right) + \left(\dot{x_2} - \frac{x_2^0}{x_2}\dot{x_2}\right) + \cdots + \left(\dot{x_1} - \frac{x_n^0}{x_n}\dot{x_n}\right) \\
&= -\frac{x_1^0}{x_1}\dot{x_1} - \frac{x_2^0}{x_2}\dot{x_2} - \cdots - \frac{x_n^0}{x_n}\dot{x_n} \\
&= -x_1^0(a_1 x_1^{c-1} - \phi) - x_2^0(a_2 x_2^{c-1} - \phi) - \cdots - x_n^0(a_n x_n^{c-1} - \phi) \\
&= (x_1^0 + x_2^0 + \cdots + x_2^0)\phi - a_1 x_1^0 x_1^{c-1} - a_2 x_2^0 x_2^{c-1} - \cdots - a_n x_n^0 x_n^{c-1} \\
&= a_1 x_1^{c-1}(x_1 - x_1^0) + a_2 x_2^{c-1}(x_2 - x_2^0) + \cdots + a_n x_n^{c-1}(x_n - x_n^0) \\
&= a_1 x_1^{c-1}(x_1 - x_1^0) + a_2 x_2^{c-1}(x_2 - x_2^0) + \cdots + a_{n-1} x_{n-1}^{c-1}(x_{n-1} - x_{n-1}^0) \\
&\quad -a_n(1 - x_1 - \cdots - x_{n-1})^{c-1}[(x_1 - x_1^0) + \cdots + (x_{n-1} - x_{n-1}^0)].
\end{aligned}$$

Let

$$\begin{aligned}
f(x_1, \cdots, x_{n-1}) &= a_1 x_1^{c-1}(x_1 - x_1^0) + a_2 x_2^{c-1}(x_2 - x_2^0) + \cdots + a_{n-1} x_{n-1}^{c-1}(x_{n-1} - x_{n-1}^0) \\
&\quad -a_n(1 - x_1 - \cdots - x_{n-1})^{c-1}[(x_1 - x_1^0) + \cdots + (x_{n-1} - x_{n-1}^0)].
\end{aligned}$$

Computing the partial derivative of f on x_1,

$$\begin{aligned}
\frac{\partial f}{\partial x_1} &= a_1(c-1)x_1^{c-1}(x_1 - x_0) + a_1 x_1^{c-1} - a_n(1 - x_1 - x_2 - \cdots - x_{n-1})^{c-1} \\
&\quad +a_n(c-1)(1 - x_1 - \cdots - x_{n-1})^{c-2}[(x_1 - x_1^0) + \cdots + (x_{n-1} - x_{n-1}^0)].
\end{aligned}$$

Hence, we have

$$\frac{\partial f}{\partial x_1}|_{(x_1^0, x_2^0, \ldots, x_{n-1}^0)} = a_1(x_1^0)^{c-1} - a_n(x_n^0)^{c-1} = 0.$$

Computing the second partial derivative of f on x_1,

$$\begin{aligned}
\frac{\partial^2 f}{\partial x_1^2} &= a_1(c-1)(c-2)x_1^{c-3}(x_1 - x_1^0) + 2a_1(c-1)x_1^{c-2} \\
&\quad +a_n(c-1)(c-2)x_n^{c-3}(x_n - x_n^0) + 2a_n(c-1)x_n^{c-2} \\
&= a_1 c(c-1)x_1^{c-2} - a_1(c-1)(c-2)x_0 x_1^{c-3} + a_n c(c-1)x_n^{c-2} \\
&\quad -a_n(c-1)(c-2)x_n^0 x_n^{c-3} \\
&< 0,
\end{aligned}$$

and computing the second partial derivative of f on x_j,

$$\begin{aligned}
\frac{\partial^2 f}{\partial x_1 \partial x_j} &= 2a_n(1 - x_1 - x_2 - \cdots - x_{n-1})^{c-1} \\
&\quad -a_n(c-1)(c-2)(1 - x_1 - \cdots - x_{n-1})^{c-3}[(x_1 - x_1^0) + \cdots + (x_{n-1} - x_{n-1}^0)] \\
&= 2a_n(c-1)x_n^{c-2} + a_n(c-1)(c-2)x_n^{c-3}(x_n - x_n^0) \\
&= a_n c(c-1)x_n^{c-2} - a_n(c-1)(c-2)x_n^0 x_n^{c-3} \\
&< 0,
\end{aligned}$$

where $j = 2, 3, ..., n-1$. Let

$$A_i = a_i c(c-1)x_i^{c-2} - a_1(c-1)(c-2)x_0 x_i^{c-3}$$

and

$$B = a_n c(c-1)x_n^{c-2} - a_n(c-1)(c-2)x_n^0 x_n^{c-3},$$

where $i = 1, 2, ..., n-1$. Then $A_i < 0$, $B < 0$, and

$$\frac{\partial^2 f}{\partial x_1^2} = A_1 + B, \quad \frac{\partial^2 f}{\partial x_1 \partial x_j} = B,$$

where $i = 1, 2, ..., n-1$ and $j = 2, 3, ..., n-1$.

In a similar way, we have that

$$\frac{\partial f}{\partial x_i}|_{(x_1^0, x_2^0, \ldots, x_{n-1}^0)} = 0, \tag{6}$$

$$\frac{\partial^2 f}{\partial x_i^2} = A_i + B \quad \text{and} \quad \frac{\partial^2 f}{\partial x_i \partial x_j} = B,$$

for $i = 2, \ldots, n-1$, $j = 1, 2, ..., n-1$, and $i \neq j$. So we conclude the Hessian of $f(x_1, x_2, \ldots, x_{n-1})$ is

$$H(f) = \begin{pmatrix} A_1 + B & B & \cdots & B \\ B & A_1 + B & \cdots & B \\ \vdots & \vdots & \ddots & \vdots \\ B & B & \cdots & A_1 + B \end{pmatrix} \tag{7}$$

Since $A_i < 0$ and $B < 0$ for $i = 2, \ldots, n-1$, we can obtain that all the eigenvalues of $H(f)$ are negative. Therefore, X_0 is the only extremum point of f inside S_n, and it is a maximum point. $f(x_1^0, x_2^0, \cdots, x_{n-1}^0) = 0$. Now we will prove that X_0 is the greatest point inside S_n.

It is easy to find that 0 is the greatest value for $n = 2$. For $n = 3$, we also have that X_0 is the greatest point because S_2 is the boundary of S_3, hence by induction, X_0 is the only greatest point inside S_n. So we have that

$$\frac{dV}{dt} = f(x_1, x_2, \cdots, x_{n-1}) \leq f(x_1^0, x_2^0, \cdots, x_{n-1}^0) = 0,$$

for all $(x_1, x_2, \cdots, x_n)$ inside S_n.

This completes the proof of Theorem 1.

3 Case 2. $c > 1$

In this case, let

$$\Omega_i = \{(x_1, x_2, \ldots, x_n) \in S_n | \ a_i x_i^c - \phi x_i > 0\}. \tag{8}$$

For the dynamics of (1) in this case, we have the following theorem.

THEOREM 2. If $c > 1$, then every vertex is locally asymptotically stable and the attractive basin of vertex i is Ω_i; the inner equilibrium X_0 is unstable.

PROOF. For the first part, without loss of generality, we may only check the vertex $(1, 0, \ldots, 0)$. We can use the Lyapunov function

$$V(x_1, x_2, \ldots, x_n) = (x_1 - \ln x_1) + x_2 + \cdots + x_n. \tag{9}$$

The Lyapunov function V satisfies

$$\begin{aligned} \frac{dV}{dt} &= (\dot{x_1} - \frac{\dot{x_1}}{x_1}) + \dot{x_2} + \cdots + \dot{x_n} \\ &= (\dot{x_1} + \dot{x_2} + \cdots + \dot{x_n}) - (a_1 x_1^{c-1} - \phi) \\ &= -x_1^{-1}(a_1 x_1^c - \phi x_1) \\ &< 0, \end{aligned}$$

for $(x_1, x_2, \ldots, x_n) \in \Omega_1$.

Suppose that $\overline{\Omega}_i$ is the closure of Ω_i, namely,

$$\overline{\Omega}_i = \{(x_1, x_2, \ldots, x_n) \in S_n : a_i x_i^c - \phi x_i\} \geq 0.$$

Because $\bigcup_{i=1}^n \overline{\Omega}_i = S_n$, it is obvious that the inner equilibrium X_0 is unstable.

This completes the proof of Theorem 2.

4 Remarks

A Volterra-type Lyapunov function has been used in this note to prove global stability of the positive equilibrium. We know that the replicator equation in n variables is equivalent to the Lotka-Volterra equation in $n-1$ variables [3]. Equation (1) can also be written in "replicator" form

$$\dot{x_i} = x_i(a_i x_i^{c-1} - \phi), i = 1, 2, \ldots, n. \tag{10}$$

The difference between equation (1) and replicator equation is that the growth rate of i (or payoff to strategy i) is given by a nonlinear function of its frequency, which has nothing to do with other subspecies. This means that equation (1) doesn't take into account the interactions within the population. Thus equation (1) can be used as an example of the replicator equation with non-linear payoff functions.

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