数理解析研究所講究録
第 1597 巻 2008 年 111-117

A mathematical analysis in discrete transition system.

Hokkaido University Takenori Takada
Hokkaido University Takashi Kohyama
Ritusmeikan University Hisao Nakajima

Introduction

It is well known that forest community is consisted of multiple layers of tree populations, from shrubs to taller tree species; especially, tropical forests have 3 or 4 layers with 30 to 50 meters tall. Individuals of the same species also occupy the different layers as they grow up from seedlings or saplings to mature trees. They transit from lower layer to middle and top layer during their lifetime. Therefore, dynamics of multi-layer population can be described as the transitions among discrete layers, using variables which represent the number of individuals at each layer. In this paper, we constructed discrete transition system and examined the local stability of the equilibrium of the system. The preceding studies examined the local stability of the two-layer system and obtained several theorems on permanence and persistence (Thieme (2003), Baer et al.(2006)). We extended the system to three-layered one and discussed about the relationship between local stability and the pattern of interaction among individuals at different layers. We showed that one-sided interaction (or asymmetric competition) through light resource promotes the stability of tree populations.

Two-layer transition system

A species is distributed both in the lower and upper layer and the number of individuals at lower and upper layer are denoted as x_1 and x_2, respectively. The new-born individuals are recruited into only the lower layer with fecundity function $f(x_1,x_2)$, and individuals step up from the lower to upper layer when they grow up with growth rate function $g(x_1,x_2)$. Only the upper-layer individuals reproduce the new-born individuals. The mortality rate functions of lower- and upper-layer individuals are denoted as $m_1(x_1,x_2)$ and $m_2(x_1,x_2)$, respectively. Then, discrete transition system can be written as:

$$\begin{cases} \dfrac{dx_1}{dt} = f(x_1,x_2)\,x_2 - g(x_1,x_2)\,x_1 - m_1(x_1,x_2)\,x_1 \\ \dfrac{dx_2}{dt} = g(x_1,x_2)\,x_1 - m_2(x_1,x_2)\,x_2 \end{cases} , \qquad (1)$$

where the first derivatives of $f(x_1,x_2)$ and $g(x_1,x_2)$ with respect to x_i are non-positive and that of $m_i(x_1,x_2)$ is non-negative because of the negative density effect.

Therefore, the system has always (0,0) and positive equilibria as long as the density effect is operated, and the number of positive equilibria depends on the functional forms of vital rate functions. Zero equilibrium is unstable, as far as

$$f(0,0)\frac{g(0,0)}{g(0,0)+m_1(0,0)} > m_2(0,0) \ . \qquad (2)$$

Under the condition (2), we examined the local stability of the positive equilibrium without specifying the functional forms of vital rates. The biological constraints of those functions are:

$$f(x_1,x_2), g(x_1,x_2), m_i(x_1,x_2) > 0 \ \text{ and } \ \frac{\partial f}{\partial x_j} \le 0, \frac{\partial g}{\partial x_j} \le 0, \frac{\partial m_i}{\partial x_j} \ge 0 . \qquad (3)$$

(i) The mode of density-dependence

The modes of density-dependence, i.e. interaction among individuals, are also defined, using the first derivative of a function with respect to stage variables. Suppose that mortality rate function of lower-layer individuals depends negatively on only the number of upper-layer individuals, which means one-sided interaction by taller individuals. Then,

$$\frac{\partial m_1}{\partial x_2} > 0 \text{ and } \frac{\partial m_1}{\partial x_1} = 0 \ \text{ (One-sided interaction).}$$

On the other hand, mortality rate function of upper-layer individuals depends negatively on only the number of lower-layer individuals, which means inverse one-sided interaction by lower individuals (we, hereafter, call it "revolution").

Then,

$$\frac{\partial m_2}{\partial x_1} > 0 \text{ and } \frac{\partial m_2}{\partial x_2} = 0 \ \text{ (Revolution).}$$

If a function depends both on lower- and upper-layer individuals, it is called both-sided interaction as:

$$\frac{\partial m_2}{\partial x_1} > 0 \text{ and } \frac{\partial m_2}{\partial x_2} > 0 \quad \text{(Both-sided interaction).}$$

(ii) Single density effect

We firstly examine the single density effect on the local stability of positive equilibrium. If only a vital rate function (h) depends on only one variable, we call it "single" density effect. It also means other vital rate functions are constant and density-independent. There are four vital rate functions and two variables in two-layer transition system. Therefore, we analyzed eight kinds of the systems with single density effect (Table 1).

We constructed the Jacobian matrix at the positive equilibrium to examine the local stability and evaluated the signs of the trace and the determinant, using the signs of vital rate functions (positive) and the derivatives (zero when it is constant or negative when it is density dependent). If the trace is always negative and the determinant is always positive, the positive equilibrium is always stable and never unstable irrespective of the specific functional forms of vital rate functions. If the sign of either the trace or the determinant is not definite, it means the equilibrium could be unstable depending on the strength of the density-dependence of the function in question or the parameters.

In Table 1, most of the single density effects lead to the stability of positive

Variables	Fecundity (f)	Mortality at lower (m_1)	Growth rate (g)	Mortality at upper (m_2)
Lower X_1	Stable	Stable	Unstable (Revolution)	Stable (Revolution)
Upper X_2	Stable (One-sided)	Stable (One-sided)	Stable	Stable

Table 1 The result of single density effect for local stability of positive equilibrium. "Stable" in the cells means the positive equilibrium is never unstable irrespective of the strength of density-dependence and "Unstable" does the equilibrium could be unstable depending on the strength of density-dependence.

equilibrium. Only the density effect by the number of lower individuals on the growth rate function could be the cause of the instability.

(iii) Multiple density effects

In general, the system (1) has several density effects at the same time. In some cases, the fecundity function depends both on x_1 and x_2. In other cases, the fecundity function depends on x_1 and the growth rate function depends on x_2. We analyzed the local stability analysis in such multiple density effects. The number of the combinations of density-dependence of the vital rates functions is 2^8-1 (Table 2). We constructed a computer program to examine the local stability of the positive equilibrium. In the program, we evaluated the signs of the trace and the determinant of the Jacobian, only using the signs of

Functions	Fecundity		Mortality at L		Growth rate		Mortality at U		Stability
Variables	Lower	Upper	Lower	Upper	Lower	Upper	Lower	Upper	
Single effect	Yes	–	–	–	–	–	–	–	Stable
	–	Yes	–	–	–	–	–	–	Stable
	–	–	Yes	–	–	–	–	–	Stable
	–	–	–	Yes	–	–	–	–	Stable
	–	–	–	–	Yes	–	–	–	Unstable
	–	–	–	–	–	Yes	–	–	Stable
	–	–	–	–	–	–	Yes	–	Stable
	–	–	–	–	–	–	–	Yes	Stable
Multiple effects	*	*	*	*	Yes	*	*	*	Unstable
	*	*	*	Yes	*	*	Yes	*	Unstable
	*	Yes	*	*	*	*	Yes	*	Unstable
	Other combinations								Stable

Table 2 The result of multiple density effects for local stability of positive equilibrium. "Yes" in the cells represents the density dependence by a variable in question. The hyphen represents no density-dependent effect. "*" represents the wild card of either "Yes" or hyphen.

vital rate functions and the derivatives.

In Table 2, the result of single density effect is also represented in the former part of the table, which shows the same result as in Table 1. In the cases of multiple density effects, two types of instability could occur. One is the case where the density dependence of growth rate function by x_1 (revolution factor). The other cause is the density dependence of mortality rate function by x_1 (revolution factor) when coupled wiith $\frac{\partial f}{\partial x_2} < 0$ or $\frac{\partial m_1}{\partial x_2} > 0$. Therefore, if two revolution factors are removed, the system is always stable. Summarizing the result of two-layer system, the positive equilibrium is never unstable if there is no "revolution".

Three-layer transition system

The same analysis was conducted in three-layer transition system. The discrete transition system can be written as:

$$\begin{cases} \frac{dx_1}{dt} = f(\mathbf{x})\,x_3 - g_1(\mathbf{x})\,x_1 - m_1(\mathbf{x})\,x_1 \\ \frac{dx_2}{dt} = g_1(\mathbf{x})\,x_1 - g_2(\mathbf{x})\,x_2 - m_2(\mathbf{x})\,x_2 \\ \frac{dx_3}{dt} = g_2(\mathbf{x})\,x_2 - m_3(\mathbf{x})\,x_3 \end{cases} \qquad \mathbf{x} = (x_1, x_2, x_3) \ . \tag{4}$$

Therefore, the system has always zero and positive equilibria as long as the density effect is operated, and the number of positive equilibria depends on the functional forms of vital rate functions. Under the condition (2), we examined the local stability of the positive equilibrium without specifying the functional forms of vital rates.

(i) Single density effect

We firstly examine the single density effect on the local stability of positive equilibrium. There are six vital rate functions and three variables in three-layer transition system. Therefore, we analyzed local stabilities of 18 kinds of the systems with single density effect (Table 3).

In Table 3, 6 kinds of single density effects lead to the instability of positive equilibrium. Four kinds of single density effects are "Revolution" type and the other two are "one-sided interaction" type.

(ii) Multiple density effects

We also analyzed the local stability analysis in the multiple density effects. The number of the

Variables	Fecun-dity (f)	Mortality at lower (m_1)	Growth at lower (g_1)	Mortality at middle (m_2)	Growth at middle (g_2)	Mortality at upper (m_3)
Lower x_1	Stable	Stable	Unstable (Revolution)	Unstable (Revolution)	Stable (Revolution)	Stable (Revolution)
Middle x_2	Stable (One-sided)	Stable (One-sided)	Stable	Stable	Unstable (Revolution)	Unstable (Revolution)
Upper x_3	Unstable (One-sided)	Unstable (One-sided)	Stable (One-sided)	Stable (One-sided)	Stable	Stable

Table 3 The result of single density effects in three-layer transition system.

---

combinations of density-dependence of the vital rates functions is $2^{18}-1$ (262,143). We examined the local stability of the positive equilibrium, using the program to evaluate the signs of the trace and the determinant. The result clarifies three types of causes for instability. The first cause is a single density effect that leads to the instability. If the combination of density effect includes the single density effect, it always causes the instability. The second is a density effect on growth rate at middle layer by lower individuals. The density effect could be the cause of instability when coupled with one or more of the following density-dependence:

$$\frac{\partial f}{\partial x_2}<0, \frac{\partial m_1}{\partial x_2}>0, \frac{\partial g_1}{\partial x_2}<0, \frac{\partial g_1}{\partial x_3}<0, \frac{\partial m_2}{\partial x_3}>0, \frac{\partial g_2}{\partial x_3}<0 \qquad (5).$$

The third is a density effect on mortality rate at upper layer by lower individuals. The density effect could be the cause of instability when coupled with one or more of the inequalities (5). Summarizing the result in three-layer system, the positive equilibrium could be unstable even if there is no "revolution".

References

Baer, S.M., Kooi, B. W. , Kuznetsov, YU. A. and Thieme, H. R. (2006) Multiparametric bifurcation analysis of a basic two-stage population model. SIAM J Appl. Math 66: 1339-1365.

Thieme, H.R. (2003) Mathematics in Population Biology. Princeton University Press.