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GLOBAL STABILITY IN A MODEL OF SINGLE-SPECIES POPULATION DYNAMICS IN A PERIODIC PATCHY ENVIRONMENT

TRINH TUAN ANH

ABSTRACT. We consider a model of single-species population dynamics in a periodic patchy environment and prove a sufficient condition for the existence of a globally asymptotically stable, strictly positive (component-wise) and periodic solution.

1. INTRODUCTION

The purpose of this paper is to study the stability of a system of nonautonomous ordinary differential equations which models the growth of a single-species population distribution over n $(n > 1)$ patches (islands or habitats) and allows for population dispersing from one to the others. This work may be throught of as a continuation of the work in [1-4, 6] where the autonomous case was considered.

The model considered in this paper is described by the following system of nonautonomous ordinary differential equations:

(1.1)

$$\dot{u}_i = u_i g_i(t, u_i) - \varepsilon_i(t) h_i(t, u_i) + \sum_{\substack{j=1 \\ j \neq i}}^{n} d_{ij}(t) \varepsilon_j(t) h_j(t, u_j), \quad i = 1, 2, \ldots, n,$$

where $g_i,\ h_i : R \times [0, +\infty) \to R$ are continuous and T-periodic in the t-variable $(T > 0)$; $\varepsilon_i,\ d_{ij}(i \neq j) : R \to R$ are continuous and T-periodic; $u_i(t)$ represents the population density of the species in the i^{th} patch at time t.

The above model is a natural generalization of the autonomous case describing the growth of the prey-population in Freedman and Takeuchi [4]. Further assumptions on the functions of the system (1.1) are given

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below, which are based on those in [4].

The function $g_i(t, u_i)$ represents the specific growth rate of the population in the i^{th} patch at time t. Due to limited resources at time t, $g_i(t, .) > 0$ if the environment is underpopulated and $g_i(t, .) < 0$ if the environment is overpopulated. Furthermore, we suppose that the growth rate slows down as population increases. Therefore the following assumptions are made on $g_i(t, u_i)$:

(H_1) $g_i(t, 0) > 0$ and $g_i(t, .)$ is strictly decreasing for any fixed $t \in [0, T]$. Moreover, there exists a positive number K_i such that $g_i(t, K_i) < 0$ for any $t \in [0, T]$.

The hypothesis (H_1) is standard in single-species models [2, 4, 6].

The function $h_i(t, u_i)$ represents the pressure or desire for the population to leave the i^{th} patch and seek another patch in the total environment at time t. Clearly, pressure to disperse increases with increasing population. Hence we assume:

(H_2) $h_i(t, 0) = 0$ and $h_i(t, .)$ is increasing for any fixed $t \in [0, T]$.

$\varepsilon_i(t)$ is an inverse barrier strength at time t. If $\varepsilon_i(t) = 0$ then the population may not leave the i^{th} patch at time t.

(H_3) $\varepsilon_i(t) \geq 0$ for any $t \in [0, T]$.

$d_{ij}(t)$ $(1 \leq i,\ j \leq n,\ i \neq j)$ is the probability that a given member of the population, having left the j^{th} patch, will arrive safely at the i^{th} patch at time t. Clearly

$$(H_4)\ 0 \leq d_{ij}(t) \leq 1,\ \sum_{\substack{i=1 \\ i \neq j}}^{n} d_{ij}(t) \leq 1, \text{ for any } t \in [0, T].$$

The following assumption is needed for technical mathematical reasons:

(H_5) The functions $g_i(t, u_i)$, $h_i(t, u_i)$ are locally Lipschitzian in u_i, uniformly in t, i.e., for each $u_i \in R_+$ there are numbers $\delta > 0$, $L > 0$ such that $|g_i(t, u_i) - g_i(t, \overline{u}_i)| \leq L|u_i - \overline{u}_i|$ for u_i, $\overline{u}_i \in R_+ : |u_i - \overline{u}_i| \leq \delta$ and $t \in R$; and similarly for h_i.

Our goal is to establish a criterion for the existence of a strictly positive (componentwise) T-periodic solution of (1.1) and to investigate its stability character in the case $h_i(t, u_i) = k_i(t)u_i$ $(1 \leq i \leq n)$.

In the next section we present some basic properties of the system (1.1). The third section is devoted to prove the existence and the global stability of a strictly positive T-periodic solution.

2. Preliminaries

First, we see that the Cauchy problem for (1.1) with the initial condition $u(t_0) = u_0 \in R^n_+$ has a unique forward solution. Indeed, the case $u(t_0) =$

$u_0 \in \mathrm{int}(R_+^n)$ is trivial, since we know from (H_5) that the right hand side function of (1.1) is locally Lipschitzian in u, uniformly in t. The case $u(t_0) = u_0 \in \partial R_+^n$ can be showed as follows. Setting $F : R \times R_+^n \to R^n$ with

$$F_i(t,u) = u_i g_i(t,u_i) - \varepsilon_i(t) h_i(t,u_i) + \sum_{\substack{j=1 \\ j\neq i}}^{n} d_{ij}(t)\varepsilon_j(t) h_j(t,u_j), \qquad i = 1,2,\dots,n.$$

Let $U_\varepsilon(R_+^n) = \{u \in R^n : d(u,R_+^n) < \varepsilon\}$, where $d(u,R_+^n) = \inf_{\overline{u}\in R_+^n} \|\overline{u} - u\|$, and $\varepsilon > 0$. It is easy to see that for each $u \in U_\varepsilon(R_+^n) \setminus R_+^n$ there exists uniquely $\overline{u} \in \partial R_+^n$ such that $d(u,R_+^n) = \|\overline{u} - u\|$. Let $\overline{F}(t,u)$ be the extension of $F(t,u)$ on $R \times U_\varepsilon(R_+^n)$ such that for $u \in U_\varepsilon(R_+^n) \setminus R_+^n$ we have $\overline{F}(t,u) = F(t,\overline{u})$, where $\overline{u} \in \partial R_+^n$ such that $d(u,R_+^n) = \|\overline{u} - u\|$. Then, by (H_5), $\overline{F}(t,u)$ is locally Lipschitzian in $u \in U_\varepsilon(R_+^n)$, uniformly in t. Therefore, the Cauchy problem

$$\dot{u} = \overline{F}(t,u), \tag{2.1}$$

$$u(t_0) = u_0 \in U_\varepsilon(R_+^n), \tag{2.2}$$

has a unique solution. Since $\overline{F}_i(t,u) = F_i(t,u) \geq 0$ for $u \in \partial R_+^n$ with $u_i = 0$, it follows that R_+^n is positively invariant with respect to (2.1). Therefore, the Cauchy problem for (1.1) with the initial condition $u(t_0) = u_0 \in \partial R_+^n$ has a unique forward solution.

The boundedness of the solutions to (1.1) is shown by the following lemma.

Lemma 2.1. *There exists $K > 0$ such that*

$$\mathcal{A} = \{(u_1,\dots,u_n) \in R_+^n : 0 \leq u_i \leq K,\ 1 \leq i \leq n\}$$

is positively invariant and strongly attractive with respect to R_+^n.

Proof. Denote

$$L = \max_{1\leq i\leq n} \{K_i\}, \quad a = \sup_{\substack{0\leq t\leq T \\ 1\leq i\leq n}} \{g_i(t,0)\}, \quad b = \sup_{\substack{0\leq t\leq T \\ 1\leq i\leq n}} \{g_i(t,L)\},$$

$$K = \left(1 - \frac{a}{b}\right) \sum_{i=1}^{n} K_i.$$

It follows from (H_1) that $a > 0$, $b < 0$ and $K > L$.

We shall prove that $\mathcal{A} = \{(u_1, \ldots, u_n) \in R_+^n : 0 \le u_i \le K,\ 1 \le i \le n\}$ is positively invariant and strongly attractive with respect to R_+^n. If $u \notin \mathcal{A}$ then there exists at least an index $k \in \{1, 2, \ldots, n\}$ such that $u_k \ge K$. Therefore

$$\begin{aligned}\sum_{i=1}^{n} u_i g_i(t, u_i) &= \sum_{\substack{i=1\\ i\neq k}}^{n} u_i g_i(t, u_i) + u_k g_k(t, u_k)\\ &\le \sum_{\substack{i=1\\ i\neq k}}^{n} K_i a + K g_k(t, L) \le a \sum_{i=1}^{n} K_i + Kb = b \sum_{i=1}^{n} K_i < 0.\end{aligned}$$

Thus, by (H_3) and (H_4) we have

$$\sum_{i=1}^{n} \dot{u}_i \le \sum_{i=1}^{n} u_i g_i(t, u_i) < 0$$

whenever $u \notin \mathcal{A}$. This proves the lemma.

By Lemma 2.1, the solution to (1.1) with $u(t_0) \in R_+^n$ is defined on $[t_0, +\infty)$, and $u(t) \in R_+^n$ for all $t \ge t_0$. Therefore, we may introduce, for any $t \ge t_0$, the Cauchy operator $G(t, t_0)$: it is defined on R_+^n and maps the initial datum $(u_{01}, \ldots, u_{0n})$ into the solution $(u_1(t), \ldots, u_n(t))$ at time t. Straightforward properties of G are: G is continuous and t-differentiable for $t \ge t_0$; $G(t, t_0)R_+^n \subset R_+^n$ for all $t \ge t_0$; $G(t, s)G(s, t_0) = G(t, t_0)$ for all $t \ge s \ge t_0$; $G(t + T, t_0 + T) = G(t, t_0)$ for all $t \ge t_0$; and $G(t_0, t_0) = E$, where E is the identity.

A basic tool in investigating T-periodic solutions is the monodromy (or Poincare) operator $H = G(T, 0)$. In fact, T-periodic solutions are in one-to-one correspondence with fixed points of H; and the stability character of a T-periodic solution can be read off from that of the corresponding fixed point of H with respect to the discrete semi-dynamical system

$$\mathbf{N} \times R_+^n \ni (k, p) \mapsto H^k p \in R_+^n. \tag{2.3}$$

In particular, if $H^k p$ converges to $\hat{p}$ as $k \to \infty$, then $\hat{p}$ is a fixed point of H. Thus, $G(t, 0)\hat{p}$ is a T-periodic solution and $\lim\limits_{t\to\infty} \|G(t, 0)p - G(t, 0)\hat{p}\| = 0$.

Now we shall prove the monotone property of the operator H. For $u, v \in R^n$, we write $u \leq v$ if $u_i \leq v_i$ for every $i = 1, 2, \ldots, n$. Similarly, $u < v$ will mean that $u_i < v_i$ for every $i = 1, 2, \ldots, n$. The most important property of (1.1) is that it is quasi-monotone increasing, because for every pair points (t, u), $(t, v) \in R \times R_+^n$ and every $i = 1, 2, \ldots, n$, one gets $F_i(t, u) \leq F_i(t, v)$ whenever $u_i = v_i$ and $u \leq v$.

Solutions to quasi-monotone systems such as (1.1) have the following comparison property (see [5, p. 318]): Let $u^+ : [t_0, \omega) \to R_+^n$ be the maximum solution through some point $(t_0, u_0) \in R \times R_+^n$ of (1.1) and $v : [t_0, \overline{\omega}) \to R_+^n$, $\overline{\omega} \leq \omega$, a continuous function such that

(i) $v(t_0) \leq u_0$,

(ii) $Dv(t) \leq F(t, v(t))$ for $t \in (t_0, \overline{\omega})$,

where Dv is any Dini derivative of v. Then $v(t) \leq u^+(t)$ for any $t \in (t_0, \overline{\omega})$.

In particular, by the forward uniqueness of solution of (1.1) we have the following:

Lemma 2.2. *If $u^1(t)$ and $u^2(t)$ are two solutions of* (1.1) *with $u^1(t_0) \leq u^2(t_0)$, $(t_0 \in R)$, then $u^1(t) \leq u^2(t)$ for all $t > t_0$. In particular, H is monotone increasing, i.e., $Hx \leq Hy$ whenever $x, y \in R_+^n : x \leq y$.*

3. Periodic solutions and global asymptotic stability

In this section we study the existence and global stability of a periodic solution whose components are strictly positive.

Theorem 3.1. *Let*

(H_6) $\inf\limits_{t \in [0,T]} \left\{ g_i(t, 0) - \varepsilon_i(t) D_{u_i^+}(h_i(t, 0)) \right\} > 0, \quad 1 \leq i \leq n,$

where $D_{u_i^+}(h_i(t, 0))$ is the lower right Dini derivative of $h_i(t, u_i)$ at $u_i = 0$. Then the system (1.1) *has at least one T-periodic solution $u^0(t)$ whose components are strictly positive. Moreover, if such a solution is unique, then $\lim\limits_{t \to +\infty} |u_i^0(t) - u_i(t)| = 0$ for every $i = 1, 2, \ldots, n$, where $u(t)$ is any solution of* (1.1) *with $u(0) > 0$.*

Proof. By (H_6), there exists a positive number δ such that

$$g_i(t, u_i) - \frac{\varepsilon_i(t) h_i(t, u)}{u_i} > 0$$

for all $0 < u_i < \delta$ and $1 \leq i \leq n$. This fact and Lemma 2.1 imply that

$$\mathcal{A}^* = \left\{ (u_1, \ldots, u_n) \in R_+^n : \delta \leq u_i \leq K,\ 1 \leq i \leq n \right\}$$

is positively invariant and strongly attractive with respect to int (R^n_+). Hence $H(\mathcal{A}^*) \subset \mathcal{A}^*$.

Denote $x = (\delta, \dots, \delta) \in R^n$ and $y = (K, \dots, K) \in R^n$. Clearly, $Hx \in \mathcal{A}^*$. Thus, $Hx \geq x$. By Lemma 2.2, $\{H^k x\}_{k=1}^{\infty}$ is monotone increasing. Moreover, $\{H^k x\}_{k=1}^{\infty}$ is bounded above by y. Consequently, $H^k x$ must converge to some point $p \in \mathcal{A}^*$. Thus, $G(t,0)p$ is a T-periodic solution of (1.1). Moreover, $G(t,0)p \in \mathcal{A}^*$ for all $t \in R$ because $\mathcal{A}^*$ is positively invariant.

We now prove the second part of the theorem. Similarly, $\{H^k y\}_{k=1}^{\infty}$ is monotone decreasing and bounded below by x. By the uniqueness of a strictly positive T-periodic solution, we have that $\{H^k x\}_{k=1}^{\infty}$ and $\{H^k y\}_{k=1}^{\infty}$ must converge to $p = u^0(0) \in \mathcal{A}^*$ as $k \to \infty$. Let z be any point in $\mathcal{A}^*$. Clearly, $x \leq z \leq y$. By Lemma 2.2, $H^k y \geq H^k z \geq H^k y$ for all $k \geq 1$. Thus $H^k z$ converges to p, as $k \to \infty$. Therefore, for the discrete semi-dynamical system (2.3) the point p absorbs every point in $\mathcal{A}^*$. Since $\mathcal{A}^*$ is strongly attractive with respect to int (R^n_+), p is globally attractive with respect to int (R^n_+). This proves the second part of the theorem. The theorem is proved.

From now on we consider the special case of the system (1.1) in which $h_i(t, u_i)$ $(1 \leq i \leq n)$ is linear in u_i, i.e., $h_i(t, u_i) = k_i(t)u_i$:

$$(3.1) \quad \dot{u}_i = u_i g_i(t, u_i) - \varepsilon_i(t)k_i(t)u_i + \sum_{\substack{j=1 \\ j \neq i}}^{n} d_{ij}(t)\varepsilon_j(t)k_j(t)u_j, \quad 1 \leq i \leq n.$$

The hypothesis (H_2) now becomes

(H_2') $k_i(t) \geq 0$ for all $t \in [0, T]$.

We now prove the uniqueness of a strictly positive T-periodic solution of the system (3.1). Before doing this, we prove the following lemma:

Lemma 3.2. *Let α be a positive number. Let $u(t)$ be a solution of* (3.1) *satisfying $u(t) > 0$ for all $t \geq 0$ and $u(x,t)$ the solution of* (3.1) *with $u(x, 0) = x := \alpha u(0)$.*

If $\alpha < 1$, then $u(x,t) > \alpha u(t)$, for all $t > 0$.

If $\alpha > 1$, then $u(x,t) < \alpha u(t)$, for all $t > 0$.

Proof. First we consider the case $\alpha < 1$. For $i = 1, 2, \dots, n$, we have

$$\frac{d}{dt}(\alpha u_i(t)) = \alpha\Big[u_i(t)g_i(t, u_i(t)) - \varepsilon_i(t)k_i(t)u_i(t)$$

$$
\begin{aligned}
&+ \sum_{\substack{j=1\\ j\neq i}}^{n} d_{ij}(t)\varepsilon_j(t)k_j(t)u_j(t)\Big] \\
&< \alpha u_i(t)g_i(t,\alpha u_i(t)) - \varepsilon_i(t)k_i(t)\alpha u_i(t) \\
&+ \sum_{\substack{j=1\\ j\neq i}}^{n} d_{ij}(t)\varepsilon_j(t)k_j(t)\alpha u_j(t),
\end{aligned}
$$

because $g_i(t,u_i(t)) < g_i(t,\alpha u_i(t))$. It follows from Lemma 2.3 of [5, p. 315] that $u(x,t) > \alpha u(t)$ for all $t > 0$.

Similarly, we can prove that $u(x,t) < \alpha u(t)$ for all $t > 0$ if $\alpha > 1$ by using Lemma 2.4 of [5, p. 316].

Theorem 3.3. *The system* (3.1) *has at most one strictly positive T-periodic solution.*

Proof. Suppose that the system (3.1) has two different strictly positive T-periodic solutions, say $\overline{u}(t)$ and $\underline{u}(t)$. Without loss of generality, we may assume that $\overline{u}_1(0) > \underline{u}_1(0)$. Therefore, there exists $\alpha \in (0,1)$ such that $\alpha\overline{u}_1(0) > \underline{u}_1(0)$. Denote $x = \alpha\overline{u}(0)$. By Lemma 3.2, we have $u(x,t) > \alpha\overline{u}(t)$ for all $t > 0$, where $u(x,t)$ is the solution with $u(x,0) = x$. Thus, by the periodicity of $\overline{u}(t)$,

$$H(\alpha\overline{u}(0)) > \alpha\overline{u}(0). \tag{3.2}$$

Since $\underline{u}(0) \notin \{z \in R^n_+ : z_i \geq x_i,\ 1 \leq i \leq n\}$, it follows that there exists $\beta > 1$ such that

$$y := \beta\underline{u}(0) \in \bigcup_{i=1}^{n} \{z \in R^n_+ : z \geq x,\ z_i = x_i\}.$$

Thus, Lemma 3.2 implies that $u(y,t) < \beta\underline{u}(t)$ for all $t > 0$, where $u(y,t)$ is the solution with $u(y,0) = y$. Hence, by the periodicity of $\underline{u}(t)$,

$$H(\beta\underline{u}(0)) < \beta\underline{u}(0). \tag{3.3}$$

Clearly, $y = \beta\underline{u}(0) \geq \alpha\overline{u}(0) = x$. Thus, it follows from Lemma 2.2 that

$$H(\beta\underline{u}(0)) \geq H(\alpha\overline{u}(0)). \tag{3.4}$$

It is easy to deduce from (3.2), (3.3) and (3.4) that

$$\beta\underline{u}(0) > H(\beta\underline{u}(0)) \geq H(\alpha\overline{u}(0)) > \alpha\overline{u}(0). \tag{3.5}$$

But there exists at least one index $j \in \{1, \dots, n\}$ such that $y_j = x_j$, i.e., $\beta\underline{u}_j(0) = \alpha\overline{u}(0)$. This contradiction proves the theorem.

We now show that the second assertion of Theorem 3.1 is valid for the system (3.1) without requiring the assumption utilized there.

Theorem 3.4. *Suppose that the system* (3.1) *has a unique strictly positive T-periodic solution. Then this solution is globally asymptotically stable in* $\operatorname{int}(R^n_+)$.

Proof. Suppose that $u^0(t)$ is the strictly positive T-periodic solution of (3.1). We consider the discrete semi-dynamical system (2.3). Let $x \in \operatorname{int}(R^n_+)$. Then there exist $\alpha \in (0,1)$ and $\beta > 1$ such that $\alpha u^0(0) \leq x \leq \beta u^0(0)$.

Thus, by Lemma 3.2, $H(\alpha u^0(0)) > \alpha u^0(0)$ and $H(\beta u^0(0)) < \beta u^0(0)$. Therefore, Lemma 2.2 implies that $\{H^k(\alpha u^0(0))\}_{k=1}^{\infty}$ is monotone increasing and bounded above by $\beta u^0(0)$, that $\{H^k(\beta u^0(0))\}_{k=1}^{\infty}$ is monotone decreasing and bounded below by $\alpha u^0(0)$, and that $H^k(\alpha u^0(0) \leq H^k(x) \leq H^k(\beta u^0(0))$ for all $k \geq 1$. Thus, the uniqueness of $u^0(t)$ implies that $H^k(\alpha u^0(0))$, $H^k(\beta u^0(0))$ and $H^k(x)$ must converge to $u^0(0)$ as $k \to \infty$. This implies that $u^0(0)$ is globally attractive with respect to $\operatorname{int}(R^n_+)$.

The stability of $u^0(0)$ follows from the fact that $\{u \in R^n_+ : \alpha u^0(0) \leq u \leq \beta u^0(0)\}$ is positively invariant (with respect to (2.3)) for all $0 < \alpha < 1$ and $\beta > 1$. Therefore, the T-periodic solution $u^0(t)$ to (3.1) is stable in $\operatorname{int}(R^n_+)$. The theorem is proved.

In the linear case, i.e. the system (3.1), the hypothesis (H_6) in Theorem 3.1 becomes

(H_6') $g_i(t,0) - \varepsilon_i(t)k_i(t) > 0$ for all $t \in [0,T]$ and $i = 1, 2, \dots, n$.

Thus the following is a direct consequence of theorems 3.1, 3.3 and 3.4.

Corollary 3.5. *Let (H_6') hold, then the system* (3.1) *has a unique strictly positive T-periodic solution which is globally asymptotically stable in* $\operatorname{int}(R^n_+)$.

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Faculty of Mathematics, Mechanics and Informatics
College of Natural Sciences, Hanoi National University
90 Nguyen Trai Str., Thanh Xuan, Hanoi, Vietnam