Existence and uniqueness of a positive steady state solution for a logistic system of differential difference equations

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ABSTRACT. We prove the existence and uniqueness of a positive solution to a logistic system of differential difference equations that arises as a population model for a single species which is composed of several habitats connected by linear migration rates. Our proof is based on the proof of a similar result for a reaction-advection-diffusion equation.

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RESUMEN. En este artículo probamos la existencia y unicidad de una solución positiva a un sistema logístico de ecuaciones diferenciales y de diferencias finitas que surge como un modelo de la población de una especie localizada en un conjunto discreto de hábitats interconectados por tasas lineales de migración. Nuestra prueba está basada en la prueba de un resultado similar para ecuaciones de reacción-advección-difusión.

1. Introduction

We consider the system of differential equations

$$u_i'(t) = \sum_{j \in I_i} \left[d_{ij} u_j(t) - d_{ji} u_i(t) \right] + u_i(t) F_i \left(u_i(t) \right), \quad i = 1, \cdots, n, \quad t \ge 0.$$
(1.1)

Here d_{ij} are positive constants, and I_i is a nonempty subset of $\{1, 2, \dots, n\}$ such that $j \in I_i$ implies $i \in I_j$, $i, j = 1, \dots, n$. We also assume that there is not a non-empty and proper subset $I \subsetneq \{1, 2, \dots, n\}$ such that $I_i \subset I$ for all 189

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 $i \in I$. This condition on I_i accounts for assuming that the matrix $A = (a_{ij})$ of the linear part of (1.1),

$$a_{ij} = \begin{cases} d_{ij}, & i \neq j \text{ and } j \in I_i, \\ 0, & i \neq j \text{ and } j \notin I_i, \\ -\sum_{j \in I_i} d_{ij}, & i = j, \end{cases}$$
(1.2)

is irreducible. The functions $F_i(s)$, $i = 1, \dots, n$, verify the following hypothesis:

Hypotheses 1.1.

- (1) F_i is continuously differentiable.
- (2) $r_i := F_i(0) > 0$, and $-\alpha_i \leq F'_i(s) \leq -\beta_i$ for given positive constants α_i, β_i , and any $s \geq 0$.

This problem arises as a population model for a single species which is composed of several habitats connected by linear migration rates and having logistic growth (see [4] and the references therein). In this case $u_i(t)$ is the population in habitat *i* at time *t*; the coefficients d_{ij} are the rates at which the individuals migrate from habitat *j* to habitat *i*; and F_i represents the net rate of population supply at habitat *i*. The second condition in Hypothesis 1.1 implies that there exists $0 < K_i < \infty$, such that f_i is positive in $(0, K_i)$ and negative in $(K_i, +\infty)$, for $i = 1, \dots, n$. The value $K_i > 0$ is called the *carrying capacity* of the population because it represents the population size that available resources can continue to support. The value $r_i > 0$ is called the *intrinsic growth rate* and represents the per capita growth rate achieved if the population size were small enough to ensure negligible resource limitations. For the standard *logistic*

growth, introduced by P.F. Verhulst [7], $F_i(s) = r_i \left(1 - \frac{s}{K_i}\right)$.

Continuous time models with multi-patch formulation have also been proposed in the study of the spatial dynamics of epidemics (see [1] and the references therein).

The first condition in Hypothesis 1.1 is technical and is needed together with the second condition to ensure, given initial data, the existence and uniqueness of solutions for (1.1) globally defined for $t \ge 0$, c.f. [3]. Since $d_{ij} > 0$ and the matrix A is irreducible, (1.1) is a cooperative and irreducible system in \mathbb{R}^n_+ . This implies that the set $C := \{\xi \in \mathbb{R}^n_+ : \lim_{t\to\infty} u(t;\xi) \text{ exists}\}$ of convergent points of (1.1) contains an open and dense subset of \mathbb{R}^n_+ , c.f. [5, Theorem 4.1.2, page 57]. Here, $u(t;\xi)$ denotes the solution of (1.1) such that $u(0;\xi) = \xi$. Thus the dynamics of (1.1) is largely determined by its equilibria.

It is clear that $u \equiv 0$ is a steady state solution of (1.1). Since $F_i(0) > 0$, $i = 1, \dots, n$, it follows that $u \equiv 0$ is unstable. Hence, by the above argument there exists at least one nontrivial equilibria \bar{u} such that $\lim_{t\to\infty} u(t;\xi) = \bar{u}$ for some ξ in an open subset of C. In fact it is not difficult to see that when

$$\sum_{j \in I_i} d_{ij} K_j = \sum_{j \in I_i} d_{ji} K_i, \qquad i = 1, \cdots, n,$$
(1.3)

the only nontrivial equilibrium of (1.1) is $\bar{u} = (K_1, K_2, \dots, K_n)$ (see [4, Theorem 1]). The purpose of this paper is to prove the following theorem regarding the existence and uniqueness of a nontrivial steady state for (1.1).

Theorem 1.1. There exists one and only one positive steady state solution for (1.1).

This result is well known for reaction-advection-diffusion equations (see [2, Proposition 3.3, page 148]). Since (1.1) can be seen as a spatially discrete model analogous to an advection-diffusion equation, the same result was expected to be true for (1.1). Nevertheless, to the best of our knowledge, its proof has not yet appeared in the literature. In order to stress the similarity of (1.1) to a reaction-advection-diffusion equation, we present a proof that is based on the corresponding proof for the PDE model.

2. Preliminary results

Consider the linear system

$$\sum_{j \in I_i} d_{ij}(x_j - x_i) + b_i x_i = f_i, \qquad i = 1, \cdots, n.$$
(2.1)

Here b_i , and f_i are given constants.

Theorem 2.1 (Strong Maximum Principle). Suppose that $b_i \leq 0, i = 1, \dots, n$. Let $x \in \mathbb{R}^n$ be a solution of (2.1), $m := \min_{\substack{1 \leq i \leq n \\ 1 \leq i \leq n}} x_i$, and $M := \max_{\substack{1 \leq i \leq n \\ 1 \leq i \leq n}} x_i$. If $f_i \leq 0, i = 1, \dots, n$, and $m \leq 0$ (resp. $f_i \geq 0, i = 1, \dots, n$, and $M \geq 0$), then $x_i = m$ (resp. $x_i = M$), and $f_i = mb_i = 0$, $i = 1, \dots, n$. In particular, if $f_i \leq 0$ (resp. $f_i \geq 0$), $i = 1, \dots, n$, and $f \neq 0$ or $b \neq 0$, then $m \geq 0$ (resp. $M \leq 0$).

Remark 2.1. This theorem is a particular version of more general maximum principles for monotone matrices (see [6, Theorem 2]). We will give an independent proof.

Proof of Theorem 2.1. Suppose that $f_i \leq 0, i = 1, \dots, n$ and $m \leq 0$, (the case that $f_i \geq 0, i = 1, \dots, n$ and $M \geq 0$ can be solved similarly). Let $I := \{i : x_i = m\}$. Clearly, I is non-empty. Suppose that $I \subsetneq \{1, \dots, n\}$. Hence, by our original assumption on the sets I_i 's, there exists $i \in I$ such that $I_i \bigcap I^c$ is non-empty. Here, I^c denotes the complement of I over the set $\{1, \dots, n\}$. For such i we have

$$f_i = \sum_{j \in I_i} d_{ij}(x_j - x_i) + b_i x_i$$

=
$$\sum_{j \in I_i \cap I^c} d_{ij}(x_j - m) + b_i m$$

> 0.

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which is a contradiction. This proves that $x_i = m, i = 1, \dots, n$. It follows, by introducing this value for x_i in (2.1), that $f_i = mb_i = 0, i = 1, \dots, n$.

We will apply the Strong Maximum Principle to obtain a monotone iteration scheme for constructing solutions to the general nonlinear system

$$\sum_{j \in I_i} d_{ij}(x_j - x_i) + e_i x_i + f_i(x_i) = 0, \qquad i = 1, \cdots, n.$$
(2.2)

Here f_i , $i = 1, \dots, n$ are given functions. We will say that x^0 is an *upper* solution of (2.2) if x^0 satisfies

$$\sum_{j \in I_i} d_{ij} \left(x_j^0 - x_i^0 \right) + e_i x_i^0 + f_i \left(x_i^0 \right) \le 0, \qquad i = 1, \cdots, n.$$
(2.3)

We will also assume that x^0 is not a solution. Similarly we define *lower* solution by interchanging the order of the inequalities in (2.3).

Theorem 2.2. Suppose that $f_i \in C^1(\mathbb{R})$ for all i, and that x^0 and y^0 are respectively upper and lower solutions of (2.2) with $y_i^0 \leq x_i^0$, $i = 1, \dots, n$. Then there exist solutions \bar{x} and \bar{y} of (2.2) such that $y_i^0 \leq \bar{y}_i \leq \bar{x}_i \leq x_i^0$, $i = 1, \dots, n$. Moreover, \bar{x} and \bar{y} are, respectively, maximal and minimal solutions of (2.2), in the sense that if x is any solution of (2.2) such that $y_i^0 \leq x_i \leq x_i^0$, $i = 1, \dots, n$ then $\bar{y}_i \leq x_i \leq \bar{x}_i$, $i = 1, \dots, n$.

Proof. Let $m := \min_{\substack{0 \le i \le n}} y_i^0$ and $M := \max_{\substack{0 \le i \le n}} x_i^0$. Let k > 0 be a constant such that $k > e_i, i = 1, \cdots, n$, and

$$f_i'(s)+k>0, \qquad 0\leq i\leq n, \qquad s\in[m,M].$$

Define the application $T: {\rm I\!R}^n \to {\rm I\!R}^n$ by $\beta = T\alpha$ where β is the solution of the problem

$$\sum_{j \in I_i} d_{ij}(\beta_j - \beta_i) + (e_i - k)\beta_i = -(f_i(\alpha_i) + k\alpha_i), \qquad i = 1, \cdots, n.$$
(2.4)

The matrix of the linear system (2.4) is of the form A - kI where A is the matrix given in (1.2). By the Gershgorin circle theorem we know that A has non-positive eigenvalues. Hence, since $e_i - k < 0, i = 1, \dots, n$, the matrix A - kI is invertible, and T is well defined.

We will see that T is a monotonic application in the sense that if $\alpha^1 \leq \alpha^2$ then $T\alpha^1 \leq T\alpha^2$, provided that $m \leq \alpha^1$, $\alpha^2 \leq M$. Here $\alpha^1 \leq \alpha^2$ means $\alpha_i^1 \leq \alpha_i^2$ for all i. We also write $\alpha^1 < \alpha^2$ if $\alpha^1 \leq \alpha^2$ and $\alpha_i^1 < \alpha_i^2$ for some i, and we write $\alpha^1 \ll \alpha^2$ if $\alpha_i^1 < \alpha_i^2$ for all i. To see this let $\beta^i = T\alpha^i$, i = 1, 2. Then

$$\sum_{j \in I_i} d_{ij} \left(\left(\beta_j^2 - \beta_j^1 \right) - \left(\beta_i^2 - \beta_i^1 \right) \right) + (e_i - k) \left(\beta_i^2 - \beta_i^1 \right) \\ = - \left(f_i \left(\alpha_i^2 \right) - f_i \left(\alpha_i^1 \right) + k \left(\alpha_i^2 - \alpha_i^1 \right) \right), \qquad i = 1, \cdots, n.$$
(2.5)

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If we assume that $\alpha^1 \leq \alpha^2$, then by the choice of k we have

$$\sum_{j \in I_i} d_{ij} \left(\left(\beta_j^2 - \beta_j^1 \right) - \left(\beta_i^2 - \beta_i^1 \right) \right) + (e_i - k) \left(\beta_i^2 - \beta_i^1 \right) \le 0, \ i = 1, \cdots, n.$$
(2.6)

This implies that $\beta^1 \ll \beta^2$. It is clear that $\beta^1 \le \beta^2$. Suppose that there exists i such that $\beta_i^1 = \beta_i^2$. By the Strong Maximum Principle $\beta^1 \equiv \beta^2$. In this case, the left hand side of (2.5) is zero. It follows by the choice of k that $\alpha^1 \equiv \alpha^2$. Hence, T is monotonic in a stronger sense, i.e. if $\alpha^1 < \alpha^2$ then $T\alpha^1 \ll T\alpha^2$.

Let us see now that $T\alpha \ll \alpha$ if α is an upper solution of (2.2). Let $\beta = T\alpha$, then

$$\sum_{j \in I_i} d_{ij} \left((\beta_j - \alpha_j) - (\beta_i - \alpha_i) \right) + (e_i - k) (\beta_i - \alpha_i)$$

$$= -\left(\sum_{j \in I_i} d_{ij} (\alpha_j - \alpha_i) + f_i (\alpha_i) \right) \ge 0, \ i = 1, \cdots, n.$$
(2.7)

Again, by the Strong Maximum Principle $\beta \ll \alpha$, otherwise $\beta \equiv \alpha$. This last option is not possible since by the definition of T, α would be a solution of (2.2) and we assumed that this was not the case.

This observations allow us to defined inductively two sequences $\{x^n\}$ and $\{y^n\}$ by letting $(x^1, y^1) := (Tx^0, Ty^0)$ and $(x^n, y^n) := (Tx^{n-1}, Ty^{n-1})$ for n > 1.

Since x^0 is an upper solution, $x^1 = Tx^0 \ll x^0$, and by the monotonicity of $T, Tx^1 \ll Tx^0 = x^1$. Hence $x^{n-1} \gg x^n$ for each n. Similarly, $y^n \gg y^{n-1}$ for each n. Also, since $x^0 > y^0$, we obtain by induction that $x^n \gg y^n$.

This allow us to conclude that $\{x^n\}$ is a decreasing sequence bounded below by y^0 . Hence

$$\bar{x}_i = \lim_{n \to \infty} x_i^n, \qquad i = 1, \cdots, n,$$

exists.

Now,

$$\bar{x} = \lim_{n \to \infty} x^n = \lim_{n \to \infty} T x^{n-1} = T \lim_{n \to \infty} x^{n-1} = T \bar{x}$$

Then \bar{x} is solution of (2.2).

Similarly we can construct a solution \bar{y} of (2.2) such that $y^0 < \bar{y} < \leq \bar{x} < x^0$. Suppose now that x is another solution of (2.2) such that $y^0 < x < x^0$. This implies that $x = Tx \ll Tx^0 = x^1$. By induction $x \ll x^n$ for all n. Hence $x \leq \bar{x}$. Similarly, one shows that $\bar{y} \leq x$. This finishes the proof of the theorem.

3. Proof of the main Theorem

The proof of Theorem 1.1 relies in the following lemmas

Lemma 3.1. If x is a solution of (2.2) with $f_i(s) := sF_i(s)$, then $x_i \leq a^*, i = 1, \cdots, n$, where $a^* := \max_{1 \leq i \leq n} \left\{ \frac{r_i}{\beta_i}, \frac{e_i + r_i}{\beta_i} \right\}$.

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Proof. Suppose that there exists i such that $x_i > a^*$. Let i_0 such that $x_{i_0} = \max_{1 \le i \le n} x_i > a^*$. Hence $e_{i_0} x_{i_0} + f_{i_0}(x_{i_0}) < 0$. It follows that

$$\sum_{j \in I_{i_0}} d_{i_0 j} \left(x_j - x_{i_0} \right) + e_{i_0} x_{i_0} + f_{i_0} \left(x_{i_0} \right) \le e_{i_0} x_{i_0} + f_{i_0} \left(x_{i_0} \right) < 0.$$

This is a contradiction which proves the lemma.

The steady state solutions of (1.1) are solutions of a system of the form

$$\sum_{j \in I_i} d_{ij}(x_j - x_i) + e_i x_i + x_i F_i(x_i) = 0, \qquad i = 1, \cdots, n.$$
(3.1)

Lemma 3.2. If the principal eigenvalue λ_1 is positive in the problem

$$\sum_{j \in I_i} d_{ij} \left(\psi_j - \psi_i \right) + e_i \psi_i + r_i \psi_i = \lambda \psi_i, \qquad i = 1, \cdots, n,$$
(3.2)

where $r_i = F_i(0)$, then system (3.1) has one and only one positive solution.

By a positive solution of (3.1) we mean a solution $x \in \mathbb{R}^n$ such that $x_i > 0, i = 1, \dots, n$.

Proof. To prove the existence of a positive solution of (3.1) we first notice that $a^* := \max_{1 \le i \le n} \left\{ \frac{r_i}{\beta_i}, \frac{e_i + r_i}{\beta_i} \right\}$ is an upper solution of (3.1).

Let ψ a positive eigenvector corresponding to the main eigenvalue λ_1 of (3.2). It follows that $\epsilon \psi$ satisfies the equation

$$\sum_{j\in I_i} d_{ij}(\epsilon\psi_j - \epsilon\psi_i) + e_i\epsilon\psi_i + \epsilon\psi_iF_i(\epsilon\psi_i) = \epsilon\psi_i(\lambda_1 - r_i + F_i(\epsilon\psi_i)), \qquad i = 1, \cdots, n.$$

Since $\lambda_1 + F_i(\epsilon \psi_i) - F_i(0) \geq \lambda_1 - \alpha_i \epsilon \psi_i$ we obtain, by choosing $\epsilon > 0$ small enough, that $\epsilon \psi$ is a positive lower solution of (3.1). We can assume without loss of generality that $\epsilon \psi_i < a^*, i = 1, \dots, n$. It follows by Theorem 2.2 that (3.1) has a positive solution.

Let \bar{x} be the maximal solution of (3.1) given by Theorem 2.2 for the upper solution a^* . Suppose that x is another positive solution of (3.1). By Lemma 3.1 $x_i \leq a^*, i = 1, \dots, n$. Since \bar{x} is a maximal solution, it follows that $0 \leq x_i \leq \bar{x}_i$, $i = 1, \dots, n$. We will show that this implies that $x = \bar{x}$.

Since x is a positive solution of (3.1) it follows that the principal eigenvalue λ_1 is zero for the problem

$$\sum_{j\in I_i} d_{ij}(\psi_j - \psi_i) + e_i\psi_i + F_i(x_i)\psi_i = \lambda\psi_i, \qquad i = 1, \cdots, n, \qquad (3.3)$$

Similarly, since \bar{x} is a positive solution of (3.1) it follows that the principal eigenvalue $\bar{\lambda}_1$ is zero for the problem

$$\sum_{j \in I_i} d_{ij}(\psi_j - \psi_i) + e_i\psi_i + F_i(\bar{x}_i)\psi_i = \lambda\psi_i, \qquad i = 1, \cdots, n.$$
(3.4)

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Assume that there exists *i* such that $x_i < \bar{x}_i$. This implies that $F_i(\bar{x}_i) < F_i(x_i)$. Hence, applying the monotonicity property of the principal eigenvalue of nonnegative irreducible matrices to problems (3.3)-(3.4), it follows that $\bar{\lambda}_1 < \lambda_1$. This is a contradiction, since $\bar{\lambda}_1 = \lambda_1 = 0$. We conclude that $x = \bar{x}$. This finished the proof of the theorem.

Proof of Theorem 1.1. Since the principal eigenvalue of the matrix A is zero then the principal eigenvalue of the problem

$$\sum_{j \in I_i} \left[d_{ij} \psi_j - d_{ji} \psi_i \right] + r_i \psi_i = \lambda \psi_i, \qquad i = 1, \cdots, n,$$
(3.5)

is positive. The theorem follows by applying Lemma 3.2 to (1.1) with $e_i = \sum_{i \in I_i} (d_{ij} - d_{ji})$.

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