

Research Article

Global Stability for a Three-Species Food Chain Model in a Patchy Environment

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We investigate a three-species food chain model in a patchy environment where prey species, mid-level predator species, and top predator species can disperse among n different patches ($n \geq 2$). By using the method of constructing Lyapunov functions based on graph-theoretical approach for coupled systems, we derive sufficient conditions under which the positive equilibrium of this model is unique and globally asymptotically stable if it exists.

1. Introduction

Coupled systems on networks are used to describe a wide variety of physical, natural, and artificial complex dynamical systems, such as neural networks, biological systems, and the spread of infectious diseases in heterogeneous populations (see [1–6] and the references therein). A mathematical description of a network is a directed graph consisting of vertices and directed arcs connecting them. At each vertex, the dynamics are given by a system of differential equations called vertex system. The directed arcs indicate interconnections and interactions among vertex systems.

Diffusion in patchy environment is one of the most prevalent phenomena of nature. Since the spatiotemporal heterogeneity incurs great impacts on the species' diversity, structure, and genetical polymorphism, scientists of biology, ecology, and biomathematics paid great attention on the population dynamics with diffusion. The stability of equilibrium is the precondition of applications of dispersal models in practice. Therefore, there are a great amount of literatures on this topic (see [7–10] and the references therein). In [10], Kuang and Takeuchi considered a predator-prey model in which preys disperse among two patches and proved the uniqueness and global stability of a positive equilibrium by constructing a Lyapunov function.

Recently, a graph theoretic approach was proposed to construct Lyapunov functions for some general coupled

systems of ordinary differential equations on networks, and the global stability was explored in [11, 12]. We refer to [13, 14] for recent applications.

In [12], Li and Shuai considered the following predator-prey model where prey species disperse among n patches ($n \geq 2$):

$$\dot{x}_i = x_i(r_i - b_i x_i - e_i y_i) + \sum_{j=1}^n d_{ij}(x_j - \alpha_{ij} x_i), \quad (1)$$

$$\dot{y}_i = y_i(-\gamma_i - \delta_i y_i + \varepsilon_i x_i),$$

where $i = 1, 2, \dots, n$. They provided a systematic method for constructing a global Lyapunov function for the coupled systems on networks and then gave some sufficient conditions of stability for system (1). In fact, there may be more species in some habitats and they can construct a food chain; in this case it is more realistic to consider a multiple species predator-prey system. Based on this fact, in this paper, we investigate the following three-species food chain model in a patchy environment:

$$\dot{x}_i = x_i(r_i - \sigma_i x_i - e_i y_i) + \sum_{j=1}^n a_{ij} x_j - \sum_{j=1}^n a_{ji} x_i,$$

$$\begin{aligned}
\dot{y}_i &= y_i (-\theta_i - \delta_i y_i + \varepsilon_i x_i - \rho_i z_i) \\
&\quad + \sum_{j=1}^n b_{ij} y_j - \sum_{j=1}^n b_{ji} y_i, \quad i = 1, 2, \dots, n, \\
\dot{z}_i &= z_i (-\gamma_i - \alpha_i z_i + \eta_i y_i) + \sum_{j=1}^n c_{ij} z_j - \sum_{j=1}^n c_{ji} z_i,
\end{aligned} \tag{2}$$

where x_i , y_i , and z_i denote the densities of prey species, mid-level predator species, and top predator species, respectively; all the parameters are nonnegative constants, and ε_i , e_i , η_i , and ρ_i are positive. Constant $a_{ij} \geq 0$ is the dispersal rate of prey species from patch j to patch i , constant $b_{ij} \geq 0$ is the dispersal rate of mid-level predator species from patch j to patch i , and constant $c_{ij} \geq 0$ is the dispersal rate of top predator species from patch j to patch i . We refer the reader to [10, 15] for interpretations of predator-prey models and parameters.

This paper is organized as follows. In Section 2, we introduce some preliminaries on graph theory which will be used in Section 3. In Section 3, the global stability of the positive equilibrium of system (2) is proved. Finally, a conclusion is given in Section 4.

2. Preliminaries

Since the coupled system considered in this paper is built on a directed graph, the following basic concepts and theorems on graph theory can be found in [12].

A directed graph or digraph $\mathcal{G} = (V, E)$ contains a set $V = \{1, 2, \dots, n\}$ of vertices and a set E of arcs (i, j) leading from initial vertex i to terminal vertex j . A subgraph \mathcal{H} of \mathcal{G} is said to be spanning if \mathcal{H} and \mathcal{G} have the same vertex set. A digraph \mathcal{G} is weighted if each arc (j, i) is assigned a positive weight a_{ij} . Here $a_{ij} > 0$ if and only if there exists an arc from vertex j to vertex i in \mathcal{G} . The weight $w(\mathcal{H})$ of a subgraph \mathcal{H} is the product of the weights on all its arcs.

Given a weighted digraph \mathcal{G} with n vertices, define the weight matrix $A = (a_{ij})_{n \times n}$ whose entry a_{ij} equals the weight of arc (j, i) if it exists and 0 otherwise. For our purpose, we denote a weighted digraph as (\mathcal{G}, A) . A digraph \mathcal{G} is strongly connected if, for any pair of distinct vertices, there exists a directed path from one to the other. A weighted digraph (\mathcal{G}, A) is strongly connected if and only if the weight matrix A is irreducible. The Laplacian matrix of (\mathcal{G}, A) is defined as

$$L = \begin{pmatrix} \sum_{k \neq 1} a_{1k} & -a_{12} & \cdots & -a_{1n} \\ -a_{21} & \sum_{k \neq 2} a_{2k} & \cdots & -a_{2n} \\ \vdots & \vdots & \ddots & \vdots \\ -a_{n1} & -a_{n2} & \cdots & \sum_{k \neq n} a_{nk} \end{pmatrix}. \tag{3}$$

Let c_i denote the cofactor of i th diagonal element of L . The following results are listed as follows from [12].

Proposition 1 (see [12]). Assume $n \geq 2$. Then,

$$c_i = \sum_{\mathcal{T} \in \mathbb{T}_i} w(\mathcal{T}), \quad i = 1, 2, \dots, n, \tag{4}$$

where \mathbb{T}_i is the set of all spanning trees \mathcal{T} of (\mathcal{G}, A) that are rooted at vertex i and $w(\mathcal{T})$ is weight of \mathcal{T} . In particular, if (\mathcal{G}, A) is strongly connected, then $c_i > 0$ for $1 \leq i \leq n$.

Theorem 2 (see [12]). Assume $n \geq 2$. Let c_i be given in Proposition 1. Then the following identity holds:

$$\sum_{i,j=1}^n c_i a_{ij} G_i(x_i) = \sum_{i,j=1}^n c_i a_{ij} G_j(x_j), \tag{5}$$

where $G_i(x_i)$, $1 \leq i \leq n$, are arbitrary functions.

3. Main Results

In this section, the stability for the positive equilibrium of a three-species food chain model in a patchy environment is considered.

Theorem 3. Assume that a positive equilibrium $E^* = (x_1^*, y_1^*, z_1^*, \dots, x_n^*, y_n^*, z_n^*)$ exists for system (2) and the following assumptions hold.

- (H₁) Dispersal matrixes $A = (a_{ij})_{n \times n}$, $B = (b_{ij})_{n \times n}$, and $C = (c_{ij})_{n \times n}$ are irreducible.
- (H₂) There exist nonnegative constants λ and β such that $\varepsilon_i a_{ij} x_j^* = \lambda e_i b_{ij} y_j^*$ and $(e_i \rho_i / \eta_i) z_j^* = \beta e_i b_{ij} y_j^*$ for all $1 \leq i, j \leq n$.

Then the positive equilibrium E^* of system (2) is unique and globally asymptotically stable in R_+^{3n} .

Proof. From equilibrium equations of (2), we obtain

$$\begin{aligned}
\sigma_i x_i^* + e_i y_i^* - \sum_{j=1}^n a_{ij} \frac{x_j^*}{x_i^*} + \sum_{j=1}^n a_{ji} &= r_i, \\
\varepsilon_i x_i^* - \delta_i y_i^* - \rho_i z_i^* + \sum_{j=1}^n b_{ij} \frac{y_j^*}{y_i^*} - \sum_{j=1}^n b_{ji} &= \theta_i, \\
-\alpha_i z_i^* + \eta_i y_i^* + \sum_{j=1}^n c_{ij} \frac{z_j^*}{z_i^*} - \sum_{j=1}^n c_{ji} &= \gamma_i.
\end{aligned} \tag{6}$$

Next, we show that E^* is globally asymptotically stable in R_+^{3n} , and thus it is unique. Let

$$\begin{aligned}
V_i(x_i, y_i, z_i) &= \varepsilon_i \left(x_i - x_i^* - x_i^* \ln \frac{x_i}{x_i^*} \right) \\
&\quad + e_i \left(y_i - y_i^* - y_i^* \ln \frac{y_i}{y_i^*} \right) \\
&\quad + \frac{e_i \rho_i}{\eta_i} \left(z_i - z_i^* - z_i^* \ln \frac{z_i}{z_i^*} \right).
\end{aligned} \tag{7}$$

Note that $1 - x + \ln x \leq 0$ for $x > 0$ and equality holds if and only if $x = 1$. Differentiating V_i along the solution of system (2), we obtain

$$\begin{aligned}
 \dot{V}_i &= \varepsilon_i (x_i - x_i^*) \left(r_i - \sigma_i x_i - e_i y_i + \sum_{j=1}^n a_{ij} \frac{x_j}{x_i} - \sum_{j=1}^n a_{ji} \right) \\
 &\quad + e_i (y_i - y_i^*) \left(-\theta_i - \delta_i y_i + \varepsilon_i x_i - \rho_i z_i \right. \\
 &\quad \left. + \sum_{j=1}^n b_{ij} \frac{y_j}{y_i} - \sum_{j=1}^n b_{ji} \right) \\
 &\quad + \frac{e_i \rho_i}{\eta_i} (z_i - z_i^*) \left(-\gamma_i - \alpha_i z_i + \eta_i y_i + \sum_{j=1}^n c_{ij} \frac{z_j}{z_i} - \sum_{j=1}^n c_{ji} \right) \\
 &= \varepsilon_i (x_i - x_i^*) \\
 &\quad \times \left[-\sigma_i (x_i - x_i^*) - e_i (y_i - y_i^*) + \sum_{j=1}^n a_{ij} \left(\frac{x_j}{x_i} - \frac{x_j^*}{x_i^*} \right) \right] \\
 &\quad + e_i (y_i - y_i^*) \\
 &\quad \times \left[-\delta_i (y_i - y_i^*) + \varepsilon_i (x_i - x_i^*) - \rho_i (z_i - z_i^*) \right. \\
 &\quad \left. + \sum_{j=1}^n b_{ij} \left(\frac{y_j}{y_i} - \frac{y_j^*}{y_i^*} \right) \right] \\
 &\quad + \frac{e_i \rho_i}{\eta_i} (z_i - z_i^*) \\
 &\quad \times \left[-\alpha_i (z_i - z_i^*) + \eta_i (y_i - y_i^*) + \sum_{j=1}^n c_{ij} \left(\frac{z_j}{z_i} - \frac{z_j^*}{z_i^*} \right) \right] \\
 &\leq \sum_{j=1}^n \varepsilon_i a_{ij} x_j^* \left(\frac{x_j}{x_j^*} - \frac{x_i}{x_i^*} - \frac{x_i^* x_j}{x_i x_j^*} + 1 \right) \\
 &\quad + \sum_{j=1}^n e_i b_{ij} y_j^* \left(\frac{y_j}{y_j^*} - \frac{y_i}{y_i^*} - \frac{y_i^* y_j}{y_i y_j^*} + 1 \right) \\
 &\quad + \sum_{j=1}^n \frac{e_i \rho_i}{\eta_i} c_{ij} z_j^* \left(\frac{z_j}{z_j^*} - \frac{z_i}{z_i^*} - \frac{z_i^* z_j}{z_i z_j^*} + 1 \right) \\
 &= \sum_{j=1}^n \varepsilon_i a_{ij} x_j^* \left(\frac{x_j}{x_j^*} - \frac{x_i}{x_i^*} - \frac{x_i^* x_j}{x_i x_j^*} + 1 \right. \\
 &\quad \left. + \ln \frac{x_i}{x_i^*} - \ln \frac{x_j}{x_j^*} + \ln \frac{x_i^* x_j}{x_i x_j^*} \right) \\
 &\quad + \sum_{j=1}^n e_i b_{ij} y_j^* \left(\frac{y_j}{y_j^*} - \frac{y_i}{y_i^*} - \frac{y_i^* y_j}{y_i y_j^*} + 1 \right.
 \end{aligned}$$

$$\begin{aligned}
 &\quad + \ln \frac{y_i}{y_i^*} - \ln \frac{y_j}{y_j^*} + \ln \frac{y_i^* y_j}{y_i y_j^*} \Big) \\
 &\quad + \sum_{j=1}^n \frac{e_i \rho_i}{\eta_i} c_{ij} z_j^* \left(\frac{z_j}{z_j^*} - \frac{z_i}{z_i^*} - \frac{z_i^* z_j}{z_i z_j^*} + 1 \right. \\
 &\quad \left. + \ln \frac{z_i}{z_i^*} - \ln \frac{z_j}{z_j^*} + \ln \frac{z_i^* z_j}{z_i z_j^*} \right) \\
 &\leq \sum_{j=1}^n \varepsilon_i a_{ij} x_j^* \left(\frac{x_j}{x_j^*} - \frac{x_i}{x_i^*} + \ln \frac{x_i}{x_i^*} - \ln \frac{x_j}{x_j^*} \right) \\
 &\quad + \sum_{j=1}^n e_i b_{ij} y_j^* \left(\frac{y_j}{y_j^*} - \frac{y_i}{y_i^*} + \ln \frac{y_i}{y_i^*} - \ln \frac{y_j}{y_j^*} \right) \\
 &\quad + \sum_{j=1}^n \frac{e_i \rho_i}{\eta_i} c_{ij} z_j^* \left(\frac{z_j}{z_j^*} - \frac{z_i}{z_i^*} + \ln \frac{z_i}{z_i^*} - \ln \frac{z_j}{z_j^*} \right) \\
 &= \sum_{j=1}^n e_i b_{ij} y_j^* \\
 &\quad \times \left[\left(\lambda \frac{x_j}{x_j^*} + \lambda \ln \frac{x_j^*}{x_j} + \beta \frac{z_j}{z_j^*} + \beta \ln \frac{z_j^*}{z_j} \right. \right. \\
 &\quad \left. \left. + \frac{y_j}{y_j^*} + \ln \frac{y_j^*}{y_j} \right) \right. \\
 &\quad \left. - \left(\lambda \frac{x_i}{x_i^*} + \lambda \ln \frac{x_i^*}{x_i} + \beta \frac{z_i}{z_i^*} + \beta \ln \frac{z_i^*}{z_i} \right. \right. \\
 &\quad \left. \left. + \frac{y_i}{y_i^*} + \ln \frac{y_i^*}{y_i} \right) \right] \\
 &= \sum_{j=1}^n e_i b_{ij} y_j^* [G_j(x_j, y_j, z_j) - G_i(x_i, y_i, z_i)],
 \end{aligned}$$

(8)

where

$$\begin{aligned}
 G_i(x_i, y_i, z_i) &= \lambda \frac{x_i}{x_i^*} + \lambda \ln \frac{x_i^*}{x_i} + \beta \frac{z_i}{z_i^*} + \beta \ln \frac{z_i^*}{z_i} \\
 &\quad + \frac{y_i}{y_i^*} + \ln \frac{y_i^*}{y_i}.
 \end{aligned}
 \tag{9}$$

Consider a weight matrix $W = (w_{ij})_{n \times n}$ with entry $w_{ij} = e_i b_{ij} y_j^*$, and denote the corresponding weighted digraph as (\mathcal{G}, W) . Let

$$\bar{L} = \begin{pmatrix} \sum_{k \neq 1} w_{1k} & -w_{12} & \cdots & -w_{1n} \\ -w_{21} & \sum_{k \neq 2} w_{2k} & \cdots & -w_{2n} \\ \vdots & \vdots & \ddots & \vdots \\ -w_{n1} & -w_{n2} & \cdots & \sum_{k \neq n} w_{nk} \end{pmatrix}. \tag{10}$$

Note that \bar{L} is the Laplacian matrix of (\mathcal{G}, W) . Since $(b_{ij})_{n \times n}$ is irreducible, we know that $(w_{ij})_{n \times n}$ is irreducible; by Proposition 1, we obtain that $c_i > 0$ for all i . Then, from Theorem 2, the following identity holds:

$$\sum_{i=1}^n c_i \sum_{j=1}^n e_i b_{ij} y_j^* (G_j(x_j, y_j, z_j) - G_i(x_i, y_i, z_i)) = 0. \quad (11)$$

Set

$$V(x_1, y_1, z_1, x_2, y_2, z_2, \dots, x_n, y_n, z_n) = \sum_{i=1}^n c_i V_i(x_i, y_i, z_i). \quad (12)$$

Using (8) and (11), we obtain

$$\begin{aligned} \dot{V} &= \sum_{i=1}^n c_i \dot{V}_i \\ &\leq \sum_{i=1}^n c_i \sum_{j=1}^n e_i b_{ij} y_j^* (G_j(x_j, y_j, z_j) - G_i(x_i, y_i, z_i)) = 0 \end{aligned} \quad (13)$$

for all $(x_1, y_1, z_1, x_2, y_2, z_2, \dots, x_n, y_n, z_n) \in R_+^{3n}$. Therefore, $V = \sum_{i=1}^n c_i V_i$ as defined in Theorem 3.1 of [12] is a Lyapunov function for the system (2); namely, $\dot{V} \leq 0$ for all $(x_1, y_1, z_1, x_2, y_2, z_2, \dots, x_n, y_n, z_n) \in R_+^{3n}$; $\dot{V} = 0$ implies that $x_i = x_i^*$, $y_i = y_i^*$, and $z_i = z_i^*$ for all i . By LaSalle Invariance Principle [16], E^* is globally asymptotically stable in R_+^{3n} ; this also implies that E^* is unique in R_+^{3n} . This completes the proof of Theorem 3. \square

Remark 4. $A = (a_{ij})_{n \times n}$, $B = (b_{ij})_{n \times n}$, and $C = (c_{ij})_{n \times n}$ are dispersal matrices; a typical assumption we impose on these matrices is that they are irreducible. In biological terms, this means individuals in each patch can disperse between any two patches directly or indirectly.

Applying the similar proof as that for Theorem 3, we have the following corollaries.

Corollary 5. Consider the model

$$\begin{aligned} \dot{x}_i &= x_i (r_i - \sigma_i x_i - e_i y_i), \\ \dot{y}_i &= y_i (-\theta_i - \delta_i y_i + \varepsilon_i x_i - \rho_i z_i) \\ &\quad + \sum_{j=1}^n b_{ij} y_j - \sum_{j=1}^n b_{ji} y_i, \quad i = 1, 2, \dots, n, \\ \dot{z}_i &= z_i (-\gamma_i - \alpha_i z_i + \eta_i y_i), \end{aligned} \quad (14)$$

where all the parameters are nonnegative constants, ε_i , e_i , η_i , and ρ_i are positive, and the dispersal matrix $B = (b_{ij})_{n \times n}$ is irreducible. Then, if a positive equilibrium E_* exists in (14), it is unique and globally asymptotically stable in the positive cone R_+^{3n} .

Corollary 6. Consider the model

$$\dot{x}_i = x_i (r_i - \sigma_i x_i - e_i y_i) + \sum_{j=1}^n a_{ij} x_j - \sum_{j=1}^n a_{ji} x_i,$$

$$\dot{y}_i = y_i (-\theta_i - \delta_i y_i + \varepsilon_i x_i - \rho_i z_i), \quad i = 1, 2, \dots, n,$$

$$\dot{z}_i = z_i (-\gamma_i - \alpha_i z_i + \eta_i y_i), \quad (15)$$

where all the parameters are nonnegative constants, ε_i , e_i , η_i , and ρ_i are positive, and the dispersal matrix $A = (a_{ij})_{n \times n}$ is irreducible. Then, if a positive equilibrium \bar{E}_* exists in (15), it is unique and globally asymptotically stable in the positive cone R_+^{3n} .

4. Conclusion

In this paper, we generalize the model of the n -patch predator-prey model of [12] to a three-species food chain model where prey species, mid-level predator species, and top predator species can disperse among n different patches ($n \geq 2$). Our proof of global stability of the positive equilibrium utilizes a graph-theoretical approach to the method of Lyapunov function.

Biologically, Theorem 3 implies that if a three-species food chain system is dispersing among strongly connected patches (which is equivalent to the irreducibility of the dispersal matrixes) and if the system is permanent (which guarantees the existence of positive equilibrium), then the numbers of prey species, mid-level predator species, and top predator species in each patch will eventually be stable at some corresponding positive values given the well-coupled dispersal (condition (H_2) of Theorem 3).

Corollaries 5 and 6 imply that if a three-species food chain system is dispersing among strongly connected patches (only one species can disperse among n different patches ($n \geq 2$)) and if the system is permanent, then the numbers of prey species, mid-level predator species, and top predator species in each patch will eventually be stable at some corresponding positive values.

Theorem 3 requires the extra condition (H_2) ; the global stability for the positive equilibrium of system (2) without condition (H_2) is still unclear. It remains an interesting problem for a three-species food chain model in patchy environment.

Conflict of Interests

The authors declare that there is no conflict of interests.

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