Global Stability for a Predator-Prey Model with Dispersal among Patches

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1. Introduction

In the literature of predator-prey population systems, both continuous reaction-diffusion systems and discrete patchy models are used to study the spatial heterogeneity \cite{1,2}; patchy models are often used to describe directed movement of population among niches or migration among habitats. It is naturally interesting to consider how the dispersal or migration of predator and prey influences the global dynamics of the interacting ecological system; thus patchy predator-prey model received lots of attentions \cite{1,3–6}.

Since the discrete patchy models usually involve high-dimensional system, it is rather mathematically challenging to study the uniqueness and stability of the positive equilibrium of the predator-prey patchy models, and the available global dynamics criteria in the literatures mainly focus on the special case of two-patch \cite{3} or on the permanence and existence of periodic solutions \cite{4–6}.

Recently, Li and Shuai \cite{7} considered the following predator-prey model with dispersal for prey among \( n \)-patch:

\begin{align}
\dot{x}_i &= x_i (r_i - b_i x_i - e_i y_i) + \sum_{j=1}^{n} d_{ij}^x (x_j - \alpha_{ij}^x x_i), \\
\dot{y}_i &= y_i (-\gamma_i - \delta_i y_i + \epsilon_i x_i), \quad i = 1, \ldots, n.
\end{align}

(1)

Here, \( x_i, y_i \) denote the densities of prey and predators on the patch \( i \), respectively. The parameters \( r_i, b_i \) and \( \gamma_i, \delta_i \) in the model are nonnegative constants. What is more, the parameters \( e_i \) and \( \epsilon_i \) in the model are positive constants. Constant \( d_{ij}^x \) is the dispersal rate of the prey from patch \( j \) to patch \( i \) and constants \( \alpha_{ij}^x \) can be selected to represent different boundary conditions in the continuous diffusion case.

In \cite{7}, the authors studied the global stability of the coexistence equilibrium of system (1), by considering (1) as a coupled \( n \) predator-prey submodels on networks. Using results from graph theory and a developed systematic approach that allows one to construct global Lyapunov functions for large-scale coupled systems from building blocks of individual vertex systems, Li and Shuai \cite{7} obtain the following sharp results for (1).

**Proposition 1** (see \cite[Theorem 6.1]{7}). Assume that \((d_{ij}^x)_{n \times n}\) is irreducible. If there exists \( k \) such that \( b_k > 0 \) or \( \delta_k > 0 \), then, whenever a positive equilibrium \( E^*_+ \) exists in (1), it is unique and globally asymptotically stable in the positive cone \( \mathbb{R}_{+n}^n \).

Although well-improved results have been seen in the above work on dispersal predator-prey model, such models are not well studied yet in the sense that model (1) assumes no dispersal for predator, which is not realistic in many cases \cite{1,3}. Thus it is interesting for us to consider the global
stability of the positive equilibrium for predator-prey model with dispersal for both predator and prey.

Motivated by the above work in [7], in this paper we generalize model (1) into the following predator-prey model with dispersal for both predator and prey:

\[
x_i = x_i(r_i - b_i x_i - e_i y_i) + \sum_{j=1}^{n} d_{ij}^x (x_j - \alpha_{ij}^x x_i)
\]

\[
y_i = y_i(-\gamma_i - \delta_i y_i + e_i x_i) + \sum_{j=1}^{n} d_{ij}^y (y_j - \alpha_{ij}^y y_i),
\]

\[
i = 1, \ldots, n.
\]

Here, the parameters \(r_i, b_i, e_i, \gamma_i, \delta_i,\) and \(e_i\) are defined the same as those in (1). The nonnegative constants \(d_{ij}^x, \alpha_{ij}^x,\) and \(d_{ij}^y\) are the dispersal rate of the predators from patch \(j\) to patch \(i\), and \(\alpha_{ij}^y\) represents the different boundary conditions in the continuous diffusion case. Clearly, when \(d_{ij}^x = 0\) for all \(i, j = 1, \ldots, n\), model (2) directly reduces to (1); thus our model (2) directly extends model (1) in [7].

The main purpose of this paper is to obtain the global stability for the coexistence equilibrium of (2). We will engage the techniques of constructing Lyapunov function based on graph-theory which were well developed by Li et al. in [7–9]; we refer to [10–12] for recent applications. Our study seems to be the first attempt in applying the network method for coupled network systems. In Section 3, we obtain the main result of system (2). This is followed by a brief conclusion section.

2. Preliminaries

In this section, we will list some definitions and Theorems that we will use in the later sections.

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

The weight \(w(H)\) of a subgraph \(H\) is the product of the weights on all its arcs. A directed path \(P\) in \(G\) is a subgraph with distinct vertices \(i_1, i_2, \ldots, i_m\) such that its set of arcs is \(\{(i_k, i_{k+1}) : k = 1, 2, \ldots, m\}\). If \(i_m = i_1\), we call \(P\) a directed cycle.

A connected subgraph \(T\) is a tree if it contains no cycles, directed or undirected.

A tree \(T\) is rooted at vertex \(i\), called the root, if \(i\) is not a terminal vertex of any arcs, and each of the remaining vertices is a terminal vertex of exactly one arc. A subgraph \(Q\) is unicyclic if it is a disjoint union of rooted trees whose roots form a directed cycle.

Given a weighted digraph \(G\) 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 \((G, A)\).

A directed graph \((G, A)\) is strongly connected if for any pair of distinct vertices, there exists a directed path from one to the other. A weighted digraph \((G, A)\) is strongly connected if and only if the weight matrix \(A\) is irreducible.

The Laplacian matrix of \((G, A)\) is denoted by \(L\). Let \(c_i\) denote the cofactor of the \(i\)th diagonal element of \(L\). The following results are listed as follows from [7].

Proposition 2 (see [7]). Assume \(n \geq 2\). Then

\[
c_i = \sum_{T \in T_i} w(T),
\]

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

Theorem 3 (see [7]). Assume \(n \geq 2\). Let \(c_i\) be given in Proposition 2. Then the following identity holds:

\[
\sum_{i,j=1}^{n} c_ia_{ij}F_{ij}(x_i, x_j) = \sum_{Q \in Q} w(Q) \sum_{(i,j) \in E(C_Q)} F_{rs}(x_r, x_s),
\]

where \(F_{ij}(x_i, x_j), 1 \leq i, j \leq n,\) are arbitrary functions, \(Q\) is the set of all spanning unicyclic graphs of \((G, A)\), \(w(Q)\) is the weight of \(Q,\) and \(C_Q\) denotes the directed cycle of \(Q\).
each vertex dynamics is described by a system of differential equations
\[ u'_i = f_i(t, u_i), \]
where \( u_i \in \mathbb{R}^m \) and \( f_i : \mathbb{R} \times \mathbb{R}^m \rightarrow \mathbb{R}^m \). Let \( g_{ij} : \mathbb{R} \times \mathbb{R}^m \times \mathbb{R}^m \rightarrow \mathbb{R}^m \) represent the influence of vertex \( j \) on vertex \( i \), and let \( g_{ij} \equiv 0 \) if there exists no arc from \( j \) to \( i \) in \( G \). Then we obtain the following coupled system on graph \( G \):
\[ u'_i = f_i(t, u_i) + \sum_{j=1}^{n} g_{ij}(t, u_i), \quad i = 1, 2, \ldots, n. \]
(6)

Here functions \( f_i \), \( g_{ij} \) are such that initial-value problems have unique solutions.

We assume that each vertex system has a globally stable equilibrium and possesses a global Lyapunov function \( V_i \).

**Theorem 4** (see [7]). Assume that the following assumptions are satisfied.

1. There exist functions \( V_i(t, u_i) \), \( F_{ij}(t, u_i, u_j) \) and constants \( a_{ij} \geq 0 \) such that
\[ \dot{V}_i(t, u_i) \leq \sum_{i,j=1}^{n} a_{ij} F_{ij}(t, u_i, u_j), \quad t > 0, \ u_i \in D_i. \]
(7)

2. Along each directed cycle \( C \) of the weighted digraph \( (G, A) \), \( A = (a_{ij}) \),
\[ \sum_{(s, r) \in (C)} F_{rs}(t, u_s, u_r) \leq 0. \]
(8)

3. Constants \( c_i \) are given by the cofactor of the \( i \)th diagonal element of \( L \).

Then the function \( V(t, u) = \sum_{i=1}^{n} c_i V_i(t, u_i) \) satisfies \( \dot{V}(t, u) \leq 0 \) for \( t > 0, \ u \in D; \) namely, \( V \) is a Lyapunov function for the system (6).

### 3. Main Results

In this section, the stability for the positive equilibrium of the \( n \)-patch predator-prey model (2) is considered. We regard (2) as a coupled system on a network. Using a Lyapunov function for the \( n \)-patch predator-prey model with dispersal and Theorem 4 of Section 2, we will establish that a positive equilibrium of the \( n \)-patch predator-prey model (2) with dispersal is globally asymptotically stable in \( \mathbb{R}_{+}^{2n} \) as long as it exists.

First of all, we will give a lemma for the system (2).

**Lemma 5.** The set \( \mathbb{R}_{+}^{2n} \) is the positive invariant set for the system (2).

The next Theorem gives the globally asymptotically stable condition for the positive equilibrium of the system (2).

**Theorem 6.** Assume that a positive equilibrium \( E^* = (x_1^*, y_1^*, x_2^*, y_2^*, \ldots, x_n^*, y_n^*) \) exists for the system (2) and the following assumptions hold.

1. Dispersal matrices \( (d_{ij}^x)_{n \times n}, (d_{ij}^y)_{n \times n} \) are irreducible; moreover there exists \( k \) such that \( b_k > 0 \) or \( \delta_k > 0 \).

2. There exists nonnegative constant \( \lambda \) such that \( \lambda \cdot d_{ij}^x e_i x_j^* = d_{ij}^y e_i y_j^* \) for \( 1 \leq i, j \leq n \), or \( d_{ij}^x e_i x_j^* = \lambda \cdot d_{ij}^y e_i y_j^* \) for \( 1 \leq i, j \leq n \).

Then, the positive equilibrium \( E^* \) is unique and globally asymptotically stable in \( \mathbb{R}_{+}^{2n} \).

**Proof.** Let
\[ Z_1^i (x_i, y_i) = r_i - b_i x_i - e_i y_i, \]
\[ Z_2^i (x_i, y_i) = -\delta_i y_i + e_i x_i. \]

In the sequel, we have
\[ Z_1^i (x_i^*, y_i^*) = -\frac{1}{x_i^*} \sum_{j=1}^{n} d_{ij}^x (x_j^* - \alpha_{ij} x_i^*), \]
\[ Z_2^i (x_i^*, y_i^*) = -\frac{1}{y_i^*} \sum_{j=1}^{n} d_{ij}^y (y_j^* - \alpha_{ij} y_i^*). \]

Set Lyapunov functions as
\[ V_i(x_i, y_i) = e_i \left( x_i - x_i^* - x_i^* \ln \frac{x_i}{x_i^*} \right) + e_i \left( y_i - y_i^* - y_i^* \ln \frac{y_i}{y_i^*} \right). \]

Direct differentiating \( V_i \) along the system (2), we have
\[ \dot{V}_i(x_i, y_i) = e_i \left( x_i - x_i^* \right) \left[ Z_1^i(x_i, y_i) - Z_1^i(x_i^*, y_i^*) \right] + e_i \left( y_i - y_i^* \right) \left[ Z_2^i(x_i, y_i) - Z_2^i(x_i^*, y_i^*) \right] \]
\[ + e_i \left( y_i - y_i^* \right) \left[ Z_1^i(x_i, y_i) - Z_1^i(x_i^*, y_i^*) \right] + e_i \left( y_i - y_i^* \right) \left[ Z_2^i(x_i, y_i) - Z_2^i(x_i^*, y_i^*) \right] \]
\[ + \sum_{j=1}^{n} d_{ij}^x e_i x_j^* F_{ij}(x_i, x_j) + \sum_{j=1}^{n} d_{ij}^y e_i y_j^* F_{ij}(y_i, y_j) \]
where

\[ F_{ij}^x(x_i, x_j) = \frac{x_j}{x_i} - \frac{x_i}{x_j} + 1 - \frac{x_j^2}{x_i x_j}, \]

\[ F_{ij}^y(y_i, y_j) = \frac{y_j}{y_i} - \frac{y_i}{y_j} + 1 - \frac{y_j^2}{y_i y_j}. \]  

(13)

Set \( a_{ij}^x = d_{ij}^x e_i x^*_j \), \( b_{ij}^y = d_{ij}^y e_i y^*_j \), \( A = (a_{ij})_{n \times n} \), and \( B = (b_{ij})_{n \times n} \).

One has

\[ G_i^x(x_i) = -\frac{x_i}{x_i^*} + \ln \frac{x_i}{x_i^*}, \quad G_i^y(y_i) = -\frac{y_i}{y_i^*} + \ln \frac{y_i}{y_i^*}. \]

(14)

Next, we have two cases to consider.

Case I. \( d_{ij}^x e_i x^*_j = \lambda \cdot d_{ij}^x e_i y^*_j \) for \( 1 \leq i, j \leq n \).

Case II. \( \lambda \cdot d_{ij}^x e_i x^*_j = d_{ij}^y e_i y^*_j \) for \( 1 \leq i, j \leq n \).

For Case I, from the fact that \( a_{ij}^x = d_{ij}^x e_i x^*_j \) and \( b_{ij}^y = d_{ij}^y e_i y^*_j \), we obtain that \( a_{ij}^x = \lambda b_{ij}^y \); thus \( A = \lambda \cdot B \). Then we obtain that

\[ \dot{V}_i(x_i, y_i) \leq -\varepsilon_b(x_i - x_i^*)^2 - \varepsilon_i \delta_i(y_i - y_i^*)^2 \]

\[ + \sum_{j=1}^n a_{ij}^x (G_i^x(x_i) - G_j^x(x_j)) \]

\[ + \sum_{j=1}^n a_{ij}^y \left( 1 - \frac{x_j^* x_j}{x_i x_j} + \ln \frac{x_j^* x_j}{x_i x_j} \right) \]

\[ + \sum_{j=1}^n b_{ij}^y (G_j^y(y_j) - G_j^y(y_j)) \]

\[ + \sum_{j=1}^n b_{ij}^y \left( 1 - \frac{y_j^* y_j}{y_i y_j} + \ln \frac{y_j^* y_j}{y_i y_j} \right). \]  

(12)

Let \( c_i^y \) denote the cofactor of the \( i \)th diagonal element of the matrix \( B \). From the irreducible character of matrix \( B \), we have \( c_i^y > 0 \).

Furthermore, set Lyapunov functions as

\[ V(x, y) = V(x_1, y_1, \ldots, x_n, y_n) \]

\[ = \sum_{i=1}^n c_i^x V_i^x(x_i) + \sum_{i=1}^n c_i^y V_i^y(y_i). \]

(16)

Then differentiating \( V \) along the solution of the system (2), we obtain that

\[ \dot{V}(x, y) \leq -\sum_{i=1}^n c_i^x \varepsilon_b(x_i - x_i^* - y_i - y_i^*)^2 \]

\[ + \sum_{i,j=1}^n \lambda b_{ij}^y c_i^y (G_i^x(x_i) - G_j^x(x_j)) \]

\[ + \sum_{i,j=1}^n b_{ij}^y c_i^y (G_j^y(y_j) - G_j^y(y_j)). \]

(17)

Let \( G \) represent the directed graph associated with matrix \( B \). Then \( G \) has vertices \( 1, 2, \ldots, n \) with a directed arc \((k, j)\) from \( k \) to \( j \) if and only if \( b_{kj}^j \neq 0 \). Then \( E(G) \) is the set of all directed arcs of \( G \). By Kirchoff’s Matrix-Tree Theorem (see Proposition 2) we know that \( t_k = C_{kk} \) can be expressed as a sum of weights of all directed spanning subtrees \( T \) of \( G \) that are rooted at vertex \( k \). Thus, each term in \( v_k a_{k,j} \) is the weight \( \omega(Q) \) of a unicyclic subgraph \( Q \) of \( G \) obtained from such a tree \( T \) by adding a directed arc \((k, j)\) from the root \( k \) to vertex \( j \). Because the arc \((k, j)\) is a part of the unique cycle \( C \) of \( Q \) and that the same unicyclic graph \( Q \) can be formed when each arc of \( C \) is added to a corresponding rooted tree \( T \), then the double sum can be expressed as a sum over all unicyclic subgraphs \( Q \) containing vertices \( 1, 2, \ldots, n \).
Therefore, following from the irreducible character of matrix $B$ and Theorem 2.3 in [7], we obtain
\begin{equation}
\sum_{i,j=1}^{n} b_{ij} y_i^* (G_i^x (x_i) - G_j^y (y_j)) = 0,
\end{equation}
which contradicts to the fact that
\begin{equation}
x_i^* (r_i - b_i x_i^* - e_i y_i^*) + \sum_{j=1}^{n} d_{ij}^x (x_j^* - \alpha_{ij} x_i^*) = 0.
\end{equation}

Next, we will prove that the largest invariant subset of $\{(x, y) \mid V(x, y) = 0\}$ is the singleton $\{E^*\}$. We only consider the case that
\begin{equation}
x_i = x_i^*, \quad \frac{y_i}{y_i^*} = \mu, \quad i = 1, 2, \ldots, n, \quad \mu \geq 0.
\end{equation}

The case that
\begin{equation}
y_i = y_i^*, \quad \frac{x_i}{x_i^*} = \mu, \quad i = 1, 2, \ldots, n, \quad \mu \geq 0
\end{equation}
is similar to this case. So we omit it.

If $\mu = 0$, we have $y_i = 0$ for any $i = 1, 2, \ldots, n$, and then we have
\begin{equation}
x_i^* (r_i - b_i x_i^* - e_i y_i^*) + \sum_{j=1}^{n} d_{ij}^x (x_j^* - \alpha_{ij} x_i^*) = 0,
\end{equation}
which contradicts to the fact that
\begin{equation}
x_i^* (r_i - b_i x_i^* - e_i y_i^*) + \sum_{j=1}^{n} d_{ij}^x (x_j^* - \alpha_{ij} x_i^*) = 0.
\end{equation}

If $\mu > 0$ and $\mu \neq 1$, we have $y_i = \mu y_i^*$ for any $i = 1, 2, \ldots, n$, and then we have
\begin{equation}
x_i^* (r_i - b_i x_i^* - e_i y_i^*) + \sum_{j=1}^{n} d_{ij}^x (x_j^* - \alpha_{ij} x_i^*) = 0,
\end{equation}
which also contradicts to the fact that
\begin{equation}
x_i^* (r_i - b_i x_i^* - e_i y_i^*) + \sum_{j=1}^{n} d_{ij}^x (x_j^* - \alpha_{ij} x_i^*) = 0.
\end{equation}

Therefore, we obtain that $\mu = 1$, which means
\begin{equation}
x_i = x_i^*, \quad y_i = y_i^*, \quad i = 1, 2, \ldots, n.
\end{equation}

Remark 7. Theorem 6 is applicable to model (1): consider model (2) with $d_{ij}^y = 0$, $i, j = 1, \ldots, n$, and let $\lambda = 0$; thus Theorem 6 directly reduces to Proposition 1 by Li and Shuai [7] for (1).

By Theorem 6 and similar arguments to Remark 7, we directly have the following global stability theorem for the predator-prey model with discrete dispersal of predator among patches.

Corollary 8. Consider the model
\begin{equation}
\begin{aligned}
x_i &= x_i (r_i - b_i x_i - e_i y_i), \\
y_i &= y_i (-y_i - \delta_i y_i + e_i x_i) + \sum_{j=1}^{n} d_{ij}^y (y_j - \alpha_{ij} y_i),
\end{aligned}
\end{equation}

Assume that the matrix $(d_{ij}^y)_{n \times n}$ is irreducible. If there exists $k$ such that $b_k > 0$ or $\delta_k > 0$; then, whenever a positive equilibrium $E_*$ exists in (32), it is unique and globally asymptotically stable in the positive cone $R^2_+$. 


4. Discussion

In this paper, we generalize the model of the $n$-patch predator-prey model of [7] to the general model (2) that both the prey and the predator have dispersal among $n$-patches. Based on the network method for coupled systems of differential equations developed in [7–9], we prove that the positive equilibrium of (2) is globally asymptotically stable given some conditions on the coupling (see Theorem 6). Our main theorem generalizes Theorem 6.1 in [7] and our results also cover the other case of (2) in that only the predators disperse among patches.

Biologically, our result of Theorem 6 implies that if predator-prey system is dispersing among strongly connected patches (which is equivalent to the irreducibility of the dispersal matrices of predator and prey) and if the system is permanent (which guarantees the existence of positive equilibrium), then the numbers of both predators and prey in each patches will eventually be stable at some corresponding positive values given the well-coupled dispersal (condition 2 of Theorem 6).

We remark that our Theorem 6 requires the extra condition 2 for the coupling dispersal coefficients and that the global dynamics for the coexistence equilibrium of (2) without condition 2 of Theorem 6 are still unclear. It remains an interesting future problem for the patchy dispersal predator-prey model.

Conflict of Interests

The authors declare that there is no conflict of interests regarding the publication of this paper.

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