The Effects of Habitat Fragmentation and Ecological Invasion on Population Sizes

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Abstract—In this paper, we consider the effects of habitat fragmentation and ecological invasion of exotic species on the survival of a native endangered species, respectively. Different from the former studies, we pay attention on the more important situation in conservation biology that species live in a weak patchy environment in the sense that species in some of the isolated patches will become extinct without the contribution from other patches. We establish some fundamental permanence and extinction results on the basic and important nonautonomous diffusive Logistic model. In addition, by using these results, we consider the effect of an introduced species on the survival of a native species through competition. Biological implications of these results are discussed. © 1999 Elsevier Science Ltd. All rights reserved.

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1. INTRODUCTION

Rare and endangered species face extinction through a variety of mechanisms, including destruction and fragmentation of their habitats and ecological invasion of exotic species [1,2]. In this article, the following important biological questions are approached using Lotka-Volterra diffusion models.

1. How does the diffusion affect the survival of an endangered species?
2. How does the introduced species affect the survival of a native endangered species through competition?

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Since the pioneering theoretical work by Skellem [3], many works have focused on the effect of diffusion on the persistence and stability of autonomous population systems (for example [4-8]). Recently, some authors have also studied the influence of diffusion on time dependent population models (see [9-14]). Assuming that the intrinsic growth rates are all continuous and bounded above and below by positive constants (this means that every species lives in a suitable environment), they obtained some sufficient conditions that guarantee permanence of every species and global stability of a unique positive periodic solution.

However, the actual situation is not always like this. Because of the ecological effects of human activities and industry, the location of manufacturing industries, the pollution of the atmosphere, of rivers, of soil, etc., more and more habitats are broken into patches and some of the patches are polluted. In some of these patches, the species will go extinct without the contribution from other patches, and hence, the species live in a weak patchy environment. The living environments of some endangered and rare species such as the giant panda [15], alligator sinensis [16], and rana temporaria [17] are some convincing examples. This fact urged us to consider the effects of habitat fragmentation and ecological invasion on the permanence and extinction of a single species living in a weak environment.

In [18], we studied the effects of diffusion on the permanence and extinction of species living in weak but periodic environments. In the present paper, we consider the effects of habitat fragmentation and ecological invasion on a single species that obeys a general nonautonomous logistic population model.

The organization of this paper is as follows. In the next section, we agree on some notations, give important definitions and state two lemmas which will be essential to our proofs. In Section 3 the effect of habitat fragmentation is considered, and some foundational results are stated and proved. We obtain that the system can be made either permanent or extinct under different appropriate diffusion conditions, even if the corresponding isolated patches are not persistent. By using the main results of Section 3, we consider the effect of an introduced competitive species on the survival of a native species in Section 4. The biological meaning of the results obtained in this paper are discussed in Section 5.

2. NOTATION, DEFINITION, AND PRELIMINARIES

In this section, we introduce a definition, some notations, and state some results which will be useful in subsequent sections. Let $C$ denotes the space of all bounded continuous functions $f : \mathbb{R} \to \mathbb{R}$ and $C_+$ is the set of all $f \in C$ such that $f$ is bounded below by a positive constant. Given $f$ in $C$, we denote

$$f^M = \sup_{t \geq 0} f(t), \quad f^L = \inf_{t \geq 0} f(t),$$

and define the lower average $A_L(f)$ and upper average $A_M(f)$ of $f$ by

$$A_L(f) = \lim_{r \to \infty} \inf_{t-s \geq r} (t-s)^{-1} \int_s^t f(\tau) \, d\tau$$

and

$$A_M(f) = \lim_{r \to \infty} \sup_{t-s \geq r} (t-s)^{-1} \int_s^t f(\tau) \, d\tau,$$

respectively. If $f \in C$ is $\omega$-periodic, then the average $A_\omega(f)$ of $f$ must be equal to $A_L(f)$ and $A_M(f)$, that is

$$A_\omega(f) = A_L(f) = A_M(f) = \omega^{-1} \int_0^\omega f(t) \, dt.$$
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DEFINITION. The system of differential equations

\[ \dot{x} = F(t, x), \quad x \in \mathbb{R}^n \]

is said to be cooperative if the off diagonal elements of $D_x F(t, x)$ are nonnegative and competitive if the off diagonal elements are nonpositive, where $D_x F(t, x)$ is the $n \times n$ matrix derivative of $F$ with respect to $x$.

**Lemma 1.** (See [19].) The problem

\[ \dot{x} = x[b(t) - a(t)x], \quad x \in C_+ \quad (1) \]

has exactly one canonical solution $U$ if $a \in C_+$, $b \in C$, and $A_L(b) > 0$. Moreover, the following properties hold.

(a) $U$ is $\omega$-periodic (almost periodic) if $a, b$ are $\omega$-periodic (almost periodic).

(b) $U$ is constant if $b/a$ is constant. In this case, $U = b/a$.

(c) $u(t) - U(t) \to 0$ as $t \to \infty$, for any positive solution $u(t)$ of equation (1).

(d) $(b/a)^L \leq U \leq (b/a)^M$.

**Lemma 2.** (See [14].) Let $x(t)$ and $y(t)$ be solutions of

\[ \dot{x} = F(t, x) \]

and

\[ \dot{y} = G(t, y), \]

respectively, where both systems are assumed to have the uniqueness property for initial value problems. Assume both $x(t)$ and $y(t)$ belong to a domain $D \subseteq \mathbb{R}^n$ for $[t_0, t_1]$ in which one of the two systems is cooperative and

\[ F(t, z) \leq G(t, z), \quad (t, z) \in [t_0, t_1] \times D. \]

If $x(t_0) \leq y(t_0)$, then $x(t_1) \leq y(t_1)$. If $F = G$ and $x(t_0) < y(t_0)$, then $x(t_1) < y(t_1)$.

3. THE EFFECT OF HABITAT FRAGMENTATION ON SINGLE SPECIES

In this section, we consider the system as composed of patches connected by discrete diffusions with each patch assumed to be occupied by a single species as follows:

\[ \dot{x}_i = x_i[b_i(t) - a_i(t)x_i] + \sum_{j=1}^{n} D_{ij}(t)(x_j - x_i), \quad (i = 1, 2, \ldots, n), \quad (2) \]

where $x_i(i = 1, 2, \ldots, n)$, defined in $\mathbb{R}^n_+ = \{(x_1, x_2, \ldots, x_n) \in \mathbb{R}^n \mid x_1 \geq 0, x_2 \geq 0, \ldots, x_n \geq 0\}$, is the concentration of species $x$ in patch $i$. $b_i \in C$, $a_i, D_{ij} \in C_+$ ($i \neq j$) and $D_{ii}(t) \equiv 0$. $b_i(t)$ is the intrinsic growth rate for species $x$ in patch $i$; $a_i(t)$ represents the self-inhibition coefficient and $D_{ij}(t)$ is the diffusion coefficient of species $x$ from patch $j$ to patch $i$.

If $1 \leq i, j \leq 2$ and the functions $a_i(t), b_i(t)$ are continuous and bounded above and below by positive constants, Wang, Chen and Lu [10] showed that the system is permanent for any continuous, nonnegative, and bounded diffusion rates $D_{ij}(t)$. In fact, by using an entirely similar argument as in Lemma 1 in [10], we can show that this result is also true for general system (2).

However, the most endangered species live in weak environments. In order to protect these species, we should investigate an important question in conservation biology, namely, to what extent does diffusion lead to the permanence or extinction of species which could not persist within some isolated patches? This is the purpose of this section.
THEOREM 1. Given any $\xi_i > 0$ ($i = 1, 2, \ldots, n$), the initial value problem

$$
\begin{align*}
\dot{x}_i &= x_i[b_i(t) - a_i(t)x_i] + \sum_{j=1}^{n} D_{ij}(t)(x_j - x_i), \\
\quad x_i(0) &= \xi_i, \quad i, j = 1, 2, \ldots, n
\end{align*}
$$

has a unique solution $x(t) = (x_1(t), x_2(t), \ldots, x_n(t))$ which exists for all $t \geq 0$. Moreover, there exists $M > 0, \tau > 0$ such that

$$0 < x_i(t) \leq M, \quad \text{for } t \geq \tau.$$  

The region $D = \{(x_1, x_2, \ldots, x_n) \mid 0 < x_i \leq M, \ i = 1, 2, \ldots, n\}$ is positively invariant with respect to (2).

PROOF. Define

$$V(x(t)) = \max_{1 \leq i \leq n} \{x_i(t)\}.$$  

Calculating the upper right derivative of $V(x(t))$ along positive solutions of (3), we have

$$D^+V \leq V \max_{1 \leq i \leq n} \{b_i(t) - a_i(t)V\}.$$  

Denote $M = \max_{1 \leq i \leq n} \{|b_i^L| + \epsilon/a_i^L\}$, where $\epsilon$ is any positive constant. If $V \geq M$, then

$$D^+V \leq -\epsilon V.$$  

Hence, there exists $\tau = \tau(x_1(0), x_2(0), \ldots, x_n(0)) > 0$, such that $V(t) \leq M$ for all $t \geq \tau$, which means that $x_i(t) \leq M$ ($i = 1, 2, \ldots, n$) for all $t \geq \tau$ if $x(t)$ exists. But the ultimate boundedness implies that $x(t)$ exists for all $t > 0$. Furthermore,

$$\dot{x}_i \big|_{x_i = 0, x_j > 0} = \sum_{j=1}^{n} D_{ij}(t)x_j > 0,$$

$$\dot{x}_i \big|_{x_i = M, x_j \geq x_j} \leq M \left(b_i^M - a_i^L M\right) < 0.$$  

Hence, all solutions of (3) initiating in the boundary of $D$ enter the region $D$ for $t \geq 0$, so $D$ is positively invariant with respect to (2). This completes the proof.

A consequence of Theorem 1 is that for $\xi_i > 0$ ($i = 1, 2, \ldots, n$), the solution of (3) is ultimately bounded above. We will show that this solution is also ultimately bounded below away from zero provided that one of the following conditions is satisfied.

(H1) There exists $i_0$ ($1 \leq i_0 \leq n$), such that $A_{L}(\theta) > 0$, where $\theta(t) = b_{i_0}(t) - \sum_{j=1}^{n} D_{i_0j}(t)$.

(H2) $A_L(\phi) > 0$, where $\phi(t) = \min_{1 \leq i \leq n} \{b_i(t) - \sum_{j=1}^{n} D_{ij}(t) + \sum_{j=1}^{n} D_{ji}(t)\}$.

THEOREM 2. Suppose that H1 or H2 holds. Then there exists $\delta_i, 0 < \delta_i < M$ and $\tau \geq 0$, such that solutions of (3) satisfies

$$x_i(t) \geq \delta_i, \quad t \geq \tau, \quad i = 1, 2, \ldots, n,$$  

where $\delta_i$ ($i = 1, 2, \ldots, n$) depend on Assumptions H1 and H2.

PROOF. Suppose that H1 holds. We have

$$\dot{x}_{i_0} > x_{i_0}[\theta(t) - a_{i_0}(t)x_{i_0}].$$  

By Lemma 1, the logistic equation

$$\dot{u} = u[\theta(t) - a_{i_0}(t)u]$$

(6)
has a unique positive globally asymptotically stable canonical solution \( \hat{u}(t) \subset [\delta_{i_0}, \delta_{i_0}] \) where \( \delta_{i_0} = (\theta/a_{i_0})^L, \delta_{i_0} = (\theta/a_{i_0})^M. \)

Let \( u(t) \) be the solution of (6) with \( u(0) = x_{i_0}(0) \). By Lemma 2, \( x_{i_0}(t) \geq u(t) > 0 \). Take \( \epsilon_{i_0} = \delta_{i_0}/2 \). Then there exists \( T_{i_0} = T_{i_0}(x_1(0), x_2(0), \ldots, x_n(0)) \), such that

\[
|u(t) - \hat{u}(t)| < \epsilon_{i_0}, \quad \text{for } t \geq T_{i_0}.
\]

Then

\[
x_{i_0}(t) \geq u(t) > \hat{u}(t) - \epsilon_{i_0} \geq \frac{\delta_{i_0}}{2} = \delta_{i_0}.
\]

Moreover, for every \( j \neq i_0 \) we have

\[
\dot{x}_j \geq -a_j^M x_j^2 + \left( b_j^L - \sum_{k=1}^n D_{j,k}^M \right) x_j + D_{j,i_0}^L \delta_{i_0} = f(x_j), \quad \text{for } t \geq T_{i_0}.
\]

The algebraic equation

\[
a_j^M x_j^2 - \left( b_j^L - \sum_{k=1}^n D_{j,k}^M \right) x_j - D_{j,i_0}^L \delta_{i_0} = 0
\]

gives us one positive root

\[
x_j = \frac{b_j^L - \sum_{k=1}^n D_{j,k}^M + \sqrt{ \left( b_j^L - \sum_{k=1}^n D_{j,k}^M \right)^2 + 4a_j^M D_{j,i_0}^L \delta_{i_0} } }{2a_j^M}.
\]

Clearly, \( f(x_j) > 0 \) for every positive number \( x_j (0 \leq x_j < \bar{x}_j) \). Choose \( \delta_j (0 < \delta_j < \bar{x}_j) \), \( \dot{x}_j|_{x_j=\delta_j} > f(\delta_j) > 0 \). If \( x_j(T_{i_0}) \geq \delta_j \), then it also holds for \( t \geq T_{i_0} \); if \( x_j(T_{i_0}) < \delta_j \), then

\[
\dot{x}_j(T_{i_0}) \geq \inf \{ f(x_j) \mid 0 \leq x_j < \delta_j \} > 0
\]

and there must exist \( T_j \geq T_{i_0} \), such that \( x_j(t) \geq \delta_j \) for \( t \geq T_j \). Therefore, (5) applies with \( r = \max_{1 \leq j \leq n} T_j \).

PROOF 2. Suppose that H2 holds. Choose the function

\[
\rho = \rho(x_1, x_2, \ldots, x_n) = x_1 + x_2 + \cdots + x_n.
\]

Calculating the derivative of \( \rho \) along solutions of (2), we have

\[
\dot{\rho}(t) = \sum_{i=1}^n \left[ b_i(t) - \sum_{j=1}^n D_{ij}(t) + \sum_{j=1}^n D_{ji}(t) \right] x_i - \sum_{i=1}^n a_i(t)x_i^2 \geq \rho(\phi(t) - a(t)\rho),
\]

where \( a(t) = \max_{1 \leq i \leq n} \{a_i(t)\} \). By Lemma 1 and H2, the logistic equation

\[
\dot{v} = v[\phi(t) - a(t)v]
\]

has a unique positive globally asymptotically canonical solution \( \hat{v}(t) \subset [p, q] (0 < p < q) \), where \( p = (\phi/a)^L, q = (\phi/a)^M \). Let \( v(t) \) be the solution of (8) with \( v(0) = \sum_{i=1}^n x_i(0) \). By Lemma 2, \( \rho(t) \geq v(t) > 0 \). Taking \( \epsilon = p/2 \), there exists \( T = T(x_1(0), x_2(0), \ldots, x_n(0)) \), such that

\[
|v(t) - \hat{v}(t)| < \epsilon, \quad \text{for } t \geq T.
\]
Then
\[ x_1(t) + x_2(t) + \cdots + x_n(t) > \bar{v} - \epsilon \geq \frac{p}{2} = \eta, \quad \text{for } t \geq T. \] (9)

Hence,
\[
\dot{x}_i = x_i \left[ b_i(t) - \sum_{j=1}^{n} D_{ij}(t) - a_i(t)x_i \right] + \sum_{j=1}^{n} D_{ij}(t)x_j
\]
\[
> x_i \left( b_i^L - D_0 - \sum_{j=1}^{n} D_{ij}^M - a_i^M x_i \right) + D_0 \eta
\]
or
\[
\dot{x}_i > -a_i^M x_i^2 - \left( \sum_{j=1}^{n} D_{ij}^M + D_0 - b_i^L \right) x_i + D_0 \eta,
\]
for \( t \geq T \) and \( i = 1, 2, \ldots, n \), where \( D_0 = \min_{1 \leq i, j, k \leq n} \{ D_{ij}^L \} > 0 \).

The algebraic equation
\[
a_i^M x_i^2 + \left( \sum_{j=1}^{n} D_{ij}^M + D_0 - b_i^L \right) x_i - D_0 \eta = 0
\]
gives us one positive root
\[
\tilde{x}_i = \frac{b_i^L - D_0 - \sum_{j=1}^{n} D_{ij}^M + \sqrt{\left( b_i^L - D_0 - \sum_{j=1}^{n} D_{ij}^M \right)^2 + 4 D_0 \eta a_i^M}}{2 a_i^M}, \quad (i = 1, 2, \ldots, n).
\]
An argument similar to Proof 1 shows that there exists \( \epsilon_i \) (\( \epsilon_i < M \), \( i = 1, 2, \ldots, n \)) and \( T' (\geq T) \) such that (5) holds for \( T' \). This completes the proof.

Theorems 1 and 2 have established that under one of the Assumptions H1 or H2, there exist positive constants \( m \) and \( M \) such that solutions of (2) with positive initial values ultimately enter the rectangular region \( \Omega = \{ (x_1, x_2, \ldots, x_n) \mid m \leq x_i \leq M, \; i = 1, 2, \ldots, n \} \), and therefore, the population is permanent.

Applying the above theorems to a two-patches system, we obtain the following result.

**COROLLARY 1.** If \( n = 2 \), let one of the following Conditions A1–A4 hold:

(A1) \( A_L(b_1(t) - D_{12}(t)) > 0 \),

(A2) \( A_L(b_2(t) - D_{21}(t)) > 0 \),

(A3) \( b_1(t) + D_{21}(t) - D_{12}(t) \geq b_2(t) + D_{12}(t) - D_{21}(t) \), and \( A_L(b_2(t) + D_{12}(t) - D_{21}(t)) > 0 \),

(A4) \( b_2(t) + D_{12}(t) - D_{21}(t) \geq b_1(t) + D_{21}(t) - D_{12}(t) \), and \( A_L(b_1(t) + D_{21}(t) - D_{12}(t)) > 0 \).

Then the population is permanent.

**REMARK 1.** According to the proof of Theorem 2, if species \( x \) is permanent in a fixed patch \( i \), then species \( x \) is also permanent in other patches for any diffusion rates \( D_{ji}(t) \) (\( i, j = 1, 2, \ldots, n \)). Assumption H1 implies that if the lower average of the sum of diffusion rates from patch \( j \) (\( j = 1, 2, \ldots, n \)) to patch \( i \) is less than that of the intrinsic growth rate of patch \( i \) (\( i \neq j \)), then species \( x \) is permanent even if the isolated patch \( j \) is not persistent.

Next we will consider the extinction of system (2). Denote
\[
\psi(t) = \max_{1 \leq i \leq n} \left\{ b_i(t) - \sum_{j=1}^{n} D_{ij}(t) + \sum_{j=1}^{n} D_{ji}(t) \right\}.
\]
THEOREM 3. Suppose that \( \int_0^{+\infty} \psi(t) \, dt = -\infty \). Then the solutions of (2) satisfy
\[
x_i(t) \to 0, \quad i = 1, 2, \ldots, n, \quad \text{as} \quad t \to +\infty.
\] (10)

PROOF. Consider the function \( \rho = \sum_{i=1}^{n} x_i \) defined in Theorem 2, and calculate the derivative of the function \( \rho \) along solutions of (2):
\[
\dot{\rho} \big|_{(2)} = \sum_{i=1}^{n} \left[ b_i(t) - \sum_{j=1}^{n} D_{ij}(t) + \sum_{j=1}^{n} D_{ji}(t) \right] x_i - \sum_{i=1}^{n} a_i(t)x_i^2 < \psi(t)\rho.
\]

Let \( u(t) \) be the solution of the equation
\[
\dot{u} = \psi(t)u,
\]
with \( u(0) = \rho(0) \). By Lemma 2, \( \rho(t) \leq \rho(0) \exp(\int_0^t \psi(\tau) \, d\tau) \). Since \( \int_0^{+\infty} \psi(t) \, dt = -\infty \), we have \( \rho \to 0 \) as \( t \to +\infty \). So \( x_i(t) \to 0 \) as \( t \to +\infty \). This completes the proof.

COROLLARY 2. If \( n = 2 \) and the following Condition A5 or A6 holds,

(A5) \( b_1(t) + D_{21}(t) - D_{12}(t) \geq b_2(t) + D_{12}(t) - D_{21}(t) \) and \( \int_0^{+\infty} [b_1(t) + D_{21}(t) - D_{12}(t)] \, dt = -\infty \);

(A6) \( b_1(t) + D_{21}(t) - D_{12}(t) \leq b_2(t) + D_{12}(t) - D_{21}(t) \) and \( \int_0^{+\infty} [b_2(t) + D_{12}(t) - D_{21}(t)] \, dt = -\infty \),

then \( x_i(t) \to 0 \) (\( i = 1, 2 \)) as \( t \to +\infty \).

In fact, Condition A5 or A6 implies \( \psi(t) = b_1(t) + D_{21}(t) - D_{12}(t) \) or \( \psi(t) = b_2(t) + D_{12}(t) - D_{21}(t) \), respectively. Applying Theorem 3, the corollary is true.

EXAMPLE 1. Consider a simple example that illustrates a biological consequence of the results in Theorems 1–3, consider the system
\[
\begin{align*}
\dot{x}_1 &= x_1 \left[ 1 + \frac{1}{4} \sin t - \frac{1}{4 + t} - a_1(t)x_1 \right] + D_{12}(t)(x_2 - x_1), \\
\dot{x}_2 &= x_2 \left[ -2 + \frac{1}{4} \sin t - a_2(t)x_2 \right] + D_{21}(t)(x_1 - x_2).
\end{align*}
\] (11)

If the patches are isolated from each other, it is clear that species \( x \) will be permanent in patch 1 and will be extinct in patch 2. Condition A5 holds if \( D_{12}(t) - D_{21}(t) \leq 1/2(3 - 1/4 + t) \) and \( \int_0^{+\infty} [1 + 1/4 \sin t + D_{21}(t) - D_{12}(t)] \, dt = -\infty \). Corollary 2 implies that system (11) goes extinct. This means that if the inherent net birth rate of species \( x \) in patch 2 is negative and small enough, then the stabilizing effect in system (11) is weaker than the destabilizing influence and causes the overall system (11) to go extinct. On the other hand, if \( A_L(D_{12}) < 1 \), then A1 holds. By Corollary 1, system (11) is permanent for any diffusion rate \( D_{21}(t) > 0 \).

REMARK 2. The above conclusion implies that the diffusion rates play an important role in the determination of the permanence and extinction of species \( x \) in a patchy environment. We can choose appropriate diffusion rates causing system (2) either to be permanent or to go extinct.

4. THE EFFECT OF ECOLOGICAL INVASION ON NATIVE SPECIES

In this section, we introduce an exotic competition species \( y \) into some patches which are occupied by native species \( x \). Assume that species \( x \) and \( y \) obey the following Lotka-Volterra diffusion model:
\[
\begin{align*}
\dot{x}_i &= x_i [b_i(t) - a_i(t)x_i - c_i(t)y_i] + \sum_{j=1}^{n} D_{ij}(t)(x_j - x_i), \\
\dot{y}_i &= y_i [d_i(t) - e_i(t)x_i - q_i(t)y_i] + \sum_{j=1}^{n} \lambda_{ij}(t)(y_j - y_i),
\end{align*}
\] (12)

\( i = 1, 2, \ldots, n \).
where \( y_i \) is the concentration of species \( y \) in patch \( i \), and \( c_i(t), e_i(t) \) and \( \lambda_{ij}(t) \) are all nonnegative and bounded continuous functions. In addition, \( d_i \in C, q_i \in C_+ \), and \( \lambda_{ii}(t) \equiv 0 \). We will consider the effect of the introduced species \( y \) on the survival of the native species \( x \).

**Theorem 4.** Let \((x_1(t), \ldots, x_n(t), y_1(t), \ldots, y_n(t))\) be a solution of (12) with positive initial conditions. Then there exist positive constants \( N_{x_i}, N_{y_i}, \) and \( \tau_1 \), such that

\[
0 < x_i(t) \leq N_{x_i}, 0 < y_i(t) \leq N_{y_i}, \quad i = 1, 2, \ldots, n, \quad t \geq \tau_1.
\]

**Proof.** Obviously, \( R^+_n \) is a positive invariant set of system (12). For every positive solution \((x_1(t), \ldots, x_n(t), y_1(t), \ldots, y_n(t))\) of (12), we have

\[
\dot{x}_i \leq x_i [b_i(t) - a_i(t)x_i] + \sum_{j=1}^{n} D_{ij}(t)(x_j - x_i),
\]

\[
\dot{y}_i \leq y_i [d_i(t) - q_i(t)y_i] + \sum_{j=1}^{n} \lambda_{ij}(t)(y_j - y_i),
\]

\( i, j = 1, 2, \ldots, n. \)

By Lemma 2 and Theorem 1, there exists \( \tau_1 > 0 \), such that

\[
0 < x_i(t) \leq N_{x_i}, \quad 0 < y_i(t) \leq N_{y_i},
\]

for \( i = 1, 2, \ldots, n \) and \( t \geq \tau_1 \), where

\[
N_{x_i} = \max_{1 \leq i \leq n} \{ |b_i| + \epsilon/a_i \}, \quad N_{y_i} = \max_{1 \leq i \leq n} \{ |d_i| + \epsilon/q_i \}
\]

and \( \epsilon \) be any positive constant. This completes the proof.

**Theorem 5. Part 1.** Suppose that Assumption H3 or H4 holds.

(H3) There exists \( i_0 \) \((1 \leq i_0 \leq n)\), such that \( A_L(\theta_1) > 0 \), where \( \theta_1(t) = b_{i_0}(t) - c_{i_0}(t)N_{y_{i_0}} - \sum_{j=1}^{n} D_{i_0j}(t). \)

(H4) \( A_L(\phi_1) > 0 \), where \( \phi_1(t) = \min_{1 \leq i \leq n} \{ b_i(t) - c_i(t)N_{y_i} - \sum_{j=1}^{n} D_{ij}(t) + \sum_{j=1}^{n} D_{ji}(t) \}. \)

Then there exist \( \zeta_{x_i}(0 < \zeta_{x_i} \leq N_{x_i}) \) and \( \tau_2 \geq \tau_1 \), such that

\[
x_i(t) \geq \zeta_{x_i}, \quad \text{for } i = 1, 2, \ldots, n, \quad t \geq \tau_2.
\]

**Theorem 5. Part 2.** Suppose that \( \lambda_{ij}(t) \) \((i \neq j)\) is continuous and bounded above and below by positive constants, and Assumption H5 or H6 holds.

(H5) There exists \( i_0 \) \((1 \leq i_0 \leq n)\), such that \( A_L(\theta_2) > 0 \), where \( \theta_2(t) = d_{i_0}(t) - e_{i_0}(t)N_{x_{i_0}} - \sum_{j=1}^{n} \lambda_{i_0j}(t). \)

(H6) \( A_L(\phi_2) > 0 \), where \( \phi_2(t) = \min_{1 \leq i \leq n} \{ d_i(t) - e_i(t)N_{x_i} - \sum_{j=1}^{n} \lambda_{ij}(t) + \sum_{j=1}^{n} \lambda_{ji}(t) \}. \)

Then there exist \( \zeta_{y_i}(0 < \zeta_{y_i} \leq N_{y_i}) \) and \( \tau_3 \geq \tau_2 \), such that

\[
y_i(t) \geq \zeta_{y_i}, \quad \text{for } i = 1, 2, \ldots, n, \quad t \geq \tau_3.
\]

**Proof 1.** By Theorem 4, there exists \( \tau_1 > 0 \), such that

\[
\dot{x}_i \geq x_i [b_i(t) - c_i(t)N_{y_i} - a_i(t)x_i] + \sum_{j=1}^{n} D_{ij}(t)(x_j - x_i), \quad t \geq \tau_1.
\]

Let \((u_1(t), \ldots, u_n(t))\) be the solution of the following initial value problem:

\[
u_i = u_i [b_i(t) - c_i(t)N_{y_i} - a_i(t)u_i] + \sum_{j=1}^{n} D_{ij}(t)(u_j - u_i),
\]

\[
u_i(\tau_1) = x_i(\tau_1), \quad i = 1, 2, \ldots, n.
\]
By Theorem 2 and Lemma 2, there exists \( x_{zi} \) \((0 < x_{zi} \leq N_{zi})\) and \( \tau_2 \) \((\tau_2 \geq \tau_1)\), such that
\[
x_i(t) \geq x_{zi}, \quad \text{for } t \geq \tau_2
\]
provided Condition H3 or H4 holds.

The proof of Theorem 5, Part 2 is entirely similar to Part 1, so we omit it. This completes the proof.

Next we will consider the extinction of species \( x \). Denote
\[
\chi(t) = \max_{1 \leq i \leq n} \left\{ \sum_{j=1}^{n} D_{ij}(t) + \sum_{j=1}^{n} D_{ji}(t) \right\}.
\]

**THEOREM 6.** Suppose that \( \int_{0}^{+\infty} \chi(t) \, dt = -\infty \). If H5 or H6 holds, then solutions of (12) satisfy
\[
\lim_{t \to +\infty} x_i(t) = 0, \quad (i = 1, 2, \ldots, n).
\]

**PROOF.** By Theorem 5, we have
\[
x_i \leq x_i \left[ \sum_{j=1}^{n} D_{ij}(t)(x_j - x_i) \right] + \sum_{j=1}^{n} D_{ij}(t)(x_j - x_i), \quad \text{for } t \geq \tau_3.
\]

Let \((v_1(t),\ldots,v_n(t))\) be the solution of the following initial value problem:
\[
\begin{align*}
v_i'(t) &= v_i \left[ \sum_{j=1}^{n} D_{ij}(t)(v_j - v_i) + \sum_{j=1}^{n} D_{ij}(t) \right], \\
v_i(\tau_3) &= x_i(\tau_3), \quad i = 1, 2, \ldots, n.
\end{align*}
\tag{17}
\]

By Theorem 3 and Lemma 2, we obtain the desired result.

**EXAMPLE 2.** For simplicity, we consider the following periodic patchy competition system:
\[
\begin{align*}
\dot{x}_1 &= x_1 \left( \frac{1}{4} \sin t - x_1 - y_1 \right) + D_{12}(t)(x_2 - x_1), \\
\dot{x}_2 &= x_2 \left( \frac{1}{2} + \frac{1}{4} \sin t - x_2 - y_2 \right) + D_{21}(t)(x_1 - x_2), \\
\dot{y}_1 &= y_1(3 + \cos t - x_1 - y_1), \\
\dot{y}_2 &= y_2(3 + \cos t - x_2 - y_2),
\end{align*}
\tag{18}
\]

where \( D_{12}(t) \) and \( D_{21}(t) \) are 2\( \pi \)-periodic functions.

Without the invasion of the competition species \( y \), we have
\[
\begin{align*}
\dot{x}_1 &= x_1 \left( \frac{1}{4} \sin t - x_1 \right) + D_{12}(t)(x_2 - x_1), \\
\dot{x}_2 &= x_2 \left( \frac{1}{2} + \frac{1}{4} \sin t - x_2 \right) + D_{21}(t)(x_1 - x_2).
\end{align*}
\tag{19}
\]

By Corollary 1, species \( x \) is permanent provided
\[
D_{21} - D_{12} \leq \frac{1}{4} \quad \text{and} \quad A_{2\pi}(D_{21} - D_{12}) > 0.
\tag{20}
\]

Moreover, for any positive solution of (18), there exists \( \tau_1 > 0 \), such that
\[
x_i(t) < 1, \quad \text{for } t \geq \tau_1.
\]
Next we consider the influence of the invasion species \( y \) on the survival of the native species \( x \).

\[
\dot{y}_i \geq y_i(2 + \cos t - y_i) \geq y_i(1 - y_i), \quad t \geq \tau_1.
\]

Hence, there exists \( \tau_2 (\tau_2 \geq \tau_1) \), such that \( \dot{y}_i(t) > 1/2 \) (\( i = 1, 2 \)), and so we have

\[
\begin{align*}
\dot{x}_1 &\leq x_1 \left( -\frac{1}{2} + \frac{1}{4} \sin t - x_1 \right) + D_{12}(t)(x_2 - x_1), \\
\dot{x}_2 &\leq x_2 \left( \frac{1}{4} \sin t - x_2 \right) + D_{21}(t)(x_1 - x_2),
\end{align*}
\]

for \( t \geq \tau_2 \). By Corollary 2 and Lemma 2 or Theorem 6 directly, species \( x \) goes extinct under the condition (20).

5. DISCUSSION

In this paper, we considered the effects of diffusion and invaded competitive species on the permanence or extinction of an indigenous species. In Section 3, we find that habitat fragmentation is a major factor in the determination of the permanence or extinction of the endangered species. Habitat fragmentation can make the species \( x \) either permanent or extinct in every patch depending on the choice of the diffusion rates. Within the context of the model (2) used here, Theorems 1–3 of this paper show that an endangered species can avoid extinction by choosing a suitable diffusion rate.

In Example 1, species \( x \) will be permanent in patch 1 and go extinct in patch 2 if the patches are isolated from each other. If we restrict the diffusion rate from patch 2 to patch 1 small enough so that it satisfies \( A_1(D_{12}) < 1 \), then the species \( x \) will be permanent. On the other hand, species \( x \) will go to extinct if we restrict the diffusion rates varying in the narrow region \( D_{12}(t) - D_{21}(t) \leq 1/2(3 - 1/4 + t) \) and \( \int_0^{\infty} [1 + 1/4\sin t + D_{21}(t) - D_{12}(t)] \, dt = -\infty \). Hence, dispersal plays an important role on the survival of an endangered species.

In Section 4, we introduced an exotic competition species \( y \) into some patches which were occupied by native species \( x \). The effect of species \( y \) on the survival of species \( x \) is profound and lasting. The exotic competition species can make the native species either permanent or extinct in different diffusion conditions. In particular, Example 2 implies that the competitor \( y \) will result in the extinction of indigenous species \( x \), although species \( x \) maintains permanence without the invasion of competitor \( y \) under the common assumption (20). Our analysis can be used to gain insight into the effect of habitat fragmentation and ecological invasion on population growth.

REFERENCES


