Periodic dynamical systems in unidirectional metapopulation models

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In periodically varying environments, population models generate periodic dynamical systems. To understand the effects of unidirectional dispersal on local patch dynamics in fluctuating environments, dynamical systems theory is used to study the resulting periodic dynamical systems. In particular, a unidirectional dispersal linked two patch nonautonomous metapopulation model is constructed and used to explain the qualitative dynamics of linked versus unlinked independent patches. As in single-patch, single-species population models, unidirectional nonautonomous models support multiple attractors where local population models support single attractors.

Keywords: Metapopulation; Multiple attractors; Nonautonomous models; Periodic dynamical systems; Unidirectional dispersal

1. Introduction

Populations are often subdivided in space and spread among independent patches that are connected via dispersal or migration [1–6,8–10,15,17,18,20–28,33–34,40–42]. The dynamics of discretely reproducing populations can be complex, especially when vital rates are density-dependent and are subject to environmental stochasticity [13,16,29,31,35–37,40]. Many scientists have used simple autonomous and nonautonomous nonlinear difference equations to model single-species discretely reproducing closed populations [2,6,7,16,25,32,35–42]. Others have used autonomous nonlinear systems of difference equations to model spatially-explicit metapopulations [1,3–5,15,22–24,33,42].

The focus of this paper is on the effects of unidirectional dispersal on local dynamics in periodically varying environments. In particular, a unidirectional dispersal linked two patch nonautonomous metapopulation model is used to study the qualitative dynamics of linked versus unlinked independent patches.

Section 2, the preliminaries section, introduces a very general single-patch single-species nonautonomous population model without dispersal [16]. In Section 3, we introduce the main model, a two-patch unidirectional dispersal linked nonautonomous metapopulation model. Such nonautonomous discrete-time models generate periodically forced dynamical systems [11,12,14,16]. In Section 4, we use dynamical systems theory to understand the relation between local patch dynamics and metapopulation dynamics. In Section 5, we test...
our results on specific metapopulation models, and the implications of our results are discussed in Section 6.

2. Single patch nonautonomous population models

In periodically varying environments, local Patch $i \in \{1, 2\}$ dynamics at generation $t$ after reproduction but before dispersal is modeled by the nonautonomous equation

$$x_i(t + 1) = x_i(t)g_i(t, x_i(t)), \quad (i = 1, 2) \quad (1)$$

where $x_i(t)$ denotes the population size, and the per capita growth rate, $g_i : \mathbb{Z}_+ \times [0, \infty) \to (0, \infty)$, is assumed to be positive and differentiable ($C^m$ on $[0, \infty)$), and where there exists a smallest positive integer $T_i$ satisfying $g_i(t + T_i, x) = g_i(t, x)$. That is, each $g_i$ is periodic with period $T_i$.

When each Patch local dynamics is governed by the Ricker model and the environment is periodic, then the uncoupled System (1) becomes

$$x_i(t + 1) = x_i(t) \exp \left( R_i \left( 1 - \frac{x_i(t)}{K_i(t)} \right) \right), \quad (i = 1, 2) \quad (2)$$

where the environmental carrying capacity satisfies $K_i(t + T_i) = K_i(t)$ for all $t \in \mathbb{Z}_+$ and $R_i > 0$ is the demographic characteristic of the species. System (2), like the classic Ricker model, is capable of supporting period-doubling bifurcations route to chaos. However, unlike the classic Ricker model, System (2) is capable of generating multiple cyclic attractors [16,39,41].

To study the population dynamics of System (1), for each Patch $i \in \{1, 2\}$, we define a general smooth function $h_i : \mathbb{Z}_+ \times [0, \infty) \to [0, \infty)$ that generates the nonautonomous difference equation

$$x_i(t + 1) = h_i(t, x_i(t)), \quad t \in \mathbb{Z}_+$$

where $h_i(t, x_i(t)) = x_i(t)g_i(t, x_i(t))$ for all $t \equiv 0$. Thus, $h_i(t + T_i, x_i(t)) = h_i(t, x_i(t))$ for all $t > 0$.

3. Two patch periodically forced unidirectional dispersal models

Hastings [27], Gyllenberg et al. [20], Doebeli [8,9], Yakubu [40], Yakubu and Castillo-Chavez [41] have studied discrete-time, autonomous, single-species metapopulation models that implicitly assume that dispersal is either bidirectional or unidirectional. A two-patch version of these metapopulation models is given by the following system of coupled nonlinear autonomous difference equations:

$$\begin{align*}
x_1(t + 1) &= (1 - d_{12})h_1(x_1(t)) + d_{21}h_2(x_2(t)), \\
x_2(t + 1) &= d_{12}h_1(x_1(t)) + (1 - d_{21})h_2(x_2(t)),
\end{align*} \quad (3)$$

where $h_i(x_i(t)) = x_i(t)g_i(x_i(t))$. In System (3), reproduction occurs prior to dispersal within
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each generation and in each patch. After reproduction, the constant fraction \( d_{12} \in (0, 1) \) of the population disperses from Patch 1 to 2 while the constant fraction \( d_{21} \in (0, 1) \) disperses from Patch 2 to 1. Dispersal is bidirectional when \( d_{12}, d_{21} \in (0, 1) \). However, when either \( d_{12} = 0 \) and \( d_{21} \in (0, 1) \) or \( d_{21} = 0 \) and \( d_{12} \in (0, 1) \), then dispersal is unidirectional.

To account for a periodic fluctuating environment, the dynamics at generation \( t \) of a single-species metapopulation under unidirectional dispersal are modeled with equations of the general form

\[
\begin{align*}
    x_1(t + 1) &= (1 - d) h_1(t, x_1(t)), \\
    x_2(t + 1) &= d h_1(t, x_1(t)) + h_2(t, x_2(t)),
\end{align*}
\]

(4)

where the dispersal coefficient \( d \in (0, 1) \) and \( h_i(t, x_i(t)) = x_i(t)g_i(t, x_i(t)) \) and \( h_i(t + T_i, x_i(t)) = h_i(t, x_i(t)) \) for each \( i \in \{1, 2\} \) and for all \( t \in \mathbb{Z}_+ \). System (4) is a nonautonomous metapopulation model under unidirectional dispersal. To study the long-term dynamics of System (4), we consider the nonautonomous hierarchical model

\[
\begin{align*}
    x(t + 1) &= f(t, x(t)), \\
    y(t + 1) &= g(t, x(t), y(t)), \\
    x(0) &= x \in \mathbb{R}_+^n, \\
    y(0) &= y \in \mathbb{R}_+^m
\end{align*}
\]

(5)

where \( f : \mathbb{Z}_+ \times \mathbb{R}_+^n \rightarrow \mathbb{R}_+^n \) and \( g : \mathbb{Z}_+ \times \mathbb{R}_+^{n+m} \rightarrow \mathbb{R}_+^m \) are continuous functions, and where there exist smallest positive integers \( T_1 \) and \( T_2 \) satisfying \( f(t + T_1, x(t)) = f(t, x(t)) \) and \( g(t + T_2, x(t), y(t)) = g(t, x(t), y(t)) \), respectively. System (5) is a generalization of the unidirectional dispersal metapopulation model, System (4).

We use the following notation, definitions and results to analyze System (5). Let \( T = \text{lcm}(T_1, T_2) \). For each \( i \in \{0, 1, \ldots, T - 1\} \), define \( F_i : \mathbb{R}_+^{n+m} \rightarrow \mathbb{R}_+^{n+m} \) by \( F_i(x, y) = (f(i, x), g(i, x, y)) \). \( F_i \) is an example of a discrete dynamical system on \( \mathbb{R}_+^{n+m} \). For \( i \geq T \), let \( F_i(x, y) = F_{i \mod T}(x, y) \). In the following general definitions, \( X \) is a locally compact metric space.

**Definition 1** A \( T \)-periodic discrete dynamical system is a sequence of maps \( \{F_0, F_1, \ldots, F_{T-1}\} \) from \( X \) to \( X \) such that \( F_i = F_{i \mod T} \) for all \( i \in \mathbb{Z}_+ \) and where \( T \) is the smallest such integer.

Consequently, a \( T \)-periodic discrete dynamical system is a finite sequence of \( T \) maps.

**Proposition 1** \( T = \text{lcm}(T_1, T_2) \) is the smallest period of the \( T \)-periodic discrete dynamical system \( \{F_0, F_1, \ldots, F_{T-1}\} \).

**Proof** \( (i + T) \mod(T_1) = i \mod(T_1) \) and \( (i + T) \mod(T_2) = i \mod(T_2) \) imply that \( F_i = F_{i \mod T} \). Suppose that there is an integer \( \hat{T} \) such that \( F_i = F_{i \mod \hat{T}} \). If \( \hat{T} \) is not a multiple of \( T_1 \), then \( \hat{T} = aT_1 + d \) where \( d \) is a positive integer less than \( T_1 \). Now since \( F_i = F_{i \mod \hat{T}} \), \( f(t, x(t)) = f(t + \hat{T}, x(t)) = f(t + aT_1 + d, x(t)) = f(t + d, x(t)) \). But this contradicts that \( T_1 \) is the smallest such positive integer. If \( \hat{T} \) is not a multiple of \( T_2 \), then \( \hat{T} = aT_2 + d \) where \( d \) is a positive integer less than \( T_2 \). Now since \( F_i = F_{i \mod \hat{T}} \), \( g(t, x(t), y(t)) = g(t + \hat{T}, x(t), y(t)) = g(t + aT_2 + d, x(t), y(t)) = g(t + d, x(t), y(t)) \). But this contradicts that \( T_2 \) is the smallest such positive integer. Thus \( \hat{T} \) is a multiple of \( T = \text{lcm}(T_1, T_2) \) and \( T \) is the smallest integer such that \( F_i = F_{i \mod T} \). \( \square \)
To define the orbit of a point $x_0 \in X$, we let $x_i = F_{i-1}(x_{i-1})$ for each $i \geq 1$.

**Definition 2.** The orbit of a point $x_0 \in X$ under the $T$-periodic discrete dynamical system $\{F_0, F_1, \ldots, F_{T-1}\}$ is $\{x_0, F_0(x_0), F_1(x_1), \ldots, F_{T-1}(x_{T-1}), \ldots\}$.

**Definition 3.** A point $x_0$ is a fixed point for the $T$-periodic discrete dynamical system $\{F_0, F_1, \ldots, F_{T-1}\}$ if its orbit is $\{x_0, x_0, \ldots, x_0, \ldots\}$.

Fixed point dynamics are rare in periodic fluctuating environments (Proposition 2).

**Proposition 2.** If for some $i \neq j$, $F_i$ and $F_j$ have unique fixed points that are not equal, then the $T$-periodic discrete dynamical system $\{F_0, F_1, \ldots, F_{T-1}\}$ has no fixed points.

**Proof.** Suppose $x_0$ is a fixed point of the $T$-periodic discrete dynamical system $\{F_0, F_1, \ldots, F_{T-1}\}$. Then $F_i(x_0) = x_0$ for each $i$. This is a contradiction, since $F_i$ and $F_j$ do not have a fixed point in common.

Recall that each $F_i$ is a single (autonomous) discrete dynamical system. A point $x_0$ is said to be a (prime) period $k$ point of $F_i$ if $k$ is the least positive integer for which $F_k(x_0) = x_0$. When $x_0$ is a (prime) period $k$ point of $F_i$, then its orbit under $F_i$ iterations,

$$\{x_0, F_i(x_0), F_i^2(x_0), \ldots, F_i^{k-1}(x_0), \ldots\},$$

is a $k$-cycle of $F_i$.

**Definition 4.** An orbit $\{x_0, x_1, \ldots, x_k, \ldots\}$ is a $k$-cycle of the $T$-periodic discrete dynamical system $\{F_0, F_1, \ldots, F_{T-1}\}$ if $x_i = x_{i \mod(k)}$ for all $i \in \mathbb{Z}_+$ and $k$ is the smallest such integer.

Henson [29], Franke and Selgrade [14] as well as Franke and Yakubu [16] have shown that $T$-periodic dynamical systems are capable of supporting $k$-cycles.

**Proposition 3.** Let $\{x_0, x_1, \ldots, x_k, \ldots\}$ be a $k$-cycle of each $F_i$. Then $\{x_0, x_1, \ldots, x_k, \ldots\}$ is a $k$-cycle of the $T$-periodic discrete dynamical system $\{F_0, F_1, \ldots, F_{T-1}\}$.

**Proof.** Since $\{x_0, x_1, \ldots, x_k, \ldots\}$ is a $k$-cycle of each $F_i$, then for each $x_i \in \{x_0, x_1, \ldots, x_k, \ldots\}$ we have

$$F_j(x_i) = x_{i+1} \quad \text{and} \quad F_j(x_i) = x_{i+1}.$$

Moreover, the orbit of $x_0$ under the $T$-periodic dynamical system $\{F_0, F_1, \ldots, F_{T-1}\}$ is $\{x_0, F_0(x_0), F_1(x_0), \ldots, F_n(F_0(x_0)), \ldots\}.$

\[\square\]

### 4. Periodically forced $T$-periodic dynamical systems

In System (5), the first set of equations are functions of the two variables, $t$ and $x$ while the second set are functions of the three variables $t$, $x$ and $y$. Once the first set of equations have a $k$-cycle, its insertion in the second set of equations makes the second set of equations periodically forced nonautonomous difference equations on $\mathbb{R}^m$. Such equations are capable of supporting cycles with periods different from $k$. In [40], Yakubu studied periodically forced autonomous difference equations.
To study *periodically forced* nonautonomous difference equations via System (5), assume \( \{f_0, f_1, \ldots, f_{T-1}\} \) is a \( T_1 \)-periodic dynamical system on \( \mathbb{R}^n \), \( \{g_0, g_1, \ldots, g_{T_2-1}\} \) is a \( T_2 \)-periodic sequence of maps from \( \mathbb{R}^{n+m} \) to \( \mathbb{R}^m \) and \( \{x_0, x_1, \ldots, x_{k-1}, \ldots\} \) is a \( k \)-cycle for the \( T_1 \)-periodic dynamical system \( \{f_0, f_1, \ldots, f_{T-1}\} \). Recall that System (5) is

\[
F_i : \mathbb{R}^{n+m} \to \mathbb{R}^{n+m} \text{ defined by } F_i(x, y) = (f_{i \mod T_1}(x), g_{i \mod T_2}(x, y)),
\]

which has period \( T = \text{lcm}(T_1, T_2) \) (see Proposition 1).

For each \( i \in \mathbb{Z}_+ \), define the *periodically forced* (nonautonomous) maps

\[
\hat{F}_i : \mathbb{R}^{n+m} \to \mathbb{R}^{n+m} \text{ by } \hat{F}_i(x, y) = (f_{i \mod T_1}(x), g_{i \mod T_2}(x, y)),
\]

and

\[
\hat{G}_i : \mathbb{R}^m \to \mathbb{R}^m \text{ by } \hat{G}_i(y) = (g_{i \mod T_2}(x, y)).
\]

**Lemma 1** There exists a \( p \) such that \( \{\hat{F}_0, \hat{F}_1, \ldots, \hat{F}_i, \ldots\} \) is a \( p \)-periodic discrete dynamical system, where \( p \) is a factor of the \( \text{lcm}(k, T_1, T_2) \).

**Proof** Let \( A = \text{lcm}(k, T_1, T_2) \). Since \((i + A) \mod T_1 = i \mod T_1, (i + A) \mod T_2 = i \mod T_2\), and \((i + A) \mod k = i \mod k\), \( \hat{F}_i = \hat{F}_{i+A} \). Thus \( \{\hat{F}_0, \hat{F}_1, \ldots, \hat{F}_i, \ldots\} \) is a \( p \)-periodic dynamical system, where \( p \) is less than or equal to \( A \). If \( p \) does not divide \( A \), then \( A = lp + d \) where \( 0 < d < p \). This would mean that \( \hat{F}_i = \hat{F}_{i+A} = \hat{F}_{i+lp+d} = \hat{F}_{i+d} \). But this contradicts that \( p \) is that smallest natural number such that \( \hat{F}_i = \hat{F}_{i+p} \). \( \square \)

Proceeding exactly as the previous proof, the following result is immediate:

**Lemma 2** There exists a \( q \) such that \( \{\hat{G}_0, \hat{G}_1, \ldots, \hat{G}_i, \ldots\} \) is a \( q \)-periodic discrete dynamical system, where \( q \) is a factor of the \( \text{lcm}(k, T_2) \).

Now, we make a connection between System (5) and doubly *periodically forced* (nonautonomous) maps.

**Lemma 3**

\[
\{(x_0, y_0), (x_1, y_1), \ldots, (x_{i-1}, y_{i-1}), \ldots\}
\]

is an \( l \)-cycle for the \( p \)-periodic dynamical system \( \{\hat{F}_0, \hat{F}_1, \ldots, \hat{F}_{i-1}\} \) if and only if

\[
\{(x_0, y_0), (x_1, y_1), \ldots, (x_{i-1}, y_{i-1}), \ldots\}
\]

is an \( l \)-cycle for the \( T \)-periodic dynamical system \( \{F_0, F_1, \ldots, F_{i-1}\} \).

**Proof** Note that the first coordinates of \( F_i \) and \( \hat{F}_i \) are identical. Since \( g_{i \mod T_2} \) is used in the second coordinate of \( F_i \) and \( \hat{F}_i \), and the orbit of \( x_0 \) under \( \{f_0, f_1, \ldots, f_{T-1}\} \) has \( x_{i \mod k} = x_i \), the second coordinates are also equal on \( (x_i, y_i) \) and the orbit of \( (x_0, y_0) \) is the same under \( \{F_0, F_1, \ldots, F_{T-1}\} \) and \( \{\hat{F}_0, \hat{F}_1, \ldots, \hat{F}_{i-1}\} \). \( \square \)

Let \( x_\infty \) be a fixed point of \( F : I \to I \). Then \( x_\infty \) is said to be *stable* if for any \( \varepsilon > 0 \), there exists \( \delta > 0 \) such that \( |x - x_\infty| < \delta \) implies \( |F^n(x) - x_\infty| < \varepsilon \) for all \( n \in \{1, 2, \ldots\} \), and all \( x \in I \). Also the fixed point \( x_\infty \) is said to be *attracting* if there exists \( \eta > 0 \) such that \( |x - x_\infty| < \delta \) implies \( \lim_{n \to \infty} F^n(x) = x_\infty \). Whenever \( \eta = \infty \), then \( x_\infty \) is said to be *globally attracting*. We use the following non-standard definition of stability to analyze cyclic “attractors” of System (5).
**Definition 5** If $X$ is a manifold, then a $k$-cycle, $\{p_0, p_1, \ldots, p_i, \ldots\}$, of a $p$-periodic dynamical system $\{H_0, H_1, \ldots, H_i, \ldots\}$ is $L$-asymptotically stable if the magnitude of all eigenvalues of $DH_{p_k-1}(\ldots (H_1(H_0(p_0))) \ldots)$ are less than one.

A $k$-cycle, $\{p_0, p_1, \ldots, p_i, \ldots\}$ is $L$-stable if the magnitude of all eigenvalues of $DH_{p_k-1}(\ldots (H_1(H_0(p_0))) \ldots)$ are less than or equal to one and those with magnitude one are simple.

We say that a $k$-cycle is attracting whenever it is $L$-asymptotically stable. In [12,13], Elaydi and Sacker proved that, when a $k$-periodic discrete dynamical system has a globally stable $l$-cycle then $l$ must be a divisor of $k$. Independent of stability, when there exists an $l$-cycle in System (5) then $k$, the period of $x_0$, must divide $l$.

**Theorem 1** Suppose
\[
\{(x_0, y_0), (x_1, y_1), \ldots, (x_{r-1}, y_{r-1}), \ldots\}
\]
is an $l$-cycle for the $T$-periodic discrete dynamical system
\[
\{F_0, F_1, \ldots F_{T-1}\} \quad \text{(System (5))},
\]
then $(l/k) \in Z_+$. 

**Proof** Since
\[
\{(x_0, y_0), (x_1, y_1), \ldots, (x_{r-1}, y_{r-1}), \ldots\}
\]
is an $l$-cycle, $\{x_0, x_1, x_2, \ldots\}$ is a cycle with period less than or equal to $l$. Since its period is $k$, proceed exactly as in the proof of Lemma 3 to show that $k$ must divide $l$. \hfill $\square$

**Theorem 2** System (5) has
\[
\{(x_0, y_0), (x_1, y_1), \ldots, (x_{r-1}, y_{r-1}), \ldots\}
\]
as an $l$-cycle if and only if
\[
\{x_0, x_1, \ldots, x_i, \ldots\}
\]
is a $k$-cycle for the $T_1$-periodic dynamical system $\{f_0, f_1, \ldots, f_{T_1-1}\}$, and
\[
\{y_0, y_1, \ldots, y_i, \ldots\}
\]
is a $r$-cycle for the $q$-periodic dynamical system $\{\hat{G}_0, \hat{G}_1, \ldots, \hat{G}_r, \ldots\}$ where $l = \text{lcm}(k, r)$.

**Proof** Suppose
\[
\{(x_0, y_0), (x_1, y_1), \ldots, (x_{r-1}, y_{r-1}), \ldots\}
\]
is an $l$-cycle, then
\[
\{x_0, x_1, \ldots, x_i, \ldots\}
\]
is a $k$-cycle for the $T_1$-periodic dynamical system $\{f_0, f_1, \ldots, f_{T_1-1}\}$ and
\[
\{y_0, y_1, \ldots, y_i, \ldots\}
\]
is an $r$-cycle for the $q$-periodic dynamical system $\{\hat{G}_0, \hat{G}_1, \ldots, \hat{G}_r, \ldots\}$ with period less than or equal to $l$. Since its period is $r$, a proof similar to that in Lemma 3 shows that $r$ must divide $l$. Combining this with Theorem 1 we have that both $r$ and $k$ divide $l$. So $l \equiv \text{lcm}(k, r)$. 

On the other hand, both the $x_i$ and the $y_j$ repeat after $\text{lcm}(k, r)$ times (that is, the orbits of $x_0$ and $y_0$ are $\{x_0, x_1, \ldots, x_{\text{lcm}(k, r) - 1}, x_0, \ldots\}$ and $\{y_0, y_1, \ldots, y_{\text{lcm}(k, r) - 1}, y_0, \ldots\}$, respectively). So
\[
\{(x_0, y_0), (x_1, y_1), \ldots, (x_{\text{lcm}(k, r) - 1}, y_{\text{lcm}(k, r) - 1}), \ldots\}
\]
is a cycle with period less than or equal to $\text{lcm}(k, r)$. Thus, $l = \text{lcm}(k, r)$.

Suppose $\{y_0, y_1, \ldots, y_r, \ldots\}$ is an $r$-cycle for the $q$-periodic dynamical system $\{\hat{G}_0, \hat{G}_1, \ldots, \hat{G}_r, \ldots\}$ and $l = \text{lcm}(k, r)$, then $\{(x_0, y_0), (x_1, y_1), \ldots, (x_l, y_l), \ldots\}$ is a cycle for System (5). Its period must be the least common multiple of the periods of $\{x_0, x_1, \ldots, x_{\text{lcm}(k, r) - 1}, x_0, \ldots\}$ and $\{y_0, y_1, \ldots, y_{\text{lcm}(k, r) - 1}, y_0, \ldots\}$. Thus, it is an $l$-cycle with $l = \text{lcm}(k, r)$.

**Theorem 3** System (5) has
\[
\{(x_0, y_0), (x_1, y_1), \ldots, (x_{\text{lcm}(k, r)}, y_{\text{lcm}(k, r)})\}
\]
as an $L$-asymptotically stable $l$-cycle if and only if
\[
\{x_0, x_1, \ldots, x_{\text{lcm}(k, r)}, \ldots\}
\]
is an $L$-asymptotically stable $k$-cycle of the $T_1$-periodic dynamical system $\{f_0, f_1, \ldots, f_{T_1 - 1}\}$ and
\[
\{y_0, y_1, \ldots, y_{\text{lcm}(k, r)}\}
\]
is an $L$-asymptotically stable $r$-cycle of the $q$-periodic dynamical system $\{\hat{G}_0, \hat{G}_1, \ldots, \hat{G}_{q - 1}\}$, where $l = \text{lcm}(k, r)$.

**Proof**
\[
D\hat{F}_i = \begin{pmatrix} D_x f_i & 0 \\ 0 & D_y \hat{G}_i \end{pmatrix}, \quad DF_i = \begin{pmatrix} D_x f_i & 0 \\ D_0 \hat{G}_i & D_y \hat{G}_i \end{pmatrix}
\]
and
\[
D_y \hat{G}_i(x_i, y) = D_y \hat{G}_{i \mod T_1}(x_i \mod k), y) = D_y \hat{G}_i(y).
\]
This implies that $DF_i$, a block triangular matrix, has diagonal entries equal to the diagonal entries of the diagonal block matrix $D\hat{F}_i$ when $x = x_i$. Thus, $DF_i$ and $D\hat{F}_i$ have the same eigenvalues when $x = x_i$.

Since $l = \text{lcm}(k, r)$, $T = \text{lcm}(T_1, T_2)$ and $q$ is a factor of $\text{lcm}(k, T_2)$, $\{x_0, x_1, \ldots, x_{\text{lcm}(k, T_2)} - 1\}$ is an $L$-asymptotically stable $k$-cycle of the $T_1$-periodic discrete dynamical system $\{F_0, f_1, \ldots, f_{T_1 - 1}\}$ and $\{y_0, y_1, \ldots, y_{\text{lcm}(k, T_2) - 1}\}$ is an $L$-asymptotically stable $r$-cycle of the $q$-periodic dynamical system $\{\hat{G}_0, \hat{G}_1, \ldots, \hat{G}_{q - 1}\}$ if and only if $DF_{T_1 - 1}(\ldots(F_1(f_0(x_0)), \ldots)$ and $D\hat{G}_{T_1 - 1}(\ldots(\hat{G}_1(\hat{G}_0(x_0))), \ldots)$ have all eigenvalues inside the unit circle. Thus the eigenvalues of $DF_{T_1 - 1}(\ldots(F_1(f_0(x_0)), \ldots)$ and $D\hat{G}_{T_1 - 1}(\ldots(\hat{G}_1(\hat{G}_0(x_0))), \ldots)$ are inside the unit circle and System (5) has $\{(x_0, y_0), (x_1, y_1), \ldots, (x_{\text{lcm}(k, T_2) - 1}, y_{\text{lcm}(k, T_2) - 1}), \ldots\}$ as an $L$-asymptotically stable $l$-cycle if and only if $\{x_0, x_1, \ldots, x_{\text{lcm}(k, T_2) - 1}, \ldots\}$ is an $L$-asymptotically stable $k$-cycle of the $T_1$-periodic discrete dynamical system $\{f_0, f_1, \ldots, f_{T_1 - 1}\}$ and $\{y_0, y_1, \ldots, y_{\text{lcm}(k, T_2) - 1}, \ldots\}$ is an $L$-asymptotically stable $r$-cycle of the $q$-periodic discrete dynamical system $\{\hat{G}_0, \hat{G}_1, \ldots, \hat{G}_{q - 1}\}$, where $l = \text{lcm}(k, r)$.

When the orbit of $x_0$ is a single point $x_\infty$, $x_i \mod k = x_\infty$ and the following result is immediate.
COROLLARY 1 If \( \{x_\omega\} \) is an \( L \)-asymptotically stable fixed point of \( f(t, x(t)) : Z_+ \times R^n \rightarrow R^n \), and
\[
\{y_0, y_1, \ldots, y_{r-1}, \ldots\}
\]
is an \( L \)-asymptotically stable \( r \)-cycle of \( g(t, x_\omega, y(t)) : Z_+ \times R^m \rightarrow R^m \), then
\[
\{(x_\omega, y_0), (x_\omega, y_1), \ldots, (x_\omega, y_{r-1}), \ldots\}
\]
is an \( L \)-asymptotically stable \( r \)-cycle of System (5).

THEOREM 4 Assume all orbits of System (5) are bounded. Then System (5) has
\[
\{(x_0, y_0), (x_1, y_1), \ldots, (x_{q-1}, y_{q-1}), \ldots\}
\]
as a globally attracting \( l \)-cycle if and only if
\[
\{x_0, x_1, \ldots, x_{k-1}, \ldots\}
\]
is a globally attracting \( k \)-cycle of the \( T_1 \)-periodic dynamical system \( \{f_0, f_1, \ldots, f_{T_1-1}\} \) and
\[
\{y_0, y_1, \ldots, y_{r-1}, \ldots\}
\]
is a globally attracting \( r \)-cycle of the \( q \)-periodic dynamical system \( \{\hat{G}_0, \hat{G}_1, \ldots, \hat{G}_{q-1}\} \), where \( l = \text{lcm}(k, r) \).

Proof Suppose System (5) has
\[
\{(x_0, y_0), (x_1, y_1), \ldots, (x_{r-1}, y_{r-1}), \ldots\}
\]
as a globally attracting \( l \)-cycle, then by Theorem 3
\[
\{x_0, x_1, \ldots, x_{k-1}, \ldots\}
\]
is an attracting \( k \)-cycle of the \( T_1 \)-periodic dynamical system \( \{f_0, f_1, \ldots, f_{T_1-1}\} \) and
\[
\{y_0, y_1, \ldots, y_{r-1}, \ldots\}
\]
is an attracting \( r \)-cycle of the \( q \)-periodic dynamical system \( \{\hat{G}_0, \hat{G}_1, \ldots, \hat{G}_{q-1}\} \), where \( l = \text{lcm}(k, r) \). In fact since the first coordinate of System (5) is precisely the \( T_1 \)-periodic dynamical system \( \{f_0, f_1, \ldots, f_{T_1-1}\} \),
\[
\{x_0, x_1, \ldots, x_{k-1}, \ldots\}
\]
is globally attracting. Independent of initial conditions, the second coordinate of System (5) limits on \( \{y_0, y_1, \ldots, y_{r-1}, \ldots\} \). So if the first coordinate of the initial condition is \( x_0 \), the second coordinate also limits on \( \{y_0, y_1, \ldots, y_{r-1}, \ldots\} \). Thus \( \{y_0, y_1, \ldots, y_{r-1}, \ldots\} \) is globally attracting for the \( q \)-periodic dynamical system \( \{\hat{G}_0, \hat{G}_1, \ldots, \hat{G}_{q-1}\} \).

Now suppose \( \{x_0, x_1, \ldots, x_{k-1}, \ldots\} \) is a globally attracting \( k \)-cycle of the \( T_1 \)-periodic dynamical system \( \{f_0, f_1, \ldots, f_{T_1-1}\} \) and \( \{y_0, y_1, \ldots, y_{r-1}, \ldots\} \) is a globally attracting \( r \)-cycle of the \( q \)-periodic dynamical system \( \{\hat{G}_0, \hat{G}_1, \ldots, \hat{G}_{q-1}\} \), where \( l = \text{lcm}(k, r) \). By Theorem 3, System (5) has \( \{(x_0, y_0), (x_1, y_1), \ldots, (x_{r-1}, y_{r-1}), \ldots\} \) as an attracting \( l \)-cycle. Thus \( \{(x_0, y_0), (x_1, y_1), \ldots, (x_{r-1}, y_{r-1}), \ldots\} \) has a bounded open neighborhood \( U \times W \) which is positively invariant under \( H = F_{T_1-1} \circ F_{T_2-2} \circ \cdots \circ F_0 \) and every point in \( U \times W \) is attracted to the \( l \)-cycle under System (5).

Let \( (x, y) \in R^{n+m} \). By boundedness of orbits, there is a compact set \( C \) that contains the \( H \) orbit of \( (x, y) \). Since \( \{y_0, y_1, \ldots, y_{r-1}, \ldots\} \) is a globally attracting \( r \)-cycle of the \( q \)-periodic
Periodic unidirectional metapopulation models

5. Application

To apply our results to a specific metapopulation model, we construct a nonautonomous unidirectional dynamical system based on the classic Ricker model. For each \( i \in \{1, 2\} \) we let

\[
h_i(t, x_i) = x_i \exp \left( R_i \left( 1 - \frac{x_i(t)}{K_i + \alpha_i(-1)^t} \right) \right)
\]

where \( R_i, K_i, \alpha_i > 0 \) and \( K_i - \alpha_i > 0 \). Then System (5) becomes

\[
\begin{align*}
x_1(t + 1) &= (1 - d)x_1(t) \exp \left( R_1 \left( 1 - \frac{x_1(t)}{K_1 + \alpha_1(-1)^t} \right) \right), \\
x_2(t + 1) &= dx_1(t) \exp \left( R_1 \left( 1 - \frac{x_1(t)}{K_1 + \alpha_1(-1)^t} \right) \right) + x_2(t) \exp \left( R_2 \left( 1 - \frac{x_2(t)}{K_2 + \alpha_2(-1)^t} \right) \right).
\end{align*}
\]

(6)

In System (6), the species persists in Patch 2. However, it goes extinct in Patch 1 whenever the unidirectional dispersal rate is high. We summarize these in the following result.

**Theorem 5** The origin is unstable, and \( (1 - d) \exp(R_1) < 1 \) implies that the \( \omega \)-limit set of every positive population vector in System (6) is a subset of \( \{0\} \times [0, \infty) \). Hence, the species goes extinct in Patch 1 while it persists in Patch 2.

**Proof** It is easy to see that all orbits of System (6) are uniformly bounded after one step. Therefore, there exist positive numbers \( I_1 \) and \( I_2 \) such that after one step initial population sizes in the set \( \{ (x_1, x_2) \in [0, \infty) \times [0, \infty) \} \) are mapped to the compact set \( \{ (x_1, x_2) \in [0, I_1] \times [0, I_2] \} \). The Jacobian of System (6) evaluated at \( (0, 0) \) is

\[
\begin{pmatrix}
(1 - d)^2 \exp(2R_1) & 0 \\
d \exp(R_1)(1 - d) \exp(R_1) + \exp(R_2) & \exp(2R_2)
\end{pmatrix}
\]

Hence, \( (0, 0) \) is unstable. To show that \( F_i(y) \to 0 \) as \( t \to +\infty \). Define the function \( V : \mathbb{R}_+ \times \mathbb{R}_+ \to \mathbb{R}_+ \) by \( V(y_1, y_2) = y_1 \). Next, we show that \( V \) is a Lyapunov function for System (6). Hence, it decreases to a limit point with first coordinate zero. If \( y_1 > 0 \), then \( V(F(y)) < (1 - d) \exp(r_1 + \alpha_1)y_1 \) and \( V(F(y)) < V(y) \) whenever \( (1 - d) \exp(R_1) < 1 \). Therefore, for all points \( y = (y_1, y_2) \) satisfying \( y_1 > 0 \) we know that \( V(F(y)) < V(y) \).

If \( (x_1, x_2) \) is an \( \omega \)-limit point and \( x_1 > 0 \), then \( V(F(x)) < V(x) \). However, this is impossible for an \( \omega \)-limit point.
Consequently, when \((1 - d) \exp(R_1) < 1\), the “limiting system” of System (6) is
\[
x_2(t + 1) = x_2(t) \exp \left( R_2 \left( 1 - \frac{x_2(t)}{K_2 + \alpha_2(-1)^t} \right) \right). \tag{7}
\]

To prove persistence, notice that \(x_2(t + 1) \geq x_2(t) \exp(R_2(1 - (x_2(t))/K_2 - \alpha_2))\). Thus \(x_2(t)\) is increasing if \(x_2(t) \in [0, K_2 - \alpha_2]\). Also, if \((x_1(t), x_2(t)) \in [0, 1] \times [K_2 - \alpha_2, 1], x_2(t + 1)\) has a positive minimum, say \(m\). Thus \(x_2\) gets larger than \(\min\{m, K_2 - \alpha_2\}/2\) and stays larger. Hence the species persists in Patch 2 while it is extinct in Patch 1.

Let \(f_0(x) = x \exp(R_1(1 - (x/K_1 - \alpha_1)))\) and \(f_1(x) = x \exp(R_1(1 - (x/K_1 - \alpha_1)))\). The positive fixed points of the Ricker maps \(f_0\) and \(f_1\) are \(X_{0\infty} = K_1 + \alpha_1\) and \(X_{1\infty} = K_1 - \alpha_1\), respectively. Since \(h_i(t + 2, x_i) = h_i(t, x_i)\) and \(h_i(t + 1, x_i) \neq h_i(t, x_i)\), then \(\{f_0, f_1, \ldots, f_n, \ldots\}\) is a two-periodic dynamical system. When \(\alpha_1 = 0, f_0\) and \(f_1\) reduce to the same classic Ricker model. In this case, it is possible for the Patch 1 population to be on a positive equilibrium at
\[
x_{1\infty} = K_1 \left( 1 + \frac{1}{R_1} \ln(1 - d) \right).
\]

**Example** Set the following parameter values in System (6):

\[
\alpha_1 = 0, \quad \alpha_2 = 0.01, \quad K_1 = K_2 = 1, \quad R_1 = 1.8, \quad R_2 = 2.1, \quad d = 0.01.
\]

With our choice of parameters, \(\{x_{0\infty} = 0.9944\}\) is an asymptotically stable fixed point of \(\{f_0, f_1\}\). For each \(i \in \mathbb{Z}_+\), define the two-periodic (nonautonomous) map by
\[
\hat{G}_i(x_2) = \frac{d}{1 - d} x_{1\infty} + x_2 \exp \left( R_2 \left( 1 - \frac{x_2}{K_2 + \alpha_2(-1)^t} \right) \right).
\]

In fact,
\[
\{0.56998 \rightarrow 1.43300\}
\]

is an asymptotically stable two-cycle of the two-periodic dynamical system \(\hat{G}_0, \hat{G}_1\). Consequently, as predicted by Theorem (2) and Corollary (1), System (6) has an asymptotically stable two-cycle at
\[
\{(0.9944, 0.56998) \rightarrow (0.9944, 1.43300)\}.
\]

To study the impact of the unidirectional dispersal rate on the two-cycle attractors, we fix the parameters \(\alpha_1, \alpha_2, K_1, K_2, R_1 = 1.8\) and \(R_2 = 2.1\) at their current values while \(d\) is varied between 0 and 1.

As predicted by Theorem (5), the Patch 1 population persists when \(d < 1 - e^{-1.8}\) while it goes extinct when \(d > 1 - e^{-1.8}\) (see Figure 1). That is, Patch 1 population decreases to zero with increasing values of the unidirectional dispersal rate. However, Patch 2 population persists on a two-cycle attractor for all values of the dispersal rate.

In a recent paper, Franke and Yakubu provided a framework for the creation of multiple attractors in single-species nonautonomous population models without dispersal. Autonomous metapopulation models are known to support multiple attractors where local populations support single attractors [16, 30]. As in the autonomous Ricker equation, increasing values of \(R_1\) in System (6) force complex bifurcations including period doubling bifurcations, chaotic attractors and multiple attractors with complex basins of attraction [16, 30].
To illustrate multiple attractors via two coexisting two-cycle attractors we set the following parameters values in System (6)
\[ a_1 = 0, \quad a_2 = 0.01, \quad K_1 = K_2 = 1, R_1 = 2.2, \quad R_2 = 2.1, \quad \text{and} \quad d = 0.01 \]

With our choice of parameters, System (6) has two coexisting two-cycle attractors at
\[ \{(1.4853, 1.4438) \rightarrow (0.5055, 0.5565)\} \]
and
\[ \{(1.4853, 0.5847) \rightarrow (0.5055, 1.4208)\}. \]

Figure 2 displays the basins of attraction of the two coexisting attractors.

6. Conclusion

This paper focuses on a generalization of unidirectional discrete-time metapopulation models connected by dispersal. The effects of unidirectional dispersal on local dynamics in periodically varying environments are explored via a very general nonautonomous dispersal linked two-patch model.
The results of Elaydi and Sacker predict that $l$ must be a divisor of $k$ whenever a $k$-periodic dynamical system supports a globally stable $l$-cycle \cite{11,12}. Our results support this prediction, and for unidirectional metapopulation models in periodically varying environments, $l$ must be a divisor of $k$ whenever the $k$-periodic dynamical system supports an $l$-cycle. This result is independent of the stability of the $l$-cycle.

Autonomous and nonautonomous unidirectional dispersal linked metapopulation models are capable of supporting multiple attractors, where local populations are governed by equations like the classic Ricker model that supports single attractors \cite{16,40,41}. Also, single species nonautonomous models support multiple attractors where the corresponding autonomous models support single attractors \cite{16}. Studies on the role of periodically varying environments in generating multiple attractors would be welcome. These results may support the need to maintain dispersal corridors in periodically fluctuating environments. The use of dispersal corridors as a mechanism to increase the number of attractors may increase the likelihood of species survival in periodically varying environments \cite{2,41}.

The interactions via dispersal of various forms of local patch dynamics has not only led to the generation of a dynamical landscape capable of supporting multiple attractors but also has aided our understanding of the role that initial population sizes play in the ultimate fate (life-history) of a metapopulation. The overall fate of a metapopulation becomes less predictable as the complexity of the local dynamics increases. That is, the complex structure of the basins of attraction and their basin boundaries increases as the complexity of the local dynamics increases to the point that it may be impossible to determine, with any degree of certainty, the fate of such metapopulations \cite{19,27,41}.

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