

Periodic dynamical systems in unidirectional metapopulation models

JOHN E. FRANKE[†] and ABDUL-AZIZ YAKUBU^{‡*}

[†]Department of Mathematics, North Carolina State University, Raleigh, N.C. 27695, USA

[‡]Department of Mathematics, Howard University, Washington, D.C. 20059, USA

(Received 7 June 2004; in final form)

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

*Corresponding author. Email: ayakubu@howard.edu

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

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

where $x_i(t)$ denotes the population size, and the per capita growth rate, $g_i : Z_+ \times [0, \infty) \rightarrow (0, \infty)$, is assumed to be positive and differentiable (C^∞ 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 i local dynamics is governed by the Ricker model and the environment is periodic, then the uncoupled System (1) becomes

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

where the environmental carrying capacity satisfies $K_i(t + T_i) = K_i(t)$ for all $t \in Z_+$ 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

$$h_i : Z_+ \times [0, \infty) \rightarrow [0, \infty)$$

that generates the nonautonomous difference equation

$$x_i(t + 1) = h_i(t, x_i(t)), \quad t \in Z_+$$

where $h_i(t, x_i(t)) = x_i(t)g_i(t, x_i(t))$ for all $t \geq 0$. 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], Gyllenburg *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:

$$\left. \begin{aligned} x_1(t + 1) &= (1 - d_{12})h_1(x_1(t)) + d_{21}h_2(x_2(t)), \\ x_2(t + 1) &= d_{12}h_1(x_1(t)) + (1 - d_{21})h_2(x_2(t)), \end{aligned} \right\} \tag{3}$$

where $h_i(x_i(t)) = x_i(t)g_i(x_i(t))$. In System (3), reproduction occurs prior to dispersal within

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 $d_{21} = d \in (0, 1)$ or $d_{21} = 0$ and $d_{12} = d \in (0, 1)$, 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

$$\left. \begin{aligned} x_1(t + 1) &= (1 - d)h_1(t, x_1(t)), \\ x_2(t + 1) &= dh_1(t, x_1(t)) + h_2(t, x_2(t)), \end{aligned} \right\} \tag{4}$$

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

$$\left. \begin{aligned} x(t + 1) &= f(t, x(t)), & x(0) &= x \in \mathbb{R}_+^n \\ y(t + 1) &= g(t, x(t), y(t)), & y(0) &= y \in \mathbb{R}_+^m \end{aligned} \right\} \tag{5}$$

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 $i \in \{0, 1, \dots, T - 1\}$, 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 $F_i(x, y) = F_{i \bmod(T)}(x, y)$. 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 $\{F_0, F_1, \dots, F_{T-1}\}$ from X to X such that $F_i = F_{i \bmod(T)}$ 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 $\{F_0, F_1, \dots, F_{T-1}\}$.

Proof $(i + T) \bmod(T_1) = i \bmod(T_1)$ and $(i + T) \bmod(T_2) = i \bmod(T_2)$ imply that $F_i = F_{i \bmod(T)}$. Suppose that there is an integer \hat{T} such that $F_i = F_{i \bmod(\hat{T})}$. 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 $F_i = F_{i \bmod(\hat{T})}$, $f(t, x(t)) = f(t + \hat{T}, x(t)) = f(t + aT_1 + d, x(t)) = f(t + d, x(t))$. 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 $F_i = F_{i \bmod(\hat{T})}$, $g(t, x(t), y(t)) = g(t + \hat{T}, x(t), y(t)) = g(t + aT_2 + d, x(t), y(t)) = g(t + d, x(t), y(t))$. 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 $F_i = F_{i \bmod(T)}$. \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* $\{F_0, F_1, \dots, F_{T-1}\}$ *is* $\{x_0, F_0(x_0), F_1(x_1), \dots, F_{T-1}(x_{T-1}), \dots\}$.

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

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* $\{F_0, F_1, \dots, F_{T-1}\}$ *has no fixed points.*

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

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 $F_i^k(x_0) = x_0$. When x_0 is a (prime) period k point of F_i , then its orbit under F_i iterations,

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

is a k -cycle of F_i .

DEFINITION 4 *An orbit* $\{x_0, x_1, \dots, x_{k-1}, \dots\}$ *is a* k -*cycle of the* T -*periodic discrete dynamical system* $\{F_0, F_1, \dots, F_{T-1}\}$ *if* $x_i = x_{i \bmod(k)}$ *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* $\{x_0, x_1, \dots, x_{k-1}, \dots\}$ *be a* k -*cycle of each* F_j . *Then* $\{x_0, x_1, \dots, x_{k-1}, \dots\}$ *is a* k -*cycle of the* T -*periodic discrete dynamical system* $\{F_0, F_1, \dots, F_{T-1}\}$.

Proof Since $\{x_0, x_1, \dots, x_{k-1}, \dots\}$ is a k -cycle of each F_j , then for each $x_i \in \{x_0, x_1, \dots, x_i, \dots\}$ we have

$$F_j(x_i) = x_{i+1} \quad \text{and} \quad F_n(\dots F_1(F_0(x_0))\dots) = x_{n+1}.$$

Moreover, the orbit of x_0 under the T -periodic dynamical system $\{F_0, F_1, \dots, F_{T-1}\}$ is

$$\{x_0, F_0(x_0), F_1(F_0(x_0)), \dots, F_n(\dots F_1(F_0(x_0))\dots), \dots\}.$$

\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 \mathfrak{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 $\{f_0, f_1, \dots, f_{T_1-1}\}$ is a T_1 -periodic dynamical system on \mathfrak{R}^n , $\{g_0, g_1, \dots, g_{T_2-1}\}$ is a T_2 -periodic sequence of maps from \mathfrak{R}^{n+m} to \mathfrak{R}^m and $\{x_0, x_1, \dots, x_{k-1}, \dots\}$ is a k -cycle for the T_1 -periodic dynamical system $\{f_0, f_1, \dots, f_{T_1-1}\}$. Recall that System (5) is

$$F_i : \mathfrak{R}^{n+m} \rightarrow \mathfrak{R}^{n+m} \text{ defined by } F_i(x, y) = (f_{i \bmod(T_1)}(x), g_{i \bmod(T_2)}(x, y)),$$

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

$$\hat{F}_i : \mathfrak{R}^{n+m} \rightarrow \mathfrak{R}^{n+m} \text{ by } \hat{F}_i(x, y) = (f_{i \bmod(T_1)}(x), g_{i \bmod(T_2)}(x_{i \bmod(k)}, y)),$$

and

$$\hat{G}_i : \mathfrak{R}^m \rightarrow \mathfrak{R}^m \text{ by } \hat{G}_i(y) = (g_{i \bmod(T_2)}(x_{i \bmod(k)}, y)).$$

LEMMA 1 *There exists a p such that $\{\hat{F}_0, \hat{F}_1, \dots, \hat{F}_i, \dots\}$ 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 $(i + A) \bmod(T_1) = i \bmod(T_1)$, $(i + A) \bmod(T_2) = i \bmod(T_2)$, and $(i + A) \bmod(k) = i \bmod(k)$, $\hat{F}_i = \hat{F}_{i+A}$. Thus $\{\hat{F}_0, \hat{F}_1, \dots, \hat{F}_i, \dots\}$ 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 $\{\hat{G}_0, \hat{G}_1, \dots, \hat{G}_i, \dots\}$ 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

$$\{(x_0, y_0), (x_1, y_1), \dots, (x_{l-1}, y_{l-1}), \dots\}$$

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

$$\{(x_0, y_0), (x_1, y_1), \dots, (x_{l-1}, y_{l-1}), \dots\}$$

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

Proof Note that the first coordinates of F_i and \hat{F}_i , are identical. Since $g_{i \bmod(T_2)}$ is used in the second coordinate of F_i and \hat{F}_i , and the orbit of x_0 under $\{f_0, f_1, \dots, f_{T_1-1}\}$ has $x_{i \bmod(k)} = x_i$, the second coordinates are also equal on (x_i, y_i) and the orbit of (x_0, y_0) is the same under $\{F_0, F_1, \dots, F_{T-1}\}$ and $\{\hat{F}_0, \hat{F}_1, \dots, \hat{F}_{T-1}\}$. \square

Let x_∞ be a fixed point of $F : I \rightarrow I$. Then x_∞ 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 $n \in \{1, 2, \dots\}$, and all $x \in I$. Also the fixed point x_∞ is said to be *attracting* if there exists $\eta > 0$ such that $|x - x_\infty| < \delta$ implies $\lim_{n \rightarrow \infty} F^n(x) = x_\infty$. Whenever $\eta = \infty$, then x_∞ 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, $\{p_0, p_1, \dots, p_i, \dots\}$, of a p -periodic dynamical system $\{H_0, H_1, \dots, H_i, \dots\}$ is L -asymptotically stable if the magnitude of all eigenvalues of $DH_{pk-1}(\dots(H_1(H_0(p_0))))$ are less than one.

A k -cycle, $\{p_0, p_1, \dots, p_i, \dots\}$ is L -stable if the magnitude of all eigenvalues of $DH_{pk-1}(\dots(H_1(H_0(p_0))))$ 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

$$\{(x_0, y_0), (x_1, y_1), \dots, (x_{l-1}, y_{l-1}), \dots\}$$

is an l -cycle for the T -periodic discrete dynamical system

$$\{F_0, F_1, \dots, F_{T-1}\} \quad \text{(System (5))},$$

then $(l/k) \in \mathbb{Z}_+$.

Proof Since

$$\{(x_0, y_0), (x_1, y_1), \dots, (x_{l-1}, y_{l-1}), \dots\}$$

is an l -cycle, $\{x_0, x_1, x_2, \dots\}$ 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 . □

THEOREM 2 System (5) has

$$\{(x_0, y_0), (x_1, y_1), \dots, (x_{l-1}, y_{l-1}), \dots\}$$

as an l -cycle if and only if

$$\{x_0, x_1, \dots, x_i, \dots\}$$

is a k -cycle for the T_1 -periodic dynamical system $\{f_0, f_1, \dots, f_{T_1-1}\}$, and

$$\{y_0, y_1, \dots, y_i, \dots\}$$

is a r -cycle for the q -periodic dynamical system $\{\hat{G}_0, \hat{G}_1, \dots, \hat{G}_i, \dots\}$ where $l = \text{lcm}(k, r)$.

Proof Suppose

$$\{(x_0, y_0), (x_1, y_1), \dots, (x_{l-1}, y_{l-1}), \dots\}$$

is an l -cycle, then

$$\{x_0, x_1, \dots, x_i, \dots\}$$

is a k -cycle for the T_1 -periodic dynamical system $\{f_0, f_1, \dots, f_{T_1-1}\}$ and

$$\{y_0, y_1, \dots, y_i, \dots\}$$

is an r -cycle for the q -periodic dynamical system $\{\hat{G}_0, \hat{G}_1, \dots, \hat{G}_i, \dots\}$ 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 $l \geq \text{lcm}(k, r)$.

On the other hand, both the x_i and the y_i repeat after $\text{lcm}(k,r)$ times (that is, the orbits of x_0 and y_0 are $\{x_0, x_1, \dots, x_{\text{lcm}(k,r)-1}, x_0, \dots\}$ and $\{y_0, y_1, \dots, y_{\text{lcm}(k,r)-1}, y_0, \dots\}$, respectively). So

$$\{(x_0, y_0), (x_1, y_1), \dots, (x_{l-1}, y_{l-1}), \dots\}$$

is a cycle with period less than or equal to $\text{lcm}(k, r)$. Thus, $l = \text{lcm}(k, r)$.

Suppose $\{y_0, y_1, \dots, y_i, \dots\}$ is an r -cycle for the q -periodic dynamical system $\{\hat{G}_0, \hat{G}_1, \dots, \hat{G}_i, \dots\}$ and $l = \text{lcm}(k, r)$, then $\{(x_0, y_0), (x_1, y_1), \dots, (x_i, y_i), \dots\}$ is a cycle for System (5). Its period must be the least common multiple of the periods of $\{x_0, x_1, \dots, x_i, \dots\}$ and $\{y_0, y_1, \dots, y_i, \dots\}$. Thus, it is an l -cycle with $l = \text{lcm}(k, r)$. \square

THEOREM 3 System (5) has

$$\{(x_0, y_0), (x_1, y_1), \dots, (x_{l-1}, y_{l-1}), \dots\}$$

as an L -asymptotically stable l -cycle if and only if

$$\{x_0, x_1, \dots, x_{k-1}, \dots\}$$

is an L -asymptotically stable k -cycle of the T_1 -periodic dynamical system $\{f_0, f_1, \dots, f_{T_1-1}\}$ and

$$\{y_0, y_1, \dots, y_{r-1}, \dots\}$$

is an L -asymptotically stable r -cycle of the q -periodic dynamical system $\{\hat{G}_0, \hat{G}_1, \dots, \hat{G}_{q-1}\}$, where $l = \text{lcm}(k, r)$.

Proof

$$D\hat{F}_i = \begin{pmatrix} D_x f_i & 0 \\ 0 & D_y \hat{G}_i \end{pmatrix}, \quad DF_i = \begin{pmatrix} D_x f_i & 0 \\ D_x g_i & D_y g_i \end{pmatrix} \quad \text{and}$$

$$D_y g_i(x_i, y) = D_y g_{i \bmod (T_2)}(x_{i \bmod (k)}, y) = D_y \hat{G}_i(y).$$

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

When the orbit of x_0 is a single point x_∞ , $x_{i \bmod (k)} = x_\infty$ and the following result is immediate.

COROLLARY 1 *If $\{x_\infty\}$ is an L -asymptotically stable fixed point of $f(t, x(t)) : Z_+ \times R^n \rightarrow R^n$, and*

$$\{y_0, y_1, \dots, y_{r-1}, \dots\}$$

is an L -asymptotically stable r -cycle of $g(t, x_\infty, y(t)) : Z_+ \times R^m \rightarrow R^m$, then

$$\{(x_\infty, y_0), (x_\infty, y_1), \dots, (x_\infty, y_{r-1}), \dots\}$$

is an L -asymptotically stable r -cycle of System (5).

THEOREM 4 *Assume all orbits of System (5) are bounded. Then System (5) has*

$$\{(x_0, y_0), (x_1, y_1), \dots, (x_{l-1}, y_{l-1}), \dots\}$$

as a globally attracting l -cycle if and only if

$$\{x_0, x_1, \dots, x_{k-1}, \dots\}$$

is a globally attracting k -cycle of the T_1 -periodic dynamical system $\{f_0, f_1, \dots, f_{T_1-1}\}$ and

$$\{y_0, y_1, \dots, y_{r-1}, \dots\}$$

is a globally attracting r -cycle of the q -periodic dynamical system $\{\hat{G}_0, \hat{G}_1, \dots, \hat{G}_{q-1}\}$, where $l = \text{lcm}(k, r)$.

Proof Suppose System (5) has

$$\{(x_0, y_0), (x_1, y_1), \dots, (x_{l-1}, y_{l-1}), \dots\}$$

as a globally attracting l -cycle, then by Theorem 3

$$\{x_0, x_1, \dots, x_{k-1}, \dots\}$$

is an attracting k -cycle of the T_1 -periodic dynamical system $\{f_0, f_1, \dots, f_{T_1-1}\}$ and

$$\{y_0, y_1, \dots, y_{r-1}, \dots\}$$

is an attracting r -cycle of the q -periodic dynamical system $\{\hat{G}_0, \hat{G}_1, \dots, \hat{G}_{q-1}\}$, where $l = \text{lcm}(k, r)$. In fact since the first coordinate of System (5) is precisely the T_1 -periodic dynamical system $\{f_0, f_1, \dots, f_{T_1-1}\}$,

$$\{x_0, x_1, \dots, x_{k-1}, \dots\}$$

is globally attracting. Independent of initial conditions, the second coordinate of System (5) limits on $\{y_0, y_1, \dots, y_{r-1}, \dots\}$. So if the first coordinate of the initial condition is x_0 , the second coordinate also limits on $\{y_0, y_1, \dots, y_{r-1}, \dots\}$. Thus $\{y_0, y_1, \dots, y_{r-1}, \dots\}$ is globally attracting for the q -periodic dynamical system $\{\hat{G}_0, \hat{G}_1, \dots, \hat{G}_{q-1}\}$.

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

dynamical system $\{\hat{G}_0, \hat{G}_1, \dots, \hat{G}_{q-1}\}$, the orbit of (x_0, y) under H gets into $U \times W$. Since C is compact, there is an integer j such that $H^j(x_0, y) \in U \times W$ for all $(x, y) \in C$. By continuity there is a $\delta > 0$ such that if $\|x - x_0\| < \delta$, then $H^j(x, y)$ stays close enough to $H^j(x_0, y)$ so that $H^j(x, y) \in U \times W$. Since $\{x_0, x_1, \dots, x_{k-1}, \dots\}$ is a globally attracting k -cycle of the T_1 -periodic dynamical system $\{f_0, f_1, \dots, f_{T_1-1}\}$, the orbit of x under $\{f_0, f_1, \dots, f_{T_1-1}\}$ eventually gets within δ of x_0 . Thus (x, y) is attracted to the l -cycle $\{(x_0, y_0), (x_1, y_1), \dots, (x_{l-1}, y_{l-1}), \dots\}$. \square

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

$$\left. \begin{aligned} x_1(t+1) &= (1-d)x_1(t) \exp\left(R_1 \left(1 - \frac{x_1(t)}{K_1 + \alpha_1(-1)^t}\right)\right), \\ x_2(t+1) &= dx_1(t) \exp\left(R_1 \left(1 - \frac{x_1(t)}{K_1 + \alpha_1(-1)^t}\right)\right) + x_2(t) \exp\left(R_2 \left(1 - \frac{x_2(t)}{K_2 + \alpha_2(-1)^t}\right)\right). \end{aligned} \right\} \quad (6)$$

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 ω -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 $F_1^t(y) \rightarrow 0$ as $t \rightarrow +\infty$. Define the function $V : \mathbb{R}_+ \times \mathbb{R}_+ \rightarrow \mathbb{R}_+$ 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 ω -limit point and $x_1 > 0$, then $V(F(x)) < V(x)$. However, this is impossible for an ω -limit point.

Consequently, when $(1 - d)\exp(R_1) < 1$, the “limiting system” of System (6) is

$$x_2(t+1) = x_2(t) \exp\left(R_2\left(1 - \frac{x_2(t)}{K_2 + \alpha_2(-1)^t}\right)\right). \quad (7)$$

To prove persistence, notice that $x_2(t+1) \geq x_2(t) \exp(R_2(1 - (x_2(t))/K_2 - a_2))$. Thus $x_2(t)$ is increasing if $x_2(t) \in [0, K_2 - \alpha_2]$. Also, if $(x_1(t), x_2(t)) \in [0, I_1] \times [K_2 - \alpha_2, I_2]$, $x_2(t+1)$ 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. \square

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 $\{f_0, f_1, \dots, f_i, \dots\}$ 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):

$$\alpha_1 = 0, \quad \alpha_2 = 0.01, \quad K_1 = K_2 = 1, \quad R_1 = 1.8, \quad R_2 = 2.1, \quad \text{and } d = 0.01.$$

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

$$\hat{G}_i(x_2) = \frac{d}{1-d} x_{1\infty} + x_2 \exp\left(R_2\left(1 - \frac{x_2}{K_2 + \alpha_2(-1)^i}\right)\right).$$

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_i in System (6) force complex bifurcations including period doubling bifurcations, chaotic attractors and multiple attractors with complex basins of attraction [16,30].

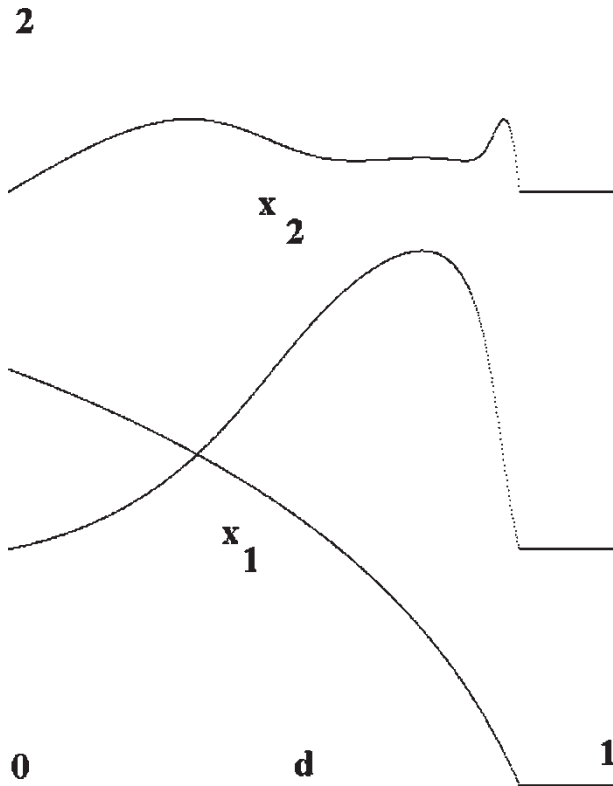


Figure 1. Patch 1 versus Patch 2 populations as d varies between 0 and 1. Patch 1 population decreases to zero with increasing values of the dispersal rate. However, Patch 2 population first increases before decreasing to its carrying capacity, and the population persists on a two-cycle attractor for all values of the dispersal rate. On the vertical axis, $0 \leq x_1, x_2 \leq 2$. On the horizontal axis, $0 \leq d \leq 1$.

To illustrate multiple attractors via two coexisting two-cycle attractors we set the following parameters values in System (6)

$$\alpha_1 = 0, \quad \alpha_2 = 0.01, \quad K_1 = K_2 = 1, \quad R_1 = 2.2, \quad R_2 = 2.1, \quad \text{and } d = 0.01$$

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.

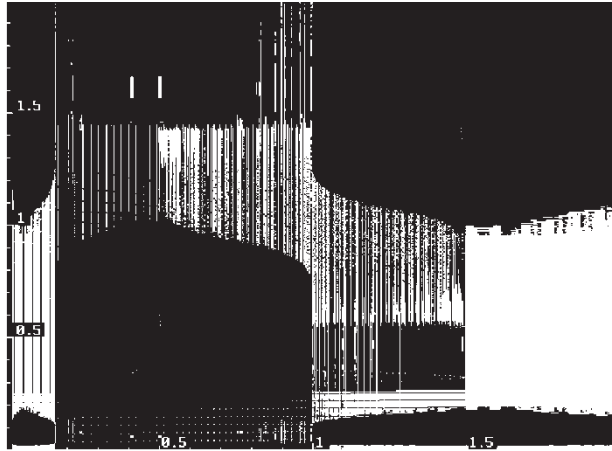


Figure 2. Basins of attraction of the two coexisting two-cycle attractors at $\{(1.4853, 1.4438) \rightarrow (0.5055, 0.5565)\}$ and $\{(1.4853, 0.5847) \rightarrow (0.5055, 1.4208)\}$. On the horizontal axis, $0 \leq x_1 \leq 2$, and on the vertical axis $0 \leq x_2 \leq 2$.

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 [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 [16,40,41]. Also, single species *nonautonomous* models support multiple attractors where the corresponding autonomous models support single attractors [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 [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 [19,27,41].

Acknowledgements

We thank the referee for useful comments and suggestions. This research has been partially supported by grants given by the National Science Foundation, National Security Agency, and the Sloan Foundation (through the Cornell-Sloan National Pipeline Program in the Mathematical Sciences). Substantial financial and moral support was also provided by

the Office of the Provost of Cornell University, the College of Agriculture and Life Science (CALs), the Department of Biological Statistics and Computational Biology and the Los Alamos National Laboratory. We especially like to thank Carlos Castillo-Chávez for his support throughout this study at MTBI 2002–2003. Abdul-Aziz Yakubu has been partially supported by the National Marine Fisheries Service (North East Fisheries Science Center) at Woods Hole, MA.

References

- [1] Allen, L.J., 1987, Persistence, extinction, and critical patch number for island populations. *Journal of Mathematical Biology*, **24**, 617–625.
- [2] Begon, M., Harper, J.L. and Townsend, C.R., 1996, *Townsend, Ecology: Individuals, Populations and Communities* (Blackwell Science Ltd).
- [3] Castillo-Chavez, C. and Yakubu, A.A., 2001, Dispersal, disease and life-history evolution. *Mathematical Biosciences*, **173**, 35–53.
- [4] Castillo-Chavez, C. and Yakubu, A.A., 2002, Intraspecific competition, dispersal and disease dynamics in discrete-time patchy environments. In: Carlos Castillo-Chavez, Sally Blower, Pauline Van den Driessche, Denise Kirschner and Abdul-Aziz Yakubu (Eds.) *Mathematical Approaches For Emerging and Reemerging Infectious Diseases: An Introduction to Models, Methods and Theory* (New York: Springer-Verlag).
- [5] Cohen, D. and Levin, S.A., 1987, The interaction between dispersal and dormancy strategies in varying and heterogeneous environments. In: E. Teramoto and M. Yamaguti (Eds.) *Mathematical Topics in Population Biology, Morphogenesis and Neurosciences*, Proc. Kyoto 1985 (Berlin: Springer Verlag), pp. 110–122.
- [6] Crutchfield, J.P., Farmer, J.D. and Huberman, B.A., 1982, Fluctuations and simple chaotic dynamics. *Physics Reports*, **92**, 45–82.
- [7] Cushing, J.M., 1977, Periodic time-dependent predator-prey systems. *SIAM Journal on Applied Mathematics*, **32**, 82–95.
- [8] Doebeli, M., 1995, Dispersal and dynamics. *Theoretical Population Biology*, **47**, 82–106.
- [9] Doebeli, M. and Ruxton, G.D., 1997, Evolution of dispersal rates in metapopulation model: Branching and cyclic dynamics in phenotype space. *Evolution*, **5**(6), 1730–1741.
- [10] Earn, D.J., Levin, S.A. and Rohani, P., 2000, Coherence and conservation. *Science*, **290**, 17.
- [11] Elaydi, S.N. and Sacker, R.J., Global stability of periodic orbits of nonautonomous difference equations and population biology. *Journal of Differential Equations*, in press.
- [12] Elaydi, S.N. and Sacker, R.J., Global stability of periodic orbits of nonautonomous difference equations in population biology and cushioning-henson conjectures. *Journal of Differential Equations*, in Press.
- [13] Elaydi, S.N. and Yakubu, A.-A., 2002, Global stability of cycles: Lotka-Volterra competition model with stocking. *Journal of Difference Equations and Applications*, **8**(6), 537–549.
- [14] Franke, J.E. and Selgrade, J.F., 2003, Attractor for periodic dynamical systems. *Journal of Mathematical Analysis and Applications*, **286**, 64–79.
- [15] Franke, J.E. and Yakubu, A.-A., 1996, Extinction and persistence of species in discrete competitive systems with a safe refuge. *Journal of Mathematical Analysis and Applications*, **23**, 746–761.
- [16] Franke, J.E. and Yakubu, A.-A. (2004) Multiple attractors via cusp bifurcation in periodically varying environments. (Preprint)
- [17] Gadgil, M., 1971, Dispersal: Population consequences and evolution. *Ecology*, **52**, 253–261.
- [18] Gonzalez-Andújar, J.L. and Perry, J.N., 1993, Chaos, metapopulations and dispersal. *Ecological Modelling*, **65**, 255–263.
- [19] Grebogi, C., Ott, E. and Yorke, J.A., 1987, Chaos, strange attractors, and fractal basin boundaries in nonlinear dynamics. *Science*, **228**, 632–638.
- [20] Gyllenberg, M., Söderbacka, G. and Ericsson, S., 1993, Does migration stabilize local population dynamics? Analysis of a discrete metapopulation model. *Mathematical Biosciences*, **118**, 25–49.
- [21] Hairston, N.G., 1993, Diapause dynamics of 2 Diaptomid copepod species in a large lake. *Hydrobiologia*, **293**, 209–218.
- [22] Hanski, I., Pöyry, J., Pakkala, T. and Kuussaari, M., 1995, Multiple equilibria in metapopulation dynamics. *Nature*, **377**, 618–621.
- [23] Hanski, I., 1991, Single-species metapopulation dynamics-concepts, models and observations. *Biological Journal of the Linnean Society*, **42**, 17–38.
- [24] Hanski, I.A., 1997, *Gilpin, Metapopulation Biology: Ecology, Genetics, and Evolution* (San Diego, CA: Academic Press Ltd.).
- [25] Hassell, M.P., 1976, *The Dynamics of Competition and Predation*, Studies in Biol. 72 (The Camelot Press Ltd.).
- [26] Hassell, M.P., Lawton, J.H. and May, R.M., 1976, Patterns of dynamical behavior in single species populations. *Journal of Animal Ecology*, **45**, 471–486.
- [27] Hastings, A., 1993, Complex interactions between dispersal and dynamics: Lessons from coupled logistic equations. *Ecology*, **75**, 1362–1372.

- [28] Hastings, A., 1982, Dynamics of a single species in a spatially varying environment: The stabilizing role of high dispersal rates. *Journal of Mathematical Biology*, **16**, 49–55.
- [29] Henson, S.M., 2000, Multiple attractors and resonance in periodically forced population models. *Physics D*, **140**, 33–49.
- [30] Henson, S.M., Costantino, R.F., Cushing, J.M., Dennis, B. and Desharnais, R.A., 1999, Multiple attractors, saddles, and population dynamics in periodic habitats. *Bulletin of Mathematical Biology*, **61**, 1121–1149.
- [31] Henson, S.M. and Cushing, J.M., 1997, The effect of periodic habitat fluctuations on a nonlinear insect population model. *Journal of Mathematical Biology*, **36**, 201–226.
- [32] Jilison, D., 1980, Insect populations respond to fluctuating environments. *Nature*, **288**, 699–700.
- [33] Levin, S.A., 1974, Dispersion and population interactions. *American Naturalist*, **108**, 207–228.
- [34] Levin, S. and Paine, R.T., 1974, Disturbance, patch formation, and community structure. *Proceedings of the National Academy Sciences of the United States of America*, **68**, 2744–2747.
- [35] May, R.M. and Oster, G.F., 1976, Bifurcations and dynamic complexity in simple ecological models. *American Naturalist*, **110**, 573–579.
- [36] May, R.M., 1977, Simple mathematical models with very complicated dynamics. *Nature*, **261**, 459–469.
- [37] May, R.M., 1974, *Stability and Complexity in Model Ecosystems* (Princeton University Press).
- [38] Nicholson, A.J., 1954, Compensatory reactions of populations to stresses, and their evolutionary significance. *Australian Journal of Zoology*, **2**, 1–65.
- [39] Ricker, W.E., 1954, Stock and recruitment. *Journal of Fisheries Research Board of Canada*, **II**(5), 559–623.
- [40] Yakubu, A.-A., 2003, Discrete-time metapopulation dynamics and unidirectional dispersal. *Journal of Difference Equations and Applications*, **9**(7), 633–653.
- [41] Yakubu, A.-A. and Castillo-Chavez, C., 2002, Interplay between local dynamics and dispersal in discrete-time metapopulation models. *Journal of Theoretical Biology*, **218**, 273–288.
- [42] Yodzis, P., 1989, *Introduction to Theoretical Ecology* (New York: Harper & Row, Publishers).