

UNIFORM PERSISTENCE AND PERIODIC COEXISTENCE STATES IN INFINITE-DIMENSIONAL PERIODIC SEMIFLOWS WITH APPLICATIONS

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ABSTRACT. This paper is devoted to the study of uniform persistence and periodic coexistence states in infinite-dimensional periodic semiflows. Under a general abstract setting, we prove that the uniform persistence of a periodic semiflow is equivalent to that of its associated Poincaré map, and that the uniform persistence implies the existence of a periodic coexistence state, which generalizes and unifies some related earlier results. As an application, we discuss in detail the periodic Kolmogorov predator-prey reaction-diffusion system with spatial heterogeneity and obtain some sufficient conditions for the uniform persistence and global extinction of the system under consideration.

1. Introduction. A central problem in population dynamics is to study the asymptotic behaviors of the model systems. Uniform persistence (permanence sometimes in the literature) characterizes a special kind of global asymptotics, that is, the long-term coexistence of interacting species. There have been extensive studies on uniform persistence (see survey paper [24], review paper [19] and references therein). Most of these discussions have centered on models governed by autonomous systems of ordinary differential equations (ODEs), delay differential equations (DDEs) and reaction-diffusion equations (RDEs). Clearly, more realistic models should include both spatial and temporal effects in the real world, which results in general nonautonomous systems. A natural consideration of a periodically varying environment (e.g., the seasonal fluctuations and periodic availability of foods) leads to the study of periodic systems of differential equations. For uniform persistence and (or) positive periodic solutions of some periodic systems, we refer to [2, 3, 7, 10, 15, 16, 22, 25, 26, 28–32]

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and references therein. With appropriate conditions, solutions of an ω -periodic system ($\omega > 0$) generate an ω -periodic semiflow $T(t) : X \rightarrow X$ (X is the initial value space) in the sense that $T(t)x$ is continuous in $(t, x) \in [0, +\infty) \times X$, $T(0) = I$ and $T(t + \omega) = T(t)T(\omega)$ for all $t \geq 0$. The purpose of this paper is to study the uniform persistence and the existence of periodic coexistence states of infinite-dimensional periodic semiflow $T(t) : X \rightarrow X$ under a general abstract setting. Our approaches are via the associated Poincaré map $T(\omega)$ (i.e., time- ω -map) and the infinite-dimensional dynamical system theory.

It is well known that the existence and stability of periodic solutions of a periodic system of differential equations are equivalent to that of the fixed point of its associated Poincaré map (see, e.g., [6, 15]). For the uniform persistence problem, one naturally expects the equivalence between a periodic semiflow and its associated Poincaré map holds as well. This will be confirmed under a general abstract setting in Section 2 (Theorem 2.1). Accordingly, some general approaches and results on the uniform persistence of maps (i.e., the discrete semi-dynamical systems generated by iterations of maps) (see, e.g., [9, 17] and references therein) may find their wide applications to infinite-dimensional periodic semiflows. In particular, we can get an acyclicity theorem on uniform persistence of maps (Theorem 2.2), which is essentially due to Freedman, Hofbauer and So [9, 17]. It is also clear that, under appropriate assumptions, the uniform persistence of periodic systems of ODEs implies the existence of a periodic coexistence solution (see [25, Theorem 4.11] and [26, Lemma 1]). In Section 2, we prove a similar conclusion for the infinite-dimensional periodic semiflow. More precisely, we prove that the uniform persistence of a map, which is defined on a closed subset of a Banach space, implies the existence of a coexistence fixed point (Theorem 2.3). Clearly, an autonomous semiflow can be viewed as an ω -periodic semiflow for any given $\omega > 0$. It follows that there is an analogous result on the existence of a stationary coexistence state (Theorem 2.4), which also generalizes and unifies earlier similar results given in [18] for one class of autonomous systems of ordinary and delay differential equations and in [5] for autonomous two-species interacting reaction-diffusion systems (Remark 2.5).

In Section 3, as an application of general results, we consider the periodic Kolmogorov predator-prey reaction-diffusion systems with spa-

tial heterogeneity and obtain some sufficient conditions for the uniform persistence (Theorem 3.1) and global extinction (Theorem 3.2) of the systems. The special case of Lotka-Volterra reaction-diffusion systems is also discussed (see Example 1 for the case where both predatory and prey have self-limitation and Example 2 for the case where only the prey has self-limitation). Moreover, Example 1 generalizes the research in [2] where only the existence of positive periodic solution is proved by bifurcation theory (Remark 3.4).

2. Uniform persistence and coexistence states. Let X be a complete metric space with metric d . According to [12], $T(t) : X \rightarrow X$, $t \geq 0$ is an ω -periodic (autonomous) semiflow on X if there is an $\omega > 0$ (for every $\omega > 0$) such that $T(t)x$ is continuous in $(t, x) \in [0, \infty) \times X$, $T(0) = I$ and $T(t+\omega) = T(t)T(\omega)$ for all $t \geq 0$. A point x_0 corresponds to an ω -periodic orbit (equilibrium point) if $T(t+\omega)x_0 = T(t)x_0$ for all $t \geq 0$ (and every $\omega > 0$). For an ω -periodic semiflow, these x_0 coincide with the fixed points of its associated Poincaré map $T(\omega)$.

Let X_0 and ∂X_0 be open and closed subsets of X , respectively, such that $X_0 \cap \partial X_0 = \emptyset$ and $X = X_0 \cup \partial X_0$, $T(t) : X \rightarrow X$, $t \geq 0$, be an ω -periodic semiflow with $T(t)X_0 \subset X_0$, $t \geq 0$, i.e., X_0 is a positively invariant subset of X for $T(t)$. Note that we don't require ∂X_0 to be positively invariant for $T(t)$.

Definition 2.1. The periodic semiflow $T(t)$ is said to be *uniformly persistent* with respect to $(X_0, \partial X_0)$ if there exists $\eta > 0$ such that for any $x \in X_0$, $\liminf_{t \rightarrow \infty} d(T(t)x, \partial X_0) \geq \eta$.

For a discrete semi-dynamical system $\{S_n\}_{n=0}^{\infty}$ defined by $S : X \rightarrow X$ with $SX_0 \subset X_0$, we have the corresponding definition of uniform persistence (see, e.g., [17]). In what follows, for some unexplained terminologies we refer to [11, 13].

We are now in a position to prove the following equivalence result between the uniform persistence of a periodic semiflow $T(t)$ and that of its associated discrete semi-dynamical system $\{S^n\}$ defined by $S = T(\omega)$.

Theorem 2.1. *Let $T(t)$ be an ω -periodic semiflow on X with $T(t)X_0 \subset X_0$, $t \geq 0$. Assume that $S = T(\omega)$ satisfies the following*

conditions:

(1) S is point dissipative in X ;

(2) S is compact; or alternatively, S is asymptotically smooth and $\gamma^+(U)$ is strongly bounded in X_0 if U is strongly bounded in X_0 .

Then the uniform persistence of S with respect to $(X_0, \partial X_0)$ implies that of $T(t) : X \rightarrow X$, $t \geq 0$. More precisely, S admits a global attractor $A_0 \subset X_0$ relative to strongly bounded sets in X_0 such that the compact set $A_0^* = \cup_{0 \leq t \leq \omega} T(t)A_0 \subset X_0$ attracts any strongly bounded sets in X_0 , i.e., for any bounded subset U of X_0 with $d(U, \partial X_0) = \inf_{x \in U} d(x, \partial X_0) > 0$, $\lim_{t \rightarrow \infty} \bar{d}(T(t)U, A_0^*) = 0$, where $\bar{d}(T(t)U, A_0^*) = \sup_{x \in T(t)U} d(x, A_0^*)$.

Proof. By the point dissipativity and uniform persistence of S , it follows that S is strongly point dissipative in X_0 , i.e., there exists a strongly bounded subset B of X_0 such that for any $x \in X_0$, there exists an $n_0 = n_0(x, B) > 0$ such that $S^n(x) \in B$ for all $n \geq n_0$. By a similar argument to [11, Theorems 2.4.6 and 2.4.7], we can prove that S admits a global attractor $A_0 \subset X_0$ which attracts strongly bounded sets in X_0 .

By the compactness of A_0 and the continuity of $T(t)x$ for $x \in X$ uniformly on the compact set $[0, \omega]$, it easily follows that for any $\varepsilon > 0$ there is $\delta > 0$ such that, for all $x \in N(A_0, \delta)$, the δ -neighborhood of A_0 , and all $t \in [0, \omega]$, $T(t)x \in N(T(t)A_0, \varepsilon)$, i.e.,

$$(2.1) \quad \lim_{x \rightarrow A_0} d(T(t)x, T(t)A_0) = 0 \quad \text{uniformly for } t \in [0, \omega].$$

Since A_0 is invariant for S (i.e., $SA_0 = A_0$) and $T(t)$ is an ω -periodic semi-flow, $A_0 = S^n A_0 = T(n\omega)A_0$ for all $n \geq 1$.

Let U be any given strongly bounded subset of X_0 ; then, by the global attractivity of A_0 relative to strongly bounded sets in X_0 ,

$$(2.2) \quad \lim_{n \rightarrow \infty} \bar{d}(S^n U, A_0) = \lim_{n \rightarrow \infty} \bar{d}(T(n\omega)U, A_0) = 0.$$

For any $t \geq 0$, let $t = n\omega + t'$, where $n = [t/\omega]$ is the greatest integer less than or equal to t/ω and $t' \in [0, \omega)$, then

$$\begin{aligned} \bar{d}(T(t)U, T(t)A_0) &= \bar{d}(T(t')T(n\omega)U, T(t')T(n\omega)A_0) \\ &= \bar{d}(T(t')T(n\omega)U, T(t')A_0), \end{aligned}$$

and hence (2.1) and (2.2) imply that

$$(2.3) \quad \lim_{t \rightarrow \infty} \bar{d}(T(t)U, T(t)A_0) = 0.$$

By the continuity of $T(t)x$ for $(t, x) \in [0, \infty) \times X$ and the compactness of $[0, \omega] \times A_0$, $A_0^* = \cup_{0 \leq t \leq \omega} T(t)A_0$ is compact, and hence $d(A_0^*, \partial X_0) > 0$ since ∂X_0 is closed and $T(t)X_0 \subset X_0, t \geq 0$, implies $A_0^* \subset X_0$. Again, by the invariance of A_0 for $S = T(\omega), \cup_{t \geq 0} T(t)A_0 = \cup_{0 \leq t \leq \omega} T(t)A_0 = A_0^*$. Therefore (2.3) implies $\lim_{t \rightarrow \infty} \bar{d}(T(t)U, A_0^*) = 0$.

This completes the proof. \square

Remark 2.1. By Theorem 2.1 above, we can reduce the uniform persistence of a given periodic (autonomous) system of differential equations to that of its associated Poincaré map (the time- ω -map for any fixed $\omega > 0$). For some illustrations, we refer to [21, Theorem 3.4] for certain autonomous systems of ODEs and [22, Theorem 1.1] for certain periodic ones.

As for the uniform persistence of discrete semi-dynamical systems defined by maps, there are unified discussions and general results in [17]. For the latter convenience of application, we give an acyclicity theorem on uniform persistence, which is essentially due to Freedman, Hofbauer and So [9, 17]. For analogous results in the case of continuous semi-dynamical systems, we refer to [13, Theorems 4.1 and 4.2]. For some terminology, again we refer to [9, 17].

Theorem 2.2 (Freedman, Hofbauer and So). *Let $S : X \rightarrow X$ be a continuous map with $S(X_0) \subset X_0$. Assume that*

(1) *$S : X \rightarrow X$ has a global attractor A , that is, A is the maximal compact invariant subset of X and $\lim_{n \rightarrow \infty} d(S^n x, A) = 0$ for any $x \in X$;*

(2) *Let A_∂ be the maximal compact invariant set of S in ∂X_0 . $\tilde{A}_\partial = \cup_{x \in A_\partial} \omega(x)$ has an isolated and acyclic covering $\cup_{i=1}^k M_i$ in ∂X_0 , that is, $A_\partial \subset \cup_{i=1}^k M_i$, where M_1, M_2, \dots, M_k are pairwise disjoint, compact and isolated invariant sets of S in ∂X_0 such that each M_i is also an isolated invariant set in X , and no subset of the M_i 's forms a cycle for $S_\partial = S|_{A_\partial}$ in A_∂ .*

Then S is uniformly persistent if and only if for each M_i , $i = 1, 2, \dots, k$,

$$W^s(M_i) \cap X_0 = \phi$$

where $W^s(M_i) = \{x; x \in X, \omega(x) \neq \phi \text{ and } \omega(x) \subset M_i\}$ is the stable set of M_i .

Proof. By the compactness and global attractivity of A , it follows that for any $x \in X$, $\gamma^+(x)$ is a precompact subset of X . Clearly, $A_\partial \subset A \cap \partial X_0$ and the closure of $\bar{A}_\partial \subset \cup_{i=1}^k M_i$. By the definition of the isolated covering $\cup_{i=1}^k M_i$, $M_i \subset A_\partial$, $i = 1, 2, \dots, k$. Therefore, [9, Propositions 2.2 and 3.2] imply that $\cup_{i=1}^k M_i$ is a Morse decomposition of A_∂ under S_∂ . Now [17, Theorem 4.2] completes the proof. \square

Remark 2.2. For fundamental results on the existence of a global attractor for $S : X \rightarrow X$, we refer to [11, Theorems 2.4.6 and 2.4.7].

In the rest of this section, we always assume that X is a closed subset of a given Banach space E , and that $X = X_0 \cup \partial X_0$ with $X_0 \cap \partial X_0 = \phi$, X_0 convex and X_0 and ∂X_0 relatively open and closed in X , respectively.

Given a set $A \subset E$, let $\text{co}(A)$ be the convex hull of A and $\overline{\text{co}}(A)$ be the closed convex hull of A , respectively. For the latter proof of the existence of coexistence states of uniformly persistent maps, we first prove the following two lemmas.

Lemma 2.1. *If A is a compact subset of X_0 , then $\overline{\text{co}}(A) \subset X_0$ and $d(\overline{\text{co}}(A), \partial X_0) > 0$.*

Proof. Since A is compact, $A \subset X_0$ and ∂X_0 is closed, $d(A, \partial X_0) > 0$. For any $x \in X$ and $\delta > 0$, denote $B(x, \delta) = \{y \in X; \|y - x\| < \delta\}$ and $\bar{B}(x, \delta) = \{y \in X; \|y - x\| \leq \delta\}$. Let $\delta_0 = (1/2)d(A, \partial X_0) > 0$, then for every $x \in A$, $\bar{B}(x, \delta_0) \subset X_0$ and $A \subset \cup_{x \in A} B(x, \delta_0)$. Again, by the compactness of A , there exist finitely many $x_1, x_2, \dots, x_k \in A$ such that $A \subset \cup_{i=1}^k B(x_i, \delta_0)$. Let $A_i = A \cap \bar{B}(x_i, \delta_0)$, $i = 1, 2, \dots, k$, then $A = \cup_{i=1}^k A_i$. Clearly, A_i is compact and $A_i \subset \bar{B}(x_i, \delta_0) \subset X_0$, and hence $\overline{\text{co}}(A_i) \subset \bar{B}(x_i, \delta_0) \subset X_0$, $i = 1, 2, \dots, k$. Therefore, since X_0 is

convex, $\text{co}(\cup_{i=1}^k \overline{\text{co}}(A_i)) \subset X_0$. By [20, Theorem 2.1 (v)] and a finite induction, it follows that for any finitely many nonempty subsets C_i of Banach space E , $i = 1, 2, \dots, n$,

$$\begin{aligned} &\text{co}\left(\bigcup_{i=1}^n C_i\right) \\ &= \left\{ \sum_{i=1}^n \alpha_i x_i; \alpha_i \geq 0, \sum_{i=1}^n \alpha_i = 1 \text{ and } x_i \in \text{co}(C_i), 1 \leq i \leq n \right\}. \end{aligned}$$

Therefore, since $\text{co}(\overline{\text{co}}(A_i)) = \overline{\text{co}}(A_i)$, $i = 1, 2, \dots, k$,

$$\begin{aligned} \text{co}\left(\bigcup_{i=1}^k \overline{\text{co}}(A_i)\right) &= \left\{ \sum_{i=1}^k \alpha_i x_i; \alpha_i \geq 0, \sum_{i=1}^k \alpha_i = 1 \right. \\ &\quad \left. \text{and } x_i \in \overline{\text{co}}(A_i), 1 \leq i \leq k \right\} \\ &= F(\Lambda_k \times \overline{\text{co}}(A_1) \times \dots \times \overline{\text{co}}(A_k)) \end{aligned}$$

where

$$F(\alpha, x_1, x_2, \dots, x_k) = \sum_{i=1}^k \alpha_i x_i,$$

$\alpha = (\alpha_1, \dots, \alpha_k) \in R^k$, $(x_1, \dots, x_k) \in E^k$ and

$$\Lambda_k = \left\{ (\alpha_1, \dots, \alpha_k) \in R^k; \alpha_i \geq 0, 1 \leq i \leq k \text{ and } \sum_{i=1}^k \alpha_i = 1 \right\}.$$

Since the closed hull of any precompact subset of a given Banach space is compact, e.g., by [27, Proposition 11.3], $\overline{\text{co}}(A)$ and $\overline{\text{co}}(A_i)$, $1 \leq i \leq k$, are all compact. By the continuity of $F : R^k \times E^k \rightarrow E$ and the compactness of $\Lambda_k \times \overline{\text{co}}(A_1) \times \dots \times \overline{\text{co}}(A_k)$ in $R^k \times E^k$, it follows that $\text{co}(\cup_{i=1}^k \overline{\text{co}}(A_i))$ is compact and hence closed. Therefore,

$$\overline{\text{co}}(A) = \overline{\text{co}}\left(\bigcup_{i=1}^k A_i\right) \subset \overline{\text{co}}\left(\bigcup_{i=1}^k \overline{\text{co}}(A_i)\right) = \text{co}\left(\bigcup_{i=1}^k \overline{\text{co}}(A_i)\right) \subset X_0.$$

Then by the compactness of $\overline{\text{co}}(A)$ and closedness of ∂X_0 , $d(\overline{\text{co}}(A), \partial X_0) > 0$. This completes the proof. \square

Lemma 2.2. *If A is a convex and compact subset of X_0 , then for any $\varepsilon > 0$ there exists an open and convex set $N_\varepsilon \subset X_0$ such that $A \subset N_\varepsilon \subset N(A, \varepsilon)$, where $N(A, \varepsilon) = \{x \in E; d(x, A) < \varepsilon\}$ is the ε -neighborhood of A .*

Proof. Since $A \subset X_0$ is compact, $\underline{d}(A, \partial X_0) > 0$. For any $\varepsilon > 0$, let $\delta = \min(\varepsilon, (1/2)\underline{d}(A, \partial X_0))$. As in the proof of Lemma 2.1, there exist $x_1, x_2, \dots, x_k \in A$ such that $A \subset \cup_{i=1}^k B(x_i, \delta) \subset X_0$. Therefore, since X_0 is convex, $A \subset \text{co}(\cup_{i=1}^k B(x_i, \delta)) \subset X_0$. Since the convex of any open subset of given linear topological space is open, $N_\varepsilon = \text{co}(\cup_{i=1}^k B(x_i, \delta))$ is open in X . Since each $B(x_i, \delta)$ is convex, as in the proof of Lemma 2.1,

$$N_\varepsilon = \left\{ \sum_{i=1}^k \alpha_i y_i; \alpha_i \geq 0, \sum_{i=1}^k \alpha_i = 1 \text{ and } y_i \in B(x_i, \delta), 1 \leq i \leq k \right\}.$$

Therefore, for any $x \in N_\varepsilon$, $x = \sum_{i=1}^k \alpha_i y_i$ for some $y_i \in B(x_i, \delta)$ and $\alpha_i \geq 0, i = 1, 2, \dots, k$, with $\sum_{i=1}^k \alpha_i = 1$. Then

$$\begin{aligned} \left\| x - \sum_{i=1}^k \alpha_i x_i \right\| &= \left\| \sum_{i=1}^k \alpha_i (y_i - x_i) \right\| \\ &\leq \sum_{i=1}^k \alpha_i \|y_i - x_i\| < \sum_{i=1}^k \alpha_i \delta = \delta \leq \varepsilon. \end{aligned}$$

Since A is convex, $\sum_{i=1}^k \alpha_i x_i \in A$ and hence $d(x, A) < \varepsilon$. Then $N_\varepsilon \subset N(A, \varepsilon)$. This completes the proof. \square

We also need the following Hale and Lopes fixed point theorem in Banach space, which is a consequence of [11, Lemmas 2.6.5 and 2.6.6] or [12, Theorems 5 and 6].

Lemma 2.3 (Hale and Lopes). *Suppose $K \subset B \subset S$ are convex subsets of a Banach space E with K compact, S closed and bounded, and B open in S . If $T : S \rightarrow E$ is α -condensing, $\gamma^+(B) \subset S$, and K attracts compact sets of B , then T has a fixed point in B .*

Recall that $T : X \rightarrow X$ is α -condensing if T is continuous, takes bounded sets into bounded sets and $\alpha(TA) < \alpha(A)$ for any bounded set $A \subset X$ with $\alpha(A) > 0$. Here $\alpha(A)$ is the Kuratowski measure of noncompactness, we refer to [11, Section 2.3] and [27, Section 11.1] for its definition and properties.

Now we turn to the discrete semi-dynamical system $\{S^n\}_{n=1}^\infty$ defined by $S : X \rightarrow X$ with $S(X_0) \subset X_0$. A point $x_0 \in X$ is called a coexistence state of $\{S^n\}_{n=1}^\infty$ if x_0 is a fixed point of S in X_0 , i.e., $x_0 \in X_0$ and $S(x_0) = x_0$. We have the following result on the existence of coexistence state.

Theorem 2.3. *Let $S : X \rightarrow X$ be a continuous map with $S(X_0) \subset X_0$. Assume that*

- (1) $S : X \rightarrow X$ is point dissipative;
- (2) S is compact; or alternatively, S is α -condensing and $\gamma^+(U)$ is strongly bounded in X_0 if U is strongly bounded in X_0 ;
- (3) S is uniformly persistent with respect to $(X_0, \partial X_0)$.

Then there exists a global attractor A_0 for S in X_0 relative to strongly bounded sets in X_0 , and S has a coexistence state $x_0 \in A_0$.

Proof. Since $S : X \rightarrow X$ is α -condensing, by [11, Lemma 2.3.5], S is asymptotically smooth. As in the proof of Theorem 2.1, the existence of global attractor A_0 in X_0 follows in both cases of assumption (2).

Let $K = \overline{\text{co}}(A_0)$. Since $A_0 \subset X_0$ is compact, K is compact. By Lemma 2.1, $K \subset X_0$ and $\underline{d}(K, \partial X_0) > 0$. Then there exists an $\varepsilon_0 > 0$ such that $N(K, \varepsilon_0) \cap X$ is strongly bounded in X_0 . By Lemma 2.2, there is an open and convex neighborhood B of K such that $B \subset N(K, \varepsilon_0) \cap X_0$, and hence B is strongly bounded in X_0 . Then K attracts B and $\gamma^+(B)$ is bounded in X_0 . Since X_0 is convex and X is closed in Banach space E , $S_0 = \overline{\text{co}}(\gamma^+(B)) \subset \overline{X_0} \subset X$, and S_0 is bounded in X . Clearly, any continuous and compact map is also an α -condensing one. Therefore, in both cases of assumption (2), $K \subset B \subset S_0$ satisfy all conditions of Lemma 2.3, and hence S has a fixed point x_0 in $B \subset X_0$ and, clearly, $x_0 \in A_0$. This completes the proof. \square

Remark 2.3. In the case where $S : X \rightarrow X$ is compact, there is an alternative proof for the existence of the coexistence state. Indeed, by Lemma 3.2, there is an open and convex neighborhood U of K such that $U \subset N(K, \varepsilon_0/2) \cap X_0$. Then $\bar{U} \subset N(K, \varepsilon_0) \cap X \subset X_0$. By the attractivity of A_0 for strongly bounded sets in X_0 , there is an $n_0 = n_0(\bar{U}) > 0$ such that, for any $n \geq n_0$, $S^n \bar{U} \subset U$. By an asymptotic generalized Schauder fixed point theorem (see [27, Theorem 17.B]), S has a fixed point x_0 in U .

Remark 2.4. By applying Theorem 2.3 above to the Poincaré map associated with a periodic semiflow, one can obtain the existence of a periodic orbit in X_0 , and hence that of periodic coexistence solutions for periodic systems of differential equations. In particular, Theorem 2.3 implies [25, Theorem 4.11]. For periodic and uniformly persistent Kolmogorov systems of ODE, Zanolin [26, Lemma 1] also proved a similar result. For the existence and global attractivity of positive periodic solutions of periodic Lotka-Volterra systems of ODE, we refer to [10, 28] and references therein.

For autonomous semiflow $T(t) : X \rightarrow X$, $t \geq 0$, we have the following result.

Theorem 2.4. *Let $T(t) : X \rightarrow X$, $t \geq 0$, be an autonomous semiflow with $T(t)X_0 \subset X_0$ for all $t \geq 0$. Assume that*

- (1) $T(t) : X \rightarrow X$ is point dissipative;
- (2) $T(t)$ is compact for each $t > 0$; or alternatively, $T(t) : X \rightarrow X$ is an α -contraction with its contracting function $k(t) \in [0, 1)$, $t > 0$, and $\gamma^+(U)$ is strongly bounded in X_0 if U is strongly bounded in X_0 ;
- (3) $T(t)$ is uniformly persistent with respect to $(X_0, \partial X_0)$.

Then there exists a global attractor A_0 for $T(t)$ in X_0 relative to strongly bounded sets in X_0 and $T(t)$ has a stationary coexistence state x_0 in A_0 , i.e., $x_0 \in X_0$ and $T(t)x_0 = x_0$ for all $t \geq 0$.

Proof. By a similar argument to [13, Proof of Theorems 3.2 and 3.3], the existence of global attractor A_0 in X_0 relative to strongly bounded sets in X_0 follows.

Let $\{\omega_m\}_{m=1}^\infty$ be any given sequence with $\omega_m > 0$, $m = 1, 2, \dots, \infty$, and $\lim_{m \rightarrow \infty} \omega_m = 0$. By Theorem 2.3, $T(\omega_m)$ has a fixed point $x_m \in X_0$, $m = 1, 2, \dots, \infty$. By the global attractivity of A_0 in X_0 , for each fixed x_m , $\lim_{t \rightarrow \infty} d(T(t)x_m, A_0) = 0$, and hence $0 = \lim_{n \rightarrow \infty} d(T(n\omega_m)x_m, A_0) = d(x_m, A_0)$. Then the compactness of A_0 implies that $x_m \in A_0$, $m = 1, 2, \dots, \infty$. Again by the compactness of A_0 , $\{x_m\}_{m=1}^\infty$ has a convergent subsequence to $x_0 \in A_0$, and hence by [12, Lemma 7], x_0 is an equilibrium point of $T(t)$, i.e., $T(t)x_0 = x_0$ for all $t \geq 0$. This completes the proof. \square

Remark 2.5. For autonomous Kolmogorov systems of ODE and one class of autonomous differential equations with finite delay, Hutson [18] proved similar results on the existence of a positive equilibrium. For autonomous Kolmogorov two-species interacting reaction-diffusion systems, Cantrell, Cosner and Hutson [5, Theorem 6.2] also showed a similar result on the existence of a stationary coexistence state under certain assumptions.

It is well-known that many of the models of population dynamics are naturally described by differential equations with delays or (and) diffusions. In many important cases and under appropriate assumptions, a (periodic) system of functional differential equations may generate an α -contractive (periodic) semiflow on some suitable Banach space (see, e.g., [11]) and a (periodic) system of parabolic differential equations may generate a (periodic) semiflow $T(t) : E \rightarrow E$, $t \geq 0$, which is compact for all $t > 0$ on some suitable Banach space E (see, e.g., [15]). Therefore, our results in this section can be applied to wide-ranging biological problems although sometimes the verification of these hypotheses involves certain technical difficulties.

3. Application to periodic predator-prey reaction-diffusion systems with spatial heterogeneity. In this section we apply the general results of Section 2 to the following two-species periodic Kolmogorov reaction-diffusion systems with spatial heterogeneity

$$(3.1) \quad \begin{cases} \partial u_i / \partial t + A_i(t)u_i = u_i F_i(x, t, u_1, u_2) & \text{in } \Omega \times (0, \infty) \\ Bu_i = 0 & \text{on } \partial\Omega \times (0, \infty) \end{cases}$$

where $\Omega \subset \mathbb{R}^N$, $N \geq 1$, is a bounded domain with boundary $\partial\Omega$ of

class $C^{2+\theta}$, $0 < \theta \leq 1$,

$$A_i(t)v = - \sum_{j,k=1}^N a_{jk}^{(i)}(x,t) \frac{\partial^2 v}{\partial x_j \partial x_k} + \sum_{j=1}^N a_j^{(i)}(x,t) \frac{\partial v}{\partial x_j} + a_0^{(i)}(x,t)v,$$

$i = 1, 2$, are linear uniformly elliptic differential expressions of second order for each $t \in [0, T]$, $T > 0$, and $A_i(t)$ and $F_i(x, t, u_1, u_2)$ are T -periodic in t , and $B_i v = v$ or $B_i v = \partial v / \partial n + b_0^{(i)}(x)v$, where $\partial / \partial n$ denotes the differentiation in the direction of the outward normal n to $\partial\Omega$. We assume that $a_{jk}^{(i)} = a_{kj}^{(i)}$, $a_j^{(i)}$ and $a_0^{(i)} \in C^{\theta, \theta/2}(\overline{Q}_T)$, $a_0^{(i)} \geq 0$, $1 \leq j, k \leq N$, $1 \leq i \leq 2$, $Q_T = \Omega \times [0, T]$, and $b_0^{(i)} \in C^{1+\theta}(\partial\Omega, R)$, $b_0^{(i)} \geq 0$, $i = 1, 2$, and that $F_i \in C(\overline{Q}_T \times R^2, R)$, $\partial F_i / \partial u_j$ exists and $\partial F_i / \partial u_j \in C(\overline{Q}_T \times R^2, R)$ with $F_i(\cdot, \cdot, u)$ and $(\partial F_i / \partial u_j)(\cdot, \cdot, u) \in C^{\theta, \theta/2}(\overline{Q}_T, R)$ uniformly for $u = (u_1, u_2)$ in bounded subsets of R^2 , $i, j = 1, 2$.

Let $X = L^p(\Omega)$, $N < p < \infty$, and for $\beta \in (1/2 + N/(2p), 1]$, let $E_i = X_\beta^{(i)}$, $i = 1, 2$, be the fractional power space of X with respect to $(A_i(0), B_i)$ (see, e.g., Henry [14]), then E_i is an ordered Banach space with the order cone P_i consisting of all nonnegative functions in E_i , and P_i has nonempty interior $\text{int}(P_i)$. Let $E = E_1 \times E_2$, then by an easy extension of some results in [15, Section III.20] to the systems, it follows that for every $u_0 = (u_1^0, u_2^0) \in E$, there exists a unique regular solution $\varphi(t, u_0)$ of (3.1) satisfying $\varphi(0, u_0) = u_0$ with its maximal existence interval $I^+(u_0) \subset [0, \infty)$ and $\varphi(t, u_0)$ is globally defined provided there is an L^∞ -bound on $I^+(u_0)$. Moreover, by an invariant principle argument (see, e.g., [1, 23]), it follows that any solution $\varphi(t, u_0)$ of (3.1) with nonnegative initial values remains nonnegative.

For any $m \in C^{\theta, \theta/2}(\overline{Q}_T)$, according to [15], there exists a unique principal eigenvalue of the periodic-parabolic eigenvalue problem

$$(3.2) \quad \begin{cases} \partial v / \partial t + A_i(t)v = m(x, t)v + \mu v & \text{in } \Omega \times R \\ B_i v = 0 & \text{on } \partial\Omega \times R \\ v \text{ } T\text{-periodic in } t, \end{cases}$$

which we denote by $\mu^{(i)}(m)$, $i = 1, 2$.

Now we turn to the periodic predator-prey models with diffusion. Assume that prey u_1 and predator u_2 live in a bounded habitat Ω . For

the global existence and dissipativity on $C(\bar{\Omega}) \times C(\bar{\Omega})$ of solutions of (3.1), we first make the following assumptions.

(A1) For any $(x, t, u_1, u_2) \in \bar{Q}_T \times R_+^2$, $F_1(x, t, u_1, u_2) \leq F_1(x, t, u_1, 0)$, and there exist $a_1 > 0$ and $M_1 > 0$ such that $F_1(x, t, u_1, 0) \leq -a_1 < 0$ for all $(x, t) \in \bar{Q}_T$ and $u_1 \geq M_1$;

(A2) For any given $(x, t, u_2) \in \bar{Q}_T \times R_+$, $F_2(x, t, u_1, u_2)$ is increasing for $u_1 \geq 0$, and for any $M > 0$, there exist $a_2(M) > 0$ and $M_2(M) > 0$ such that $F_2(x, t, M, u_2) \leq -a_2 < 0$ for all $(x, t) \in \bar{Q}_T$ and $u_2 \geq M_2$.

By a standard comparison argument (see, e.g., [31, Lemma 4.1]), we can readily prove the following result.

Lemma 3.1. *Let (A1) and (A2) hold. Then there exists an $M > 0$ such that for any $u \in P_1 \times P_2$, $\varphi(t, u) = (\varphi_1(t, u), \varphi_2(t, u))$ exists globally on $[0, +\infty)$ and there is a $t_0 = t_0(u) > 0$ such that*

$$0 \leq \varphi_i(t, u)(x) \leq M, \quad t \geq t_0, \quad x \in \bar{\Omega}, \quad i = 1, 2.$$

In the case where the predator may have no self-limitation (see, e.g., [3, 8] for some examples), we can make the following assumption.

(A3) For any $\rho > 0$ there exists $K(\rho) > 0$ such that for all $(x, t, u_1, u_2) \in \bar{Q}_T \times [0, \rho] \times R_+$, $F_2(x, t, u_1, u_2) \leq K(\rho)$, and there exist positive constants α, β and γ and a continuous function $F_3(t, u_1)$, T -periodic in t , such that for all $(x, t, u_1, u_2) \in \bar{Q}_T \times R_+^2$,

$$\alpha u_1 [F_1(x, t, u_1, u_2) + \gamma] + \beta u_2 [F_2(x, t, u_1, u_2) + \gamma] \leq F_3(t, u_1).$$

By a similar argument to [5, Lemma 4.5] and [31, Lemma 4.2], we can also easily prove the following result.

Lemma 3.2. *Let $A_i = -k_i(t)\Delta$, $k_i(t) \in C^{\theta/2}([0, T])$ and $k_i(t) > 0$, $i = 1, 2$, and assume that (A1) and (A3) hold. Then the conclusions of Lemma 3.1 are valid.*

Remark 3.1. The conclusions of Lemmas 3.1 and 3.2 also hold if we replace assumptions (A1) and (A2) respectively by the following ones:

(A1)' There exists a Lipschitz function $F_1^*(t, u_1)$, T -periodic in t , such that

$$\sup\{F_1(x, t, u_1, u_2); x \in \bar{\Omega}, u_2 \geq 0\} \leq F_1^*(t, u_1), \quad t \in [0, T], u_1 \geq 0$$

and solutions of $du_1/dt = u_1 F_1^*(t, u_1)$ are ultimately bounded in R_+ ;

(A2)' For any $M > 0$ there exists a Lipschitz function $F_2^*(t, M, u_2)$, T -periodic in t , such that

$$\sup\{F_2(x, t, u_1, u_2); x \in \bar{\Omega}, 0 \leq u_1 \leq M\} \leq F_2^*(t, M, u_2), \\ t \in [0, T], u_2 \geq 0$$

and solutions of $du_2/dt = u_2 F_2^*(t, M, u_2)$ are ultimately bounded in R_+ .

In the absence of predator u_2 , the prey u_1 often has self-limitation and cannot increase infinitely. Therefore, we further impose the following condition.

(C1) For any given $(x, t) \in \bar{Q}_T$, $F_1(x, t, u_1, 0)$ is decreasing in $u_1 \in R_+$, for at least one $(x_0, t_0) \in \bar{Q}_T$, $F_1(x_0, t_0, u_1, 0)$ is strictly decreasing in $u_1 \in R_+$, and there exists $M > 0$ such that $F_1(x, t, M, 0) \leq 0$ for all $(x, t) \in \bar{Q}_T$.

Then by [30, Theorem 3.3], we have the following result on the global dynamics of single species u_1 in the absence of predator u_2 .

Lemma 3.3. *Let (C1) hold. If $\mu^{(1)}(F_1(x, t, 0, 0)) < 0$, then the scalar equation*

$$(3.3) \quad \begin{cases} \partial u_1/\partial t + A_1(t)u_1 = u_1 F_1(x, t, u_1, 0) & \text{in } \Omega \times (0, \infty) \\ B_1 u_1 = 0 & \text{on } \partial\Omega \times (0, \infty) \end{cases}$$

admits a unique positive T -periodic solution $u_1^(t, x)$ and $u_1^*(t, x)$ is globally asymptotically stable with respect to the initial values in $P_1 \setminus \{0\}$.*

In the absence of prey u_1 , we expect that the predator u_2 will die out. According to two possible cases of predator u_2 : one with self-limitation and the other without self-limitation, we distinguish between the following two conditions.

(C2) For any $(x, t) \in \bar{Q}_T$ and $u_2 \geq 0$, $F_2(x, t, 0, u_2) \leq F_2(x, t, 0, 0)$, and for at least one $(x_0, t_0) \in \bar{Q}_T$ and all $u_2 > 0$, $F_2(x_0, t_0, 0, u_2) < F_2(x_0, t_0, 0, 0)$;

(C3) For any $(x, t) \in \overline{Q}_T$ and $u_2 \geq 0$, $F_2(x, t, 0, u_2) \leq F_2(x, t, 0, 0)$.

Therefore, by [30, Theorem 3.2] and the proof of [30, Theorem 2.2], we have the following result.

Lemma 3.4. *Assume either (C2) and $\mu^{(2)}(F_2(x, t, 0, 0)) \geq 0$, or alternatively, (C3) and $\mu^{(2)}(F_2(x, t, 0, 0)) > 0$ hold. Then for the scalar equation*

$$(3.4) \quad \begin{cases} \partial u_2 / \partial t + A_2(t)u_2 = u_2 F_2(x, t, 0, u_2) & \text{in } \Omega \times (0, \infty) \\ B_2 u_2 = 0 & \text{on } \partial\Omega \times (0, \infty) \end{cases}$$

$u_2 = 0$ is globally asymptotically stable with respect to the initial values in P_2 .

We are now in a position to prove the main result of this section.

Theorem 3.1. *Assme that (A1), (A2) (or alternatively, (A3) with $A_i = -k_i(t)\Delta$, $i = 1, 2$), (C1) with $\mu^{(1)}(F_1(x, t, 0, 0)) < 0$, and (C2) with $\mu^{(2)}(F_2(x, t, 0, 0)) \geq 0$ (or alternatively, (C3) with $\mu^{(2)}(F_2(x, t, 0, 0)) > 0$) hold. If $\mu^{(2)}(F_2(x, t, u_1^*(t, x), 0)) < 0$, then system (3.1) is uniformly persistent and admits at least one periodic coexistence solution. More precisely, there exists a $\beta > 0$ such that for any $u = (u_1, u_2) \in P_1 \times P_2$ with $u_1(x) \not\equiv 0$ and $u_2(x) \not\equiv 0$, there exists $t_0 = t_0(u) > 0$ such that $\varphi(t, u) = (\varphi_1(t, u), \varphi_2(t, u))$ satisfies*

$$\varphi_i(t, u)(x) \geq \beta e_i(x) \quad \text{for } t \geq t_0, x \in \overline{\Omega} \text{ and } i = 1, 2,$$

where $u_1^*(t, x)$ is the unique positive T -periodic solution of equation (3.3) and

$$e_i(x) = \begin{cases} e(x) & \text{if } B_i v = v \\ 1 & \text{if } B_i v = \partial v / \partial n + b_0^{(i)} \end{cases}$$

$e \in C^2(\overline{\Omega})$ is given such that for $x \in \Omega$, $e(x) > 0$ and for $x \in \partial\Omega$, $e(x) = 0$ and $\partial e / \partial n < -\gamma < 0$.

Proof. By Lemmas 3.1 and 3.2, we can define a T -periodic semiflow $\Phi(t) : X = P_1 \times P_2 \rightarrow X$ by

$$\Phi(t)u = \varphi(t, u), \quad u \in X, t \geq 0.$$

Let $X_0 = \{(u_1, u_2) \in X; u_i(x) \neq 0, i = 1, 2\}$ and $\partial X_0 = \{(u_1, u_2) \in X; u_1(x) \equiv 0 \text{ or } u_2(x) \equiv 0\}$, then $X = X_0 \cup \partial X_0$, X_0 and ∂X_0 are relatively open and closed in X , respectively, and X_0 is convex. Clearly, $\Phi(t)X_0 \subset X_0$ and $\Phi(t)(\partial X_0) \subset \partial X_0$, $t \geq 0$. By a similar argument to the proof of [15, Proposition 21.2], it follows that $\Phi(t) : X \rightarrow X$ is continuous and compact for any $t > 0$. With the properties of the fractional power space $E_i = X_\beta^{(i)}$ and by a standard argument (see, e.g., [7, Theorem 23.3]), Lemmas 3.1 and 3.2 imply that $\Phi(t)$, $t \geq 0$, is point dissipative in $E_1 \times E_2$, i.e., there exists a $B > 0$ such that for any $u \in P_1 \times P_2$, there exists $t_0 = t_0(u) > 0$ such that $\Phi(t)u = (\varphi_1(t, u), \varphi_2(t, u))$ satisfies

$$\|\Phi(t)u\|_{E_1 \times E_2} = \|\varphi_1(t, u)\|_{E_1} + \|\varphi_2(t, u)\|_{E_2} \leq B, \quad \text{for } t \geq t_0.$$

We first prove the uniform persistence of the Poincaré map $S : X \rightarrow X$ defined by $S(u) = \Phi(T)u = \varphi(T, u)$, $u \in X$. Clearly, $S : X \rightarrow X$ is a continuous, point dissipative and compact map with $S(X_0) \subset X_0$ and $S(\partial X_0) \subset \partial X_0$. By [11, Theorem 2.4.7], $S : X \rightarrow X$ has a global attractor A . By Lemmas 3.3 and 3.4, $\cup_{u \in \partial X_0} \omega(u) = \{(0, 0), (u_1^*(0), 0)\}$. Let $M_1 = (0, 0)$, $M_2 = (u_1^*(0), 0)$ and A_∂ be the maximal compact invariant set of S in ∂X_0 , then $\hat{A}_\partial = \cup_{x \in A_\partial} \omega(x) = \{M_1, M_2\}$ and M_1 and M_2 are disjoint, compact and isolated invariant sets for $S_\partial = S|_{A_\partial}$ in A_∂ .

Claim. For each M_i , $i = 1, 2$, there exists $\delta_i > 0$ such that $\overline{\lim}_{n \rightarrow \infty} d(S^n(u), M_i) \geq \delta_i$ for all $u \in X_0$.

It suffices to prove that there exists $\delta_i > 0$, $i = 1, 2$, such that for any $u \in N(M_i, \delta_i) \cap X_0$, where $N(M_i, \delta_i)$ is the δ_i -neighborhood of M_i , there exists $n_i = n_i(u) \geq 1$ such that $S^{n_i}(u) \notin N(M_i, \delta_i)$. We first prove this for M_2 . Let $\mu^{(2)} = \mu^{(2)}(F_2(x, t, u_1^*(t, x), 0))$, then by our assumption, $\mu^{(2)} < 0$. For any given $\varepsilon_0 \in (0, -\mu^{(2)})$, by the uniform continuity of $F_2(x, t, u_1, u_2)$ on the compact set $\bar{Q}_T \times ([0, b])^2$, where $b = \max_{(x,t) \in \bar{Q}_T} u_1^*(t, x) + 1$, there exists $\delta_0 \in (0, 1)$ such that for any (u_1, u_2) and $(v_1, v_2) \in ([0, b])^2$ with $|u_1 - v_1| < \delta_0$, $|u_2 - v_2| < \delta_0$, and all $(x, t) \in \bar{Q}_T$,

$$|F_2(x, t, u_1, u_2) - F_2(x, t, v_1, v_2)| < \varepsilon_0.$$

Since $\lim_{u \rightarrow M_2} \varphi(t, u) = \varphi(t, M_2) = (u_1^*(t), 0)$ in $E_1 \times E_2 = X_\beta^{(1)} \times X_\beta^{(2)}$ uniformly for $t \in [0, T]$ and $E_1 \times E_2 \hookrightarrow C(\bar{\Omega}) \times C(\bar{\Omega})$, there exists $\delta_2 > 0$ such that for any $u \in N(M_2, \delta_2) \subset E_1 \times E_2$,

$$\|\varphi_1(t, u) - u_1^*(t)\|_{C(\bar{\Omega})} < \delta_0, \quad \|\varphi_2(t, u)\|_{C(\bar{\Omega})} < \delta_0, \quad \text{for all } t \in [0, T].$$

Assume that, by contradiction, there exists $u_0 \in N(M_2, \delta_2) \cap X_0$ such that for all $n \geq 1$, $S^n(u_0) = \varphi(nT, u_0) \in N(M_2, \delta_2)$. For any $t \geq 0$, let $t = nT + t'$, where $t' \in [0, T)$ and $n = [t/T]$ is the greatest integer less than or equal to t/T , then

$$\|\varphi_1(t, u_0) - u_1^*(t)\|_{C(\bar{\Omega})} = \|\varphi_1(t', \varphi(nT, u_0)) - u_1^*(t')\|_{C(\bar{\Omega})} < \delta_0$$

and

$$\|\varphi_2(t, u_0)\|_{C(\bar{\Omega})} = \|\varphi_2(t', \varphi(nT, u_0))\|_{C(\bar{\Omega})} < \delta_0.$$

Let $(u_1(t, x), u_2(t, x)) = (\varphi_1(t, u_0)(x), \varphi_2(t, u_0)(x))$, by the T -periodicity of $F_2(x, t, u_1, u_2)$ with respect to t ,

$$F_2(x, t, u_1(t, x), u_2(t, x)) > F_2(x, t, u_1^*(t, x), 0) - \varepsilon_0$$

for all $x \in \bar{\Omega}$, $t \geq 0$.

According to [15], let $\varphi_2(t, x)$ be a positive eigenfunction corresponding to the principal eigenvalue $\mu^{(2)}$, that is, $\varphi_2(t, x)$ satisfies

$$(3.5) \quad \begin{cases} \partial\varphi_2/\partial t + A_2(t)\varphi_2 = F_2(x, t, u_1^*(t, x), 0)\varphi_2 + \mu^{(2)}\varphi_2 & \text{in } \Omega \times (0, \infty) \\ B_2\varphi_2 = 0 & \text{on } \partial\Omega \times (0, \infty) \\ \varphi_2 & T\text{-periodic in } t. \end{cases}$$

Then $\varphi_2(0, x) \gg 0$ in $E_2 = X_\beta^{(2)}$, i.e., $\varphi_2(0, x) \in \text{int}(P_2)$. Since $(u_1(0, x), u_2(0, x)) = u_0 \in X_0$, by applying the parabolic maximum principle (see, e.g., [15]) to each component of systems (3.1), it follows that $u_1(t, x) \gg 0$ in E_1 and $u_2(t, x) \gg 0$ in E_2 for all $t > 0$. Therefore, without loss of generality, we can assume that $u_0 \in \text{int}(P_1) \times \text{int}(P_2)$. Then there exists $k > 0$ such that $u_2(0, x) \geq k\varphi_2(0, x)$, $x \in \bar{\Omega}$. Therefore, $u_2(t, x)$ satisfies

$$(3.6) \quad \begin{cases} \partial u_2/\partial t + A_2(t)u_2 \geq u_2(F_2(x, t, u_1^*(t, x), 0) - \varepsilon_0) & \text{in } \Omega \times (0, \infty) \\ u_2(0, x) \geq k\varphi_2(0, x) & \text{on } \bar{\Omega}. \end{cases}$$

By (3.5), it easily follows that $v(t, x) = ke^{(-\mu^{(2)} - \varepsilon_0)t} \varphi_2(t, x)$ satisfies

$$(3.7) \quad \begin{cases} \partial v / \partial t + A_2(t)v = v(F_2(x, t, u_1^*(t, x), 0) - \varepsilon_0) & \text{in } \Omega \times (0, \infty) \\ v(0, x) = k\varphi_2(0, x) & \text{on } \bar{\Omega} \end{cases}$$

By (3.6), (3.7) and standard comparison principle of scalar parabolic equations,

$$u_2(t, x) \geq ke^{(-\mu^{(2)} - \varepsilon_0)t} \varphi_2(t, x), \quad t \geq 0, x \in \Omega.$$

Then, since $\varphi_2(t, x)$ is a positive T -periodic function on $[0, \infty) \times \Omega$, $\lim_{t \rightarrow \infty} u_2(t, x) = +\infty$ for any $x \in \Omega$, which implies that $\lim_{t \rightarrow \infty} \|u_2(t, \cdot)\|_{E_2} = +\infty$ since $E_2 = X_\beta^{(2)} \hookrightarrow C(\bar{\Omega})$. This contradicts our assumption that $S^n(u_0) = (u_1(nT), u_2(nT)) \in N(M_2, \delta_2)$ for all $n \geq 1$. Therefore, for all $u \in X_0$, $\overline{\lim}_{n \rightarrow \infty} d(S^n(u), M_2) \geq \delta_2$. In a similar way, by using the uniform continuity of $F_1(x, t, u_1, u_2)$ on the compact set $\bar{Q}_T \times ([0, 1])^2$ and the assumption $\mu^{(1)}(F_1(x, t, 0, 0)) < 0$, we can prove that there exists a $\delta_1 > 0$ such that for all $u \in X_0$, $\overline{\lim}_{n \rightarrow \infty} d(S^n(u), M_1) \geq \delta_1$.

The claim above implies that M_i , $i = 1, 2$, is isolated for S in X since M_i is isolated for $S|_\partial$ in ∂X_0 and $S : X_0 \rightarrow X_0$ and $S : \partial X_0 \rightarrow \partial X_0$. Therefore, by Lemmas 3.3 and 3.4, $M_1 \cup M_2$ is an isolated and acyclic covering of \tilde{A}_∂ in ∂X_0 . Since the claim above also implies $W^s(M_i) \cap X_0 = \emptyset$, $i = 1, 2$, the uniform persistence of S with respect to $(X, \partial X_0)$ follows from Theorem 2.2. Therefore, by Theorem 2.3, S has a global attractor $A_0 \subset X_0$ relative to strongly bounded sets in X_0 and admits a fixed point $u_0 \in A_0$. Then (3.1) has a periodic coexistence solution $\varphi(t, u_0)$.

By Theorem 2.1, $\Phi(t)$ is uniformly persistent with respect to $(X_0, \partial X_0)$. More precisely, the compact set $A_0^* = \cup_{t \in [0, T]} \Phi(t)A_0 = \varphi([0, T] \times A_0)$ attracts any strongly bounded sets in X_0 . Since $A_0 = \Phi(T)A_0$, $A_0^* = \cup_{t \in (0, T]} \Phi(t)A_0 = \varphi((0, T] \times A_0)$ and hence for any $u \in A_0^*$, there exist a $v \in A_0 \subset A_0^*$ and a $t \in (0, T]$ such that $u = \Phi(t)v = \varphi(t, v)$. By using the compactness of A_0^* and the fact that $E_1 \times E_2 = X_\beta^{(1)} \times X_\beta^{(2)} \hookrightarrow C^1(\bar{\Omega}) \times C^1(\bar{\Omega})$, and by a similar argument to [5, Lemma 3.6, Corollary 3.7 and Remark 3.8], we can prove the required uniform persistence of system (3.1) in the theorem. This completes the proof. \square

Remark 3.2. For the various estimates of the principal eigenvalue of a periodic-parabolic eigenvalue problem, we refer to [15, Lemma

15.6 and Section II.17]. As an illustration, let $Bv = \partial v / \partial n$ and $A = -k(t)\Delta$, where $k \in C^{\theta/2}(R, R)$ is T -periodic and positive. For any $m \in C^{\theta, \theta/2}(\overline{Q_T})$, let $\mu(m(x, t))$ be the principal eigenvalue of the problem (3.2) with A_i and B_i replaced by A and B , respectively. By the results of [15, Example 17.2], it follows that

(I) $\mu(m(x, t)) < 0$ if either $\iint_{Q_T} m(x, t) dx dt > 0$ or $\iint_{Q_T} m(x, t) dx dt \geq 0$ with $m(x, t)$ depending nontrivially on x ;

(II) $\mu(m(x, t)) > 0$ if $\iint_{Q_T} m(x, t) dx dt < 0$ and $\int_0^T \max_{x \in \overline{\Omega}} m(x, t) dt \leq 0$.

Remark 3.3. By a similar approach to that of Theorem 3.1, we can discuss the uniform persistence and existence of a periodic coexistence solution for periodic two-species Kolmogorov competition reaction-diffusion systems with spatial heterogeneity. For more complete results on periodic two-species Lotka-Volterra competition reaction-diffusion systems and a different approach (i.e., using monotone dynamical system theory), we refer to [15, Section IV.33] or [16]. For general periodic N -species competition reaction-diffusion systems and another approach, we refer to [29].

Example 3.1. For periodic Lotka-Volterra predator-prey systems with diffusion,

$$(3.8) \quad \begin{cases} \partial u_1 / \partial t + A_1(t)u_1 = u_1[b_1(x, t) - a_{11}(x, t)u_1 - a_{12}(x, t)u_2] \\ \partial u_2 / \partial t + A_2(t)u_2 = u_2[b_2(x, t) + a_{21}(x, t)u_1 - a_{22}(x, t)u_2] \\ B_i u_i = 0, \quad i = 1, 2 \end{cases}$$

assume that $a_{11} > 0$, $a_{22} > 0$, $a_{12} \geq 0$ and $a_{21} \geq 0$ on $\overline{Q_T}$, and that $\mu^{(1)}(b_1(x, t)) < 0$, $\mu^{(2)}(b_2(x, t)) \geq 0$ and $\mu^{(2)}(b_2(x, t) + a_{21}(x, t)u_1^*(t, x)) < 0$, where $u_1^*(t, x)$ is the unique positive T -periodic solution of the logistic equation $\partial u_1 / \partial t + A_1(t)u_1 = u_1[b_1(x, t) - a_{11}(x, t)u_1]$ with $B_1 u_1 = 0$. Then conditions (A1), (A2), (C1) and (C2) in Theorem 3.1 are all satisfied and hence system (3.8) is uniformly persistent and admits at least one T -periodic coexistence solution.

Remark 3.4. By using bifurcation theory, Brown and Hess [2, Theorem 4.3] or [15, Theorem 37.1]) proved the existence of a T -periodic

coexistence solution of (3.8) under the same conditions as in Example 3.1 above. For autonomous Lotka-Volterra predator-prey systems with Dirichlet boundary conditions, Dancer [6, Theorem 1] also obtained a similar condition on the stationary coexistence solution by degree arguments in cones. However, they didn't give any information on the uniform persistence of system (3.8).

Example 3.2. For periodic Lotka-Volterra predator-prey systems with diffusion,

$$(3.9) \quad \begin{cases} \partial u_1/\partial t = k_1(t)\Delta u_1 + u_1[b_1(x, t) - a_{11}(x, t)u_1 - a_{12}(x, t)u_2] \\ \partial u_2/\partial t = k_2(t)\Delta u_2 + u_2[b_2(x, t) + a_{21}(x, t)u_1] \\ B_i u_i = 0, \quad i = 1, 2, \end{cases}$$

assume that $a_{11} > 0$, $a_{12} > 0$, $a_{21} \geq 0$ and $b_2 < 0$ on $\overline{Q_T}$ and that $\mu^{(1)}(b_1(x, t)) < 0$, $\mu^{(2)}(b_2(x, t)) > 0$ and $\mu^{(2)}(b_2(x, t) + a_{21}(x, t)u_1^*(t, x)) < 0$, where $u_1^*(t, x)$ is the unique positive T -periodic solution of the logistic equation $\partial u_1/\partial t = k_1(t)\Delta u_1 + u_1[b_1(x, t) - a_{11}(x, t)u_1]$ with $B_1 u_1 = 0$. Then conditions (A1), (A3), (C1) and (C3) in Theorem 3.1 are all satisfied, and, hence, system (3.9) is uniformly persistent and admits at least one T -periodic coexistence solution.

Remark 3.5. In general, the unique positive T -periodic solution $u_1^*(t, x)$ of the logistic equation

$$(3.10) \quad \begin{cases} \partial u_1/\partial t + A_1(t)u_1 = u_1[b_1(x, t) - a_{11}(x, t)u_1] & \text{in } \Omega \times (0, \infty) \\ B_1 u_1 = 0, & \text{on } \partial\Omega \times (0, \infty) \end{cases}$$

is not known explicitly. If, however, $A_1(t) = -k_1(t)\Delta$, $B_1 v = \partial v/\partial n$ and b_1 is positive on $\overline{Q_T}$, we have $u_1^*(t, x) \geq \min_{\overline{Q_T}}(b_1(x, t)/a_{11}(x, t)) = (b_1/a_{11})_l$, see, e.g., [2]. Therefore, in the case where $A_2(t) = -k_2(t)\Delta$ and $B_2 v = \partial v/\partial n$, by Remark 3.2, $\mu^{(2)}(b_2(x, t) + a_{21}(x, t)u_1^*(t, x)) < 0$ if $\iint_{Q_T} (b_2 + a_{21}(b_1/a_{11})_l) dx dt > 0$.

Finally, as a complement to Theorem 3.1, we discuss global extinction in system (3.1). The following conditions will be imposed on (3.1).

(H1) For any given $(x, t, u_2) \in \overline{Q}_T \times R_+$, $F_1(x, t, u_1, u_2)$ is strictly decreasing in $u_1 \geq 0$;

(H2) For any given $(x, t, u_1) \in \overline{Q}_T \times R_+$, $F_2(x, t, u_1, u_2)$ is strictly decreasing in $u_2 \geq 0$;

(H3) For any $(x, t, u_1, u_2) \in \overline{Q}_T \times R_+^2$, $F_2(x, t, u_1, u_2) \leq F_2(x, t, u_1, 0)$.

By a similar argument to [15, Proposition 37.3], we can easily prove the following result.

Theorem 3.2. *Assume that (A1), (A2) (or alternatively, (A3) with $A_i(t) = -k_i(t)\Delta$, $i = 1, 2$) (H1) and (H2) with $\mu^{(2)}(F_2(x, t, 0, 0)) \geq 0$ (or alternatively, (H3) with $\mu^{(2)}(F_2(x, t, 0, 0)) > 0$) hold.*

(1) *If $\mu^{(1)}(F_1(x, t, 0, 0)) \geq 0$, then the trivial solution $(0, 0)$ is globally attractive with respect to initial values in $P_1 \times P_2$;*

(2) *If $\mu^{(1)}(F_1(x, t, 0, 0)) < 0$ but $\mu^{(2)}(F_2(x, t, u_1^*(t, x), 0)) \geq 0$, where $u_1^*(t, x)$ is the unique positive T -periodic solution of the logistic equation (3.3), then the semitrivial solution $(u_1^*(t, x), 0)$ is globally attractive with respect to initial values in X_0 .*

Clearly, by Theorem 3.2, one can give sufficient conditions for the global extinction of the periodic Lotka-Volterra predator-prey reaction-diffusion systems in Examples 3.1 and 3.2.

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REFERENCES

1. N.D. Alikakos, *An application of the invariant principle to reaction-diffusion equations*, J. Differential Equations **33** (1979), 201–225.
2. K.J. Brown and P. Hess, *Positive periodic solutions of predator-prey reaction-diffusion systems*, Nonlinear Anal. **16** (1991), 1147–1158.
3. G.J. Butler and H.I. Freedman, *Periodic solutions of a predator-prey system with periodic coefficients*, Math. Biosci. **55** (1981), 27–38.
4. G.J. Butler, H.I. Freedman and P. Waltman, *Uniformly persistent systems*, Proc. Amer. Math. Soc. **96** (1986), 425–430.

5. R.S. Cantrell, C. Cosner and V. Hutson, *Permanence in ecological systems with spatial heterogeneity*, Proc. Roy. Soc. Edinburgh Sect. A **123** (1993), 533–559.
6. E.N. Dancer, *On positive solutions of some pairs of differential equations II*, J. Differential Equations **60** (1985), 236–258.
7. D. Daners and P.K. Medina, *Abstract evolution equations, periodic problems and applications*, Pitman Res. Notes Math., Ser. 279, Longman Sci. Tech., Harlow, 1992.
8. S.R. Dunbar, K.P. Rybakowski and K. Schmitt, *Persistence in models of predator-prey populations with diffusion*, J. Differential Equations **65** (1986), 117–138.
9. H.I. Freedman and J.W.-H. So, *Persistence in discrete semi-dynamical systems*, SIAM J. Math. Anal. **20** (1989), 930–938.
10. K. Gopalsamy, *Global asymptotic stability in a periodic Lotka-Volterra system*, J. Austral. Math. Soc. **27** (1985), 66–72.
11. J.K. Hale, *Asymptotic behavior of dissipative systems*, Math. Surveys Monographs **25**, Amer. Math. Soc., Providence, RI, 1988.
12. J.K. Hale and O. Lopes, *Fixed point theorems and dissipative processes*, J. Differential Equations **13** (1973), 391–402.
13. J.K. Hale and P. Waltman, *Persistence in infinite-dimensional systems*, SIAM J. Math. Anal. **20** (1989), 388–395.
14. D. Henry, *Geometric theory of semilinear parabolic equations*, Lecture Notes in Math **840**, Springer-Verlag, Berlin, 1981.
15. P. Hess, *Periodic-parabolic boundary value problems and positivity*, Pitman Res. Notes Math., Ser. 247, Longman Sci. Tech., Harlow, 1991.
16. P. Hess and A.C. Lazer, *On an abstract competition model and applications*, Nonlinear Anal. **16** (1991), 917–940.
17. J. Hofbauer and J.W.-H. So, *Uniform persistence and repellers for maps*, Proc. Amer. Math. Soc. **107** (1989), 1137–1142.
18. V. Hutson, *The existence of an equilibrium for permanent systems*, Rocky Mountain J. Math. **20** (1990), 1033–1040.
19. V. Hutson and K. Schmitt, *Permanence and the dynamics of biological systems*, Math. Biosci. **111** (1992), 1–71.
20. J.K. Kelley, I. Namioka, et al., *Linear topological spaces*, Springer-Verlag, Berlin-New York, 1963.
21. X. Lin and J.W.-H. So, *Global stability of the endemic equilibrium and uniform persistence in epidemic models with subpopulations*, J. Austral. Math. Soc., Ser. B, **34** (1993), 282–295.
22. H.L. Smith, *Periodic rotating waves in a model of microbial competition in a circular gradient*, Canad. Appl. Math. Quart. **1** (1993), 83–113.
23. J. Smoller, *Shock waves and reaction-diffusion equations*, Springer, Berlin, 1983.
24. P. Waltman, *A brief survey of persistence in dynamical systems*, in *Delay-differential equations and dynamical systems*, Lecture Notes in Math. **1475** (1991), 31–40.

25. F. Yang and H.I. Freedman, *Competing predators for a prey in a chemostat model with periodic nutrient input*, J. Math. Biol. **29** (1991), 715–732.
26. F. Zanolin, *Permanence and positive periodic solutions for Kolmogorov competing species systems*, Results Math. **21** (1992), 224–250.
27. E. Zeidler, *Nonlinear functional analysis and its applications I: Fixed-point theorems*, Springer-Verlag, New York, 1986.
28. X.-Q. Zhao, *The qualitative analysis of N -species Lotka-Volterra periodic competition systems*, Math. Comp. Modelling **15** (1991), 3–8.
29. ———, *Permanence and positive periodic solutions of N -species competition reaction-diffusion systems with spatial inhomogeneity*, J. Math. Anal. Appl., 1995.
30. ———, *Global attractivity and stability for discrete strongly monotone dynamical systems with applications to biology*, Tech. Report No. 005, Inst. Appl. Math., Academia Sinica, 1994.
31. X.-Q. Zhao and V. Hutson, *Permanence in Kolmogorov periodic predator-prey models with diffusion*, Nonlinear Anal. **23** (1994), 651–668.
32. X.-Q. Zhao and B.D. Sleeman, *Permanence in Kolmogorov competition models with diffusion*, IMA J. Appl. Math. **51** (1993), 1–11.

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