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A Lotka–Volterra competition model with seasonal succession

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Abstract A complete classification for the global dynamics of a Lotka–Volterra two species competition model with seasonal succession is obtained via the stability analysis of equilibria and the theory of monotone dynamical systems. The effects of two death rates in the bad season and the proportion of the good season on the competition outcomes are also discussed.

Keywords Lotka–Volterra model · Seasonal succession · The period map · Periodic solutions · Global stability · Saddle-point structure

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1 Introduction

Temporal variation of environmental conditions is important for growth and survival of species. Seasonal forcing in nature is a common cause of environmental change,

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which not only affects species growth but also composition of communities (DeAngelis et al. 2009; DuBowy 1988). The growth of species is in fact driven by the combination of external forcing and internal dynamics. In temperate lakes there is a growing season for the phytoplankton and zooplankton during warmer months after which species die off or form resting stages in the winter. It has been a fascinating subject for plankton ecologists to study the modeling of non-equilibrium food chains dynamics by means of seasonal succession. Litchman and Klausmeier (2001) studied a mathematical model of competition of two genera, *Nitschia* (opportunist) and *Sphaerocystis* (gleaner), under fluctuating light with season succession in a well-mixed water column. Klausmeier (2008) applied the Floquet theory to several mathematical models including structured populations and food chains to obtain some analytic results. Klausmeier (2010) also chose the well-known Rosenzweig–McArthur model as a prototypical predator-prey system to study the effect of season succession. In their numerical simulations, they found that in addition to the expected periodic oscillations, chaos may happen in some parameter range. In Steiner et al. (2009) and Hu and Tessier (1995), there are some experimental data about the effect of season succession on the competition of phytoplankton species. In a much earlier paper, Koch (1974) studied numerically a two species competition model, where he assumed the Lotka–Volterra competition dynamics in good seasons from spring to autumn, and the reduction of populations by some constant factors due to adverse conditions in bad seasons from autumn to spring through winter. Koch (1974) also considered a model of exploitative competition with the type II functional responses and investigated effects of seasonal harvesting. However, there are few analytic results on these ecological models with season succession. Mathematically, the vector fields of these models are discontinuous and periodic in time t, but the associated period maps are continuous. In this paper, we choose two species competition model of Lotka–Voltera type as starting point to study analytically the possible effect of season succession. Indeed, this model is phenomenological and even conceptual, but we are able to give a complete mathematical classification for its global dynamics in terms of the involved parameters. From these analytical results, we further gain insights into effects of season succession on the competition outcomes.

The organization of the paper is as follows. Section 2 is devoted to the study of the long-time behavior of solutions of our two species competition model. We first establish a series of results on the global convergence of forward orbits, stability of semitrivial and positive fixed points, and nonexistence and uniqueness of positive fixed point for the discrete-time dynamical system generated by the period map of the two species competition model of Lotka–Volterra type with season succession. Then we use these results to obtain a complete classification for the global dynamics. More precisely, we give several sets of sufficient conditions for the global extinction of both species (Theorem 2.1), the competitive exclusion (Theorem 2.2), the competitive coexistence of two species (Theorem 2.3), and the saddle-point structure (Theorem 2.4), respectively. It turns out that four possible outcomes of the classical Lotka–Volterra two species competition model are preserved by the period map of our competition model with season succession. In Sect. 3, we discuss in detail the effects of two death rates in the bad season and the proportion of the good season on the competition outcomes.

2 Global dynamics

Let $\mathbb{R}_+ := [0, \infty)$, $\mathbb{Z}_+$ be the set of all nonnegative integers, and $\omega > 0$ be given. We first consider the logistic equation with seasonal succession:

$$\begin{aligned} &\frac{dx}{dt} = -\lambda x, \quad m\omega \le t \le m\omega + (1-\phi)\omega, \\ &\frac{dx}{dt} = rx\left[1 - \frac{x}{K}\right], \quad m\omega + (1-\phi)\omega \le t \le (m+1)\omega, \\ &x(0) = x_0 \in \mathbb{R}_+, \end{aligned} \tag{2.1}$$

where $m \in \mathbb{Z}_+$, λ, r and K are positive constants, and $\phi \in (0, 1]$.

For any $y_0 \in \mathbb{R}_+$, let $y(t, y_0)$ be the unique solution of the logistic equation

$$\frac{dy}{dt} = ry\left[1 - \frac{y}{K}\right], \qquad y(0, y_0) = y_0 \in \mathbb{R}_+. \tag{2.2}$$

It then follows that the solution $x(t, x_0)$ can be determined uniquely as follows:

$$\begin{aligned} x(t, x_0) &= e^{-\lambda(t - m\omega)} x(m\omega, x_0), \ \forall t \in [m\omega, m\omega + (1-\phi)\omega], \\ x(t, x_0) &= y\left(t - [m\omega + (1-\phi)\omega], \quad x(m\omega + (1-\phi)\omega, x_0)\right), \\ &\qquad \forall t \in [m\omega + (1-\phi)\omega, (m+1)\omega], \end{aligned}$$

where $m \in \mathbb{Z}_+$. This implies that the solution $x(t, x_0)$ exists globally on $[0, \infty)$. We further have the following threshold dynamics for (2.1).

Lemma 2.1 (Threshold dynamics) *Let $x(t, x_0)$ be the unique solution of system* (2.1). *Then the following two statements are valid:*

(i) *If $r\phi - \lambda(1-\phi) \le 0$, then $\lim_{t\to\infty} x(t, x_0) = 0$ for all $x_0 \in \mathbb{R}_+$.*
(ii) *If $r\phi - \lambda(1-\phi) > 0$, then system* (2.1) *admits a unique positive ω-periodic solution $x^*(t)$, and $\lim_{t\to\infty} (x(t, x_0) - x^*(t)) = 0$ for all $x_0 \in \mathbb{R}_+ \setminus \{0\}$.*

Proof This threshold type result is a straightforward consequence of Zhao (2003, Theorem 2.3.4), as applied to the period map M associated with system (2.1), that is, $M(x_0) = x(\omega, x_0)$, $\forall x_0 \in \mathbb{R}_+$. Here we provide a more elementary proof. It is easy to see that $M(x_0) = y\left(\phi\omega, e^{-\lambda(1-\phi)\omega} x_0\right)$. Clearly, $M(0) = 0$, and M is increasing on $\mathbb{R}_+$. Note that the solution $y(t, y_0)$ of the logistic equation (2.2) has the following explicit expression:

$$y(t, y_0) = \frac{K y_0}{(K - y_0)e^{-rt} + y_0}, \quad \forall t \ge 0, \ \ y_0 \in \mathbb{R}_+. \tag{2.3}$$

Then the period map M of system (2.1) can be expressed as

$$M(x_0) = \frac{K x_0 e^{-\lambda(1-\phi)\omega}}{\left(K - x_0 e^{-\lambda(1-\phi)\omega}\right) e^{-r\phi\omega} + x_0 e^{-\lambda(1-\phi)\omega}}, \quad \forall x_0 \in \mathbb{R}_+.$$

A simple computation shows that M has no positive fixed point in the case where $r\phi - \lambda(1-\phi) \le 0$, while M has a unique positive fixed point

$$x^* = \frac{K\left(1 - e^{\lambda(1-\phi)\omega - r\phi\omega}\right)}{1 - e^{-r\phi\omega}}$$

in the case where $r\phi - \lambda(1-\phi) > 0$. Thus, conclusions (i) and (ii) follow from the convergence of the monotone sequence $M^n(x_0)$. □

Now we consider the Lotka–Volterra two species competition model with seasonal succession:

$$\begin{aligned}
&\frac{dx_i}{dt} = -\lambda_i x_i, \quad m\omega \le t \le m\omega + (1-\phi)\omega, \quad i = 1, 2,\\
&\frac{dx_1}{dt} = r_1 x_1 \left[1 - \frac{x_1}{K_1}\right] - \alpha x_1 x_2, \quad m\omega + (1-\phi)\omega \le t \le (m+1)\omega,\\
&\frac{dx_2}{dt} = r_2 x_2 \left[1 - \frac{x_2}{K_2}\right] - \beta x_1 x_2, \quad m\omega + (1-\phi)\omega \le t \le (m+1)\omega,\\
&(x_1(0), x_2(0)) = x^0 \in \mathbb{R}^2_+,
\end{aligned} \tag{2.4}$$

where $m \in \mathbb{Z}_+$, $\lambda_i, r_i, K_i, \alpha$ and β are all positive constants, and $\phi \in (0, 1]$.

By a similar way of induction as in system (2.1), it follows that for any $x^0 \in \mathbb{R}^2_+$, system (2.4) admits a unique nonnegative global solution $x(t, x^0)$ on $[0, \infty)$. Since system (2.4) is ω-periodic, it suffices to investigate its associated the period map S on $\mathbb{R}^2_+$, that is,

$$S(x^0) = x(\omega, x^0), \quad \forall x^0 \in \mathbb{R}^2_+.$$

We define a linear map $L : \mathbb{R}^2_+$ by

$$L(x_1, x_2) = \left(e^{-\lambda_1(1-\phi)\omega} x_1, e^{-\lambda_2(1-\phi)\omega} x_2\right), \quad \forall (x_1, x_2) \in \mathbb{R}^2_+.$$

Let $\{Q_t\}_{t\ge 0}$ be solution semiflow associated with the Lotka–Volterra competition system:

$$\begin{aligned}
&\frac{dx_1}{dt} = r_1 x_1 \left[1 - \frac{x_1}{K_1}\right] - \alpha x_1 x_2,\\
&\frac{dx_2}{dt} = r_2 x_2 \left[1 - \frac{x_2}{K_2}\right] - \beta x_1 x_2,\\
&(x_1(0), x_2(0)) = x^0 \in \mathbb{R}^2_+,
\end{aligned} \tag{2.5}$$

that is, $Q_t(x^0)$, as a function of t, is the unique global solution of system (2.5) on $[0, \infty)$. It then easily follows that $S(x^0) = Q_{\phi\omega}(Lx^0)$, $\forall x^0 \in \mathbb{R}^2_+$, i.e., $S = Q_{\phi\omega} \circ L$.

For $x, y \in \mathbb{R}^2$, we write $x \leq y$ if $y-x \in \mathbb{R}^2_+$; $x < y$ if $y-x \in \mathbb{R}^2_+ \setminus \{0\}$; and $x \ll y$ if $y - x \in Int(\mathbb{R}^2_+)$. Let $K := \{(x_1, x_2) \in \mathbb{R}^2 : x_1 \geq 0, x_2 \leq 0\}$. Then we write $x \leq_K y$ if $y - x \in K$; $x <_K y$ if $y - x \in K \setminus \{0\}$; and $x \ll_K y$ if $y - x \in Int(K)$.

2.1 The period map S

To describe the long-term behavior of solutions of the model system (2.4), we first study the discrete-time dynamical system $\{S^n\}_{n\geq 0}$, which is generated by the period map S.

Lemma 2.2 (Monotonicity and convergence) *The map S has the following properties on $\mathbb{R}^2_+$:*

(i) *If $x \leq_K y$, then $S(x) \leq_K S(y)$.*
(ii) *If $S(x) \leq S(y)$, then $x \leq y$.*
(iii) *For any $x^0 \in \mathbb{R}^2_+$, the sequence of points $S^n(x^0)$ converges to a fixed point of S as $n \to \infty$.*

Proof By the comparison theorem of competitive systems (see, e.g., Smith and Waltman 1995, Theorem B.4), it follows that $Q_t(x^0) \leq_K Q_t(y^0)$, $\forall t \geq 0$, $x^0, y^0 \in \mathbb{R}^2_+$ with $x^0 \leq_K y^0$, and hence, the property (i) holds for the map S. For any given $t_0 \geq 0$, and $x, y \in \mathbb{R}^2_+$ with $Q_{t_0}(x) \leq Q_{t_0}(y)$, it is easy to see that $u(t) := Q_{t_0-t}(x)$ and $v(t) := Q_{t_0-t}(y)$ are two solutions of a two dimensional cooperative system for $t \in [0, t_0]$. Since $u(0) = Q_{t_0}(x) \leq Q_{t_0}(y) = v(0)$, the comparison theorem of cooperative systems (see, e.g., Smith and Waltman 1995, Corollary B.2) implies that $x = u(t_0) \leq v(t_0) = y$. By this property of the semiflow $\{Q_t\}_{t\geq 0}$ and the expression of the linear map L, it then follows that the property (ii) holds for the map S. Now the property (iii) is a consequence of (i), (ii), and the same arguments as in Smith and Waltman (1995, Theorem 7.4.2) (see also the proof of, de Mottoni and Schiaffino 1981, Theorem 4.1). □

Lemma 2.3 (Stability of semitrivial fixed points) *Assume that $r_1\phi - \lambda_1(1-\phi) > 0$ and let $x_1^*(t)$ be the unique positive ω-periodic solution of system (2.1) with $r = r_1$ and $K = K_1$. Let $x^* = (x_1^*(0), 0)$, $DS(x^*)$ be the Jacobian matrix (i.e., the Frechét derivative) of S at x^*, and $r(DS(x^*))$ be the spectral radius of the linear operator $DS(x^*)$. Then following statements are valid:*

(i) *If $r_2\phi - \lambda_2(1-\phi) > \frac{\beta K_1}{r_1}(r_1\phi - \lambda_1(1-\phi))$, then $r(DS(x^*)) > 1$, and hence, x^* is an unstable fixed point of S.*
(ii) *If $r_2\phi - \lambda_2(1-\phi) < \frac{\beta K_1}{r_1}(r_1\phi - \lambda_1(1-\phi))$, then $r(DS(x^*)) < 1$, and hence, x^* is an asymptotically stable fixed point of S.*

An analogous stability result also holds for the case where $r_2\phi - \lambda_2(1-\phi) > 0$.

Proof Let $f(x)$ be the right-hand side vector field of system (2.5). Then we have

$$Df(x) = \begin{bmatrix} r_1 - \frac{2r_1}{K_1}x_1 - \alpha x_2 & -\alpha x_1 \\ -\beta x_2 & r_2 - \frac{2r_2}{K_2}x_2 - \beta x_1 \end{bmatrix}. \tag{2.6}$$

Let $u(t,x) := Q_t(x)$, and $V(t,x) := D_x u(t,x)$. It then follows that for any given $x \in \mathbb{R}^2_+$, the matrix function $V(t,x)$ satisfies

$$\frac{dV(t)}{dt} = Df(u(t,x))V(t), \quad V(0) = I.$$

Since $S = Q_{\phi\omega} \circ L$, the chain rule implies that

$$DS(x^*) = DQ_{\phi\omega}(Lx^*) \begin{bmatrix} e^{-\lambda_1(1-\phi)\omega} & 0 \\ 0 & e^{-\lambda_2(1-\phi)\omega} \end{bmatrix}.$$

Thus, $DQ_{\phi\omega}(Lx^*) = D_x u(\phi\omega, Lx^*) = V(\phi\omega, Lx^*)$. Let $x^* = (x_1^*, 0)$. Then $Lx^* = \left(e^{-\lambda_1(1-\phi)\omega}x_1^*, 0\right)$. By the expression (2.3), we have $u(t, Lx^*) = (u_1^*(t), 0)$ with

$$u_1^*(t) = \frac{K_1 x_1^* e^{-\lambda_1(1-\phi)\omega}}{\left(K_1 - x_1^* e^{-\lambda_1(1-\phi)\omega}\right) e^{-r_1 t} + x_1^* e^{-\lambda_1(1-\phi)\omega}}, \tag{2.7}$$

and hence,

$$Df(u(t, Lx^*)) = \begin{bmatrix} r_1 - \frac{2r_1}{K_1}u_1^*(t) & -\alpha u_1^*(t) \\ 0 & r_2 - \beta u_1^*(t) \end{bmatrix}.$$

It then follows that

$$V(\phi\omega, Lx^*) = \begin{bmatrix} e^{\int_0^{\phi\omega}\left(r_1 - \frac{2r_1}{K_1}u_1^*(t)\right)dt} & * \\ 0 & e^{\int_0^{\phi\omega}(r_2 - \beta u_1^*(t))dt} \end{bmatrix}.$$

Thus, the matrix $DS(x^*)$ has two positive eigenvalues μ_1 and μ_2 given by

$$\mu_1 = e^{\int_0^{\phi\omega}\left(r_1 - \frac{2r_1}{K_1}u_1^*(t)\right)dt} \cdot e^{-\lambda_1(1-\phi)\omega}, \quad \mu_2 = e^{\int_0^{\phi\omega}(r_2 - \beta u_1^*(t))dt} \cdot e^{-\lambda_2(1-\phi)\omega}.$$

By the formula (2.7) and elementary computations, or by integrating the logistic equation for $u_1^*(t)$ (see, e.g., the proof of Lemma 2.5(i)), it then follows that

$$\int_0^{\phi\omega} u_1^*(t)dt = \frac{K_1}{r_1}\left(r_1\phi - \lambda_1(1-\phi)\right)\omega.$$

A straightforward calculation further shows that

$$\mu_1 = e^{-(r_1\phi - \lambda_1(1-\phi))\omega} < 1, \quad \mu_2 = e^{\left(r_2\phi - \lambda_2(1-\phi) - \frac{\beta K_1}{r_1}(r_1\phi - \lambda_1(1-\phi))\right)\omega},$$

which implies that the statements (i) and (ii) hold. □

Lemma 2.4 (Stability of positive fixed point) *Let $\bar{x}$ be a positive fixed point of S, and $r(DS(\bar{x}))$ be the spectral radius of the linear operator $DS(\bar{x})$. Then following statements are valid:*

(i) *If $\frac{r_1 r_2}{K_1 K_2} < \alpha\beta$, then $r(DS(\bar{x})) > 1$, and hence, $\bar{x}$ is an unstable fixed point of S.*
(ii) *If $\frac{r_1 r_2}{K_1 K_2} > \alpha\beta$, then $r(DS(\bar{x})) < 1$, and hence, $\bar{x}$ is an asymptotically stable fixed point of S.*

Proof Let $f(x)$, $u(t,x)$ and $V(t,x)$ be defined as in the proof of Lemma 2.3. It then follows that

$$DS(\bar{x}) = V(\phi\omega, L\bar{x}) \begin{bmatrix} e^{-\lambda_1(1-\phi)\omega} & 0 \\ 0 & e^{-\lambda_2(1-\phi)\omega} \end{bmatrix}.$$

Let $\bar{u}(t) = (\bar{u}_1(t), \bar{u}_2(t)) := Q_t(L\bar{x})$ and $V(t) := V(t, L\bar{x})$. Then

$$\frac{dV(t)}{dt} = Df(\bar{u}(t))V(t), \quad V(0) = I.$$

Let

$$P(t) := \begin{bmatrix} \frac{1}{\bar{u}_1(t)} & 0 \\ 0 & \frac{1}{\bar{u}_2(t)} \end{bmatrix}.$$

By the expression of $Df(x)$ in (2.6) and a straightforward computation, it then follows that under a change of variable $w = P(t)v$, the linear equation $\frac{dv}{dt} = Df(\bar{u}(t))v$ becomes the following one:

$$\frac{dw}{dt} = \begin{bmatrix} -\frac{r_1}{K_1}\bar{u}_1(t) & -\alpha\bar{u}_2(t) \\ -\beta\bar{u}_1(t) & -\frac{r_2}{K_2}\bar{u}_2(t) \end{bmatrix} w := A(t)w. \tag{2.8}$$

Let $W(t)$ be the monodromy matrix of system (2.8), that is, $W(t)$ satisfies

$$\frac{dW(t)}{dt} = A(t)W(t), \quad W(0) = I.$$

Thus, we have $W(t) = P(t)V(t)P^{-1}(0)$, and hence, $V(t) = P^{-1}(t)W(t)P(0)$, $\forall t \geq 0$. Let $\bar{x} = (\bar{x}_1, \bar{x}_2)$. Note that

$$\bar{u}(0) = L\bar{x} = \left(e^{-\lambda_1(1-\phi)\omega}\bar{x}_1, e^{-\lambda_2(1-\phi)\omega}\bar{x}_2\right),$$

and $\bar{u}(\phi\omega) = Q_{\phi\omega}(L\bar{x}) = S(\bar{x}) = \bar{x}$. It then follows that

$$P(0) = \begin{bmatrix} \frac{e^{\lambda_1(1-\phi)\omega}}{\bar{x}_1} & 0 \\ 0 & \frac{e^{\lambda_2(1-\phi)\omega}}{\bar{x}_2} \end{bmatrix}, \quad P(\phi\omega) = \begin{bmatrix} \frac{1}{\bar{x}_1} & 0 \\ 0 & \frac{1}{\bar{x}_2} \end{bmatrix},$$

and hence,

$$\begin{aligned} DS(\bar{x}) &= V(\phi\omega)\begin{bmatrix} e^{-\lambda_1(1-\phi)\omega} & 0 \\ 0 & e^{-\lambda_2(1-\phi)\omega} \end{bmatrix} \\ &= P^{-1}(\phi\omega)W(\phi\omega)P(0)\begin{bmatrix} e^{-\lambda_1(1-\phi)\omega} & 0 \\ 0 & e^{-\lambda_2(1-\phi)\omega} \end{bmatrix} \\ &= \begin{bmatrix} \bar{x}_1 & 0 \\ 0 & \bar{x}_2 \end{bmatrix} W(\phi\omega) \begin{bmatrix} \bar{x}_1 & 0 \\ 0 & \bar{x}_2 \end{bmatrix}^{-1}, \end{aligned}$$

which implies that $DS(\bar{x})$ is similar to $W(\phi\omega)$. Thus, we have $r(DS(\bar{x})) = r(W(\phi\omega))$. Let

$$Z(t) = \begin{bmatrix} 1 & 0 \\ 0 & -1 \end{bmatrix} W(t) \begin{bmatrix} 1 & 0 \\ 0 & -1 \end{bmatrix}^{-1}.$$

Then $Z(t)$ satisfies

$$\frac{dZ}{dt} = \begin{bmatrix} -\frac{r_1}{K_1}\bar{u}_1(t) & \alpha\bar{u}_2(t) \\ \beta\bar{u}_1(t) & -\frac{r_2}{K_2}\bar{u}_2(t) \end{bmatrix} Z := B(t)Z, \quad Z(0) = I. \tag{2.9}$$

Since the matrix $B(t)$ is cooperative and irreducible, it follows from Smith and Waltman (1995, Theorem B.3) that for each $t > 0$, every element of $Z(t)$ is positive. Clearly, $W(\phi\omega)$ is similar to $Z(\phi\omega)$, and hence, $r(W(\phi\omega)) = r(Z(\phi\omega))$. By Perron–Frobenius theorem (see, e.g., Smith and Waltman 1995, Theorem A.4), $\rho_2 := r(Z(\phi\omega))$ is a simple eigenvalue of $Z(\phi\omega)$ with a positive eigenvector $e = (e_1, e_2)^T$. Let ρ_1 be another eigenvalue of $Z(\phi\omega)$. By Liouville's formula, we have $0 < \rho_1\rho_2 = det Z(\phi\omega) = e^{\int_0^{\phi\omega} trace(B(s))ds} < 1$, and hence, $0 < \rho_1 < \rho_2$. Let $z(t) = (z_1(t), z_2(t))^T := Z(t)e$. Then $z(\phi\omega) = Z(\phi\omega)e = \rho_2 e$, and $z_i(t) > 0$, $\forall t \geq 0$, $i = 1, 2$. Since

$$\begin{aligned} \frac{dz_1(t)}{dt} &= -\frac{r_1}{K_1}\bar{u}_1(t)z_1(t) + \alpha\bar{u}_2(t)z_2(t), \\ \frac{dz_2(t)}{dt} &= \beta\bar{u}_1(t)z_1(t) - \frac{r_2}{K_2}\bar{u}_2(t)z_2(t), \end{aligned}$$

it follows that

$$\beta\frac{dz_1(t)}{dt} + \frac{r_1}{K_1}\frac{dz_2(t)}{dt} = \left(\alpha\beta - \frac{r_1r_2}{K_1K_2}\right)\bar{u}_2(t)z_2(t), \quad \forall t \geq 0.$$

Integrating the above equation for t from 0 to $\phi\omega$, we then obtain

$$\left(\beta e_1 + \frac{r_1}{K_1}e_2\right)(\rho_2 - 1) = \left(\alpha\beta - \frac{r_1r_2}{K_1K_2}\right)\int_0^{\phi\omega} \bar{u}_2(t)z_2(t)dt.$$

Since $\left(\beta e_1 + \frac{r_1}{K_1} e_2\right) > 0$ and $\int_0^{\phi\omega} \bar{u}_2(t) z_2(t) dt > 0$, we see that $\rho_2 - 1$ has the same sign as $\alpha\beta - \frac{r_1 r_2}{K_1 K_2}$. This implies that the statements (i) and (ii) hold. □

For the sake of convenience, we introduce the following notations:

$$A := \begin{bmatrix} \frac{r_1}{K_1} & \alpha \\ \beta & \frac{r_2}{K_2} \end{bmatrix}, \quad B := \begin{bmatrix} (r_1\phi - \lambda_1(1-\phi))\,\omega \\ (r_2\phi - \lambda_2(1-\phi))\,\omega \end{bmatrix}.$$

Then we have the following observation.

Lemma 2.5 (Uniqueness of positive fixed point) *The following two statements are valid:*

(i) *If S has a positive fixed point $\bar{x}$, then $y := \int_0^{\phi\omega} Q_t(L\bar{x}) dt$ is a positive solution of the linear algebraic system $Ay = B$.*

(ii) *If $\frac{r_1 r_2}{K_1 K_2} \neq \alpha\beta$, then S has at most one positive fixed point.*

Proof Let $x(t) = (x_1(t), x_2(t)) := Q_t(L\bar{x})$ and $y_i := \int_0^{\phi\omega} x_i(t) dt$, $i = 1, 2$. Then $x(\phi\omega) = Q_{\phi\omega}(L\bar{x}) = S(\bar{x}) = \bar{x}$, and $x_i(t) > 0$, $\forall t \geq 0$, $i = 1, 2$. Since $(x_1(t), x_2(t))$ satisfies equation (2.5), it follows that

$$r_1\left[1 - \frac{x_1(t)}{K_1}\right] - \alpha x_2(t) = \frac{x_1'(t)}{x_1(t)},$$
$$r_2\left[1 - \frac{x_2(t)}{K_2}\right] - \beta x_1(t) = \frac{x_2'(t)}{x_2(t)}.$$

Integrating the above two equations for t from 0 to $\phi\omega$, we then obtain

$$r_1\phi\omega - \frac{r_1}{K_1} y_1 - \alpha y_2 = \ln \bar{x}_1 - \ln\left(e^{-\lambda_1(1-\phi)\omega}\bar{x}_1\right) = \lambda_1(1-\phi)\omega,$$
$$r_2\phi\omega - \frac{r_2}{K_2} y_2 - \beta y_1 = \ln \bar{x}_2 - \ln\left(e^{-\lambda_2(1-\phi)\omega}\bar{x}_2\right) = \lambda_2(1-\phi)\omega.$$

This implies that the statement (i) holds.

Now we prove the uniqueness of the positive fixed point of S. Suppose, by contradiction, that S has two distinct positive fixed points $\bar{x}$ and $\bar{y}$. Since $det A = \frac{r_1 r_2}{K_1 K_2} - \alpha\beta \neq 0$, the linear system $Ay = B$ has a unique solution. By the statement (i), it then follows that

$$\int_0^{\phi\omega} Q_t(L\bar{x}) dt = \int_0^{\phi\omega} Q_t(L\bar{y}) dt. \tag{2.10}$$

Since any two points in $\mathbb{R}^2$ are ordered with respect to one of two orderings $\leq$ and $\leq_K$, we can assume, without loss of generality, that either $\bar{y} < \bar{x}$, or $\bar{y} <_K \bar{x}$. In the case where $\bar{y} < \bar{x}$, we have $Q_{\phi\omega}(L\bar{y}) = \bar{y} \leq \bar{x} = Q_{\phi\omega}(L\bar{x})$. By the comparison theorem of two dimensional competition systems in the negative direction (see, e.g., the proof of Lemma 2.2(ii)), it then follows that $Q_t(L\bar{y}) \leq Q_t(L\bar{x})$, $\forall t \in [0, \phi\omega]$. Since $L\bar{y} < L\bar{x}$, we see that $Q_t(L\bar{y}) \not\equiv Q_t(L\bar{x})$ on $[0, \phi\omega]$. Thus, we have $\int_0^{\phi\omega} Q_t(L\bar{y})dt < \int_0^{\phi\omega} Q_t(L\bar{x})dt$, a contradiction to (2.10). In the case where $\bar{y} <_K \bar{x}$, we have $L\bar{y} <_K L\bar{x}$. By the comparison theorem of two dimensional competition systems (see, e.g., Smith and Waltman 1995, Theorem B.4), it then follows that $Q_t(L\bar{y}) \leq_K Q_t(L\bar{x})$, $\forall t \in [0, \phi\omega]$. Since $L\bar{y} <_K L\bar{x}$, we have $Q_t(L\bar{y}) \not\equiv Q_t(L\bar{x})$ on $[0, \phi\omega]$, and hence, $\int_0^{\phi\omega} Q_t(L\bar{y})dt <_K \int_0^{\phi T} Q_t(L\bar{x})dt$. This also contradicts (2.10). □

2.2 Long-term behavior

With the help of Lemmas 2.1–2.5, we are now ready to give a complete classification for the global dynamics of the model system (2.4).

For the sake of convenience, we also use the notations $\mathbf{0} = (0, 0)$, $C_1 := \{(x_1, 0) : x_1 \in \mathbb{R}_+\}$, and $C_2 := \{(0, x_2) : x_2 \in \mathbb{R}_+\}$. A vector function $f(t)$ is said to be asymptotic to an ω-periodic function $g(t)$ provided that $\lim_{t\to\infty} |f(t) - g(t)| = 0$.

Theorem 2.1 (Global extinction) *The following statements are valid:*

(i) *If* $r_i\phi - \lambda_i(1-\phi) < 0$, $\forall i = 1, 2$, *then the zero solution is globally asymptotically stable for system* (2.4) *in* $\mathbb{R}^2_+$.
(ii) *If* $r_1\phi - \lambda_1(1-\phi) > 0$ *and* $r_2\phi - \lambda_2(1-\phi) < 0$, *then any solution of system* (2.4) *in* $\mathbb{R}^2_+ \setminus C_2$ *is asymptotic to* $(x_1^*(t), 0)$.
(iii) *If* $r_1\phi - \lambda_1(1-\phi) < 0$ *and* $r_2\phi - \lambda_2(1-\phi) > 0$, *then any solution of system* (2.4) *in* $\mathbb{R}^2_+ \setminus C_1$ *is asymptotic to* $(0, x_2^*(t))$.

Proof In three cases (i), (ii) and (iii), at least one component of the vector B is negative, and hence, $Ax = B$ has no positive solution. By Lemma 2.5(i), it then follows that the map S has no positive fixed point.

In case (i), Lemma 2.1(i) implies that S has no nonzero fixed point on the boundary of $\mathbb{R}^2_+$. By Lemma 2.2(iii), it follows that every forward orbit of S^n in $\mathbb{R}^2_+$ converges to $\mathbf{0}$. As in the proof of Lemma 2.3, it is easy to see that

$$\begin{aligned} DS(\mathbf{0}) &= DQ_{\phi\omega}(\mathbf{0}) \begin{bmatrix} e^{-\lambda_1(1-\phi))\omega} & 0 \\ 0 & e^{-\lambda_2(1-\phi)\omega} \end{bmatrix} \\ &= \begin{bmatrix} e^{(r_1\phi-\lambda_1(1-\phi))\omega} & 0 \\ 0 & e^{(r_2\phi-\lambda_2(1-\phi))\omega} \end{bmatrix}. \end{aligned}$$

Thus, we see that $r(DS(\mathbf{0})) < 1$, and hence, $\mathbf{0}$ is a linearly stable fixed point of S. Consequently, we obtain the global asymptotic stability of the zero solution for the periodic system (2.4).

In case (ii), Lemma 2.1(i) implies that S has exactly one nonzero fixed point $(x_1^*(0), 0)$ on the boundary of $\mathbb{R}^2_+$. Note that $DS(\mathbf{0})$ has two positive eigenvalues: one is greater than 1 and the other is less than 1. Thus, $\mathbf{0}$ is a saddle fixed point of S. By Lemma 2.2(iii), it then follows that every forward orbit for S in $\mathbb{R}^2_+ \setminus C_2$ converges to $(x_1^*(0), 0)$. This implies that the statement (ii) is valid. By symmetric arguments, we see that the statement (iii) also holds. □

Theorem 2.2 (Competitive exclusion) *Assume that* $r_i\phi - \lambda_i(1-\phi) > 0$, $\forall i = 1, 2$. *Then the following statements are valid:*

(i) *If* $r_2\phi - \lambda_2(1-\phi) < \frac{\beta K_1}{r_1}(r_1\phi - \lambda_1(1-\phi))$ *and* $r_1\phi - \lambda_1(1-\phi) > \frac{\alpha K_2}{r_2}(r_2\phi - \lambda_2(1-\phi))$, *then the solution* $(x_1^*(t), 0)$ *is globally asymptotically stable for system* (2.4) *in* $\mathbb{R}_+^2 \setminus C_2$.

(ii) *If* $r_2\phi - \lambda_2(1-\phi) > \frac{\beta K_1}{r_1}(r_1\phi - \lambda_1(1-\phi))$ *and* $r_1\phi - \lambda_1(1-\phi) < \frac{\alpha K_2}{r_2}(r_2\phi - \lambda_2(1-\phi))$, *then the solution* $(0, x_2^*(t))$ *is globally asymptotically stable for system* (2.4) *in* $\mathbb{R}_+^2 \setminus C_1$.

Proof We consider two lines on y_1-y_2 plane

$$l_1: \quad \frac{r_1}{K_1}y_1 + \alpha y_2 = (r_1\phi - \lambda_1(1-\phi))\,\omega > 0,$$

and

$$l_2: \quad \beta y_1 + \frac{r_2}{K_2}y_2 = (r_2\phi - \lambda_2(1-\phi))\,\omega > 0.$$

It is easy to verify that the y_1 and y_2 intercepts of l_1 are greater than those of l_2 in case (i); and the y_1 and y_2 intercepts of l_2 are greater than those of l_1 in case (ii). This implies that both l_1 and l_2 do not intersect in $\mathbb{R}_+^2$. Then Lemma 2.5(i) implies that S has no positive fixed point. By the expression of $DS(\mathbf{0})$ as in the proof of Theorem 2.1, it follows that $\mathbf{0}$ is a unstable fixed point of S in both x_1 and x_2 directions. From Lemma 2.3 and its proof, we further see that in case (i), $(x_1^*(0), 0)$ is an asymptotic stable fixed point of S and $(0, x_2^*(0))$ is a unstable fixed point of the saddle type. By Lemma 2.2(iii), it then follows that $(x_1^*(0), 0)$ globally asymptotically stable for S in $\mathbb{R}_+^2 \setminus C_2$, which implies the statement (i). The statement (ii) can be proved in a similar way. □

Theorem 2.3 (Competitive coexistence) *Assume that* $r_i\phi - \lambda_i(1-\phi) > 0$, $\forall i = 1, 2$. *If* $r_2\phi - \lambda_2(1-\phi) > \frac{\beta K_1}{r_1}(r_1\phi - \lambda_1(1-\phi))$ *and* $r_1\phi - \lambda_1(1-\phi) > \frac{\alpha K_2}{r_2}(r_2\phi - \lambda_2(1-\phi))$, *then system* (2.4) *admits a unique positive* ω*-periodic solution* $\bar{x}(t)$, *and* $\bar{x}(t)$ *is globally asymptotically stable for system* (2.4) *in* $Int(\mathbb{R}_+^2)$.

Proof As in the proof of Theorem 2.2, $\mathbf{0}$ is a unstable fixed point of S in both x_1 and x_2 directions. By Lemma 2.3 and its proof, it follows that both $(x_1^*(0), 0)$ and $(0, x_2^*(0))$ are two unstable fixed points of the saddle type. Thus, Lemma 2.2(iii) implies that for any $x^0 \in Int(\mathbb{R}_+^2)$, $S^n(x^0)$ converges to a fixed point of S in $Int(\mathbb{R}_+^2)$ as $n \to \infty$. Since $r_2\phi - \lambda_2(1-\phi) > 0$ and

$$\begin{aligned} r_2\phi - \lambda_2(1-\phi) &> \frac{\beta K_1}{r_1}(r_1\phi - \lambda_1(1-\phi)) \\ &> \frac{\beta K_1}{r_1} \cdot \frac{\alpha K_2}{r_2}(r_2\phi - \lambda_2(1-\phi)), \end{aligned}$$

we then have $\frac{r_1 r_2}{K_1 K_2} > \alpha\beta$. In view of Lemma 2.5(ii), S has a unique positive fixed point $\bar{x}$, and hence, $\bar{x}$ is globally attractive for S in $Int(\mathbb{R}^2_+)$. Further, Lemma 2.4(ii) implies the local stability of the fixed point $\bar{x}$. Consequently, we have the above stated conclusion for solutions of system (2.4). □

Theorem 2.4 (Saddle-point structure) *Assume that* $r_i\phi - \lambda_i(1-\phi) > 0$, $\forall i = 1, 2$. *If* $r_2\phi - \lambda_2(1-\phi) < \frac{\beta K_1}{r_1}(r_1\phi - \lambda_1(1-\phi))$ *and* $r_1\phi - \lambda_1(1-\phi) < \frac{\alpha K_2}{r_2}(r_2\phi - \lambda_2(1-\phi))$, *then system* (2.4) *admits a unique positive* ω*-periodic solution* $\bar{x}(t)$, *and there exists a continuous, unbounded and one-dimensional curve* $\Gamma \subset \mathbb{R}^2_+$ *such that both* $\mathbf{0}$ *and* $\bar{x}(0)$ *are in* Γ, *and the following statements are valid:*

(a) *If* $x^0 \in \Gamma \setminus \{\mathbf{0}\}$, *then the solution* $x(t, x^0)$ *is asymptotic to* $\bar{x}(t)$.
(b) *If* $x^0 >_K y^0$ *for some* $y^0 \in \Gamma$, *then the solution* $x(t, x^0)$ *is asymptotic to* $(x_1^*(t), 0)$.
(c) *If* $x^0 <_K z^0$ *for some* $z^0 \in \Gamma$, *then the solution* $x(t, x^0)$ *is asymptotic to* $(0, x_2^*(t))$.

Proof In view of Lemma 2.3, both $(x_1^*(0), 0)$ and $(0, x_2^*(0))$ are asymptotic stable fixed points of S. Let B_1 and B_2 be the basins of attraction of $(x_1^*(0), 0)$ and $(0, x_2^*(0))$ for S in $\mathbb{R}^2_+$, respectively. It then follows that B_1 and B_2 are relatively open in $\mathbb{R}^2_+$. Now we claim that S has at least one fixed point $\bar{x}$ in $Int(\mathbb{R}^2_+)$. Otherwise, Lemma 2.2(iii) implies that $\mathbb{R}^2_+ \setminus \{\mathbf{0}\} = B_1 \cup B_2$, which contradicts the connectedness of $\mathbb{R}^2_+ \setminus \{\mathbf{0}\}$. Note that the existence of the positive fixed point $\bar{x}$ is also a straightforward consequence of Hsu et al. (1996, Proposition 2.1) on connecting orbits for abstract competitive systems. Since $r_2\phi - \lambda_2(1-\phi) > 0$ and

$$\begin{aligned} r_2\phi - \lambda_2(1-\phi) &< \frac{\beta K_1}{r_1}(r_1\phi - \lambda_1(1-\phi)) \\ &< \frac{\beta K_1}{r_1} \cdot \frac{\alpha K_2}{r_2}(r_2\phi - \lambda_2(1-\phi)), \end{aligned}$$

we then have $\frac{r_1 r_2}{K_1 K_2} < \alpha\beta$. Thus, Lemma 2.5(ii) implies that $\bar{x}$ is a unique positive fixed point of S. Further, we see from Lemma 2.4 and its proof that $DS(\bar{x})$ has two positive eigenvalues ρ_1 and ρ_2 such that $\rho_1\rho_2 < 1$ and $\rho_2 > 1$. Since $\rho_1 = (\rho_1\rho_2) \cdot \frac{1}{\rho_2} < 1$, the fixed point $\bar{x}$ is of the saddle point type. As in the proof of Lemma 2.4, we see that $det DS(\bar{x}) = \rho_1\rho_2 > 0$. Since S is invertible, it follows that $S(x) = \bar{x}$ only for $x = \bar{x}$. Thus, condition 3 (b) in Kulenovic and Merino (2006, Theorem 5) is satisfied. For any given $(x_1, 0) \geq_K (x_1^*(0), 0)$, we have $S(x_1, 0) = (M_1(x_1), 0)$, where M_1 is the period map of system (2.1) with $\lambda = \lambda_1, r = r_1$ and $K = K_1$. We claim that $M_1(x_1) \leq x_1$. Otherwise, $M_1^n(x_1)$ is a strictly increasing sequence of points, and hence, we obtain $\lim_{n\to\infty} M_1^n(x_1) > x_1 \geq x_1^*(0)$, which contradicts the global attactivity of $x_1^*(0)$ for M_1^n on $\mathbb{R}_+ \setminus \{0\}$ (see Lemma 2.1(ii)). It then follows that $S(x_1, 0) \leq_K (x_1, 0)$. Similarly, we can show that $S(0, x_2) \geq_K (0, x_2)$ for any $(0, x_2) \leq_K (0, x_2^*(0))$. Thus, two conditions in Kulenovic and Merino (2006, Theorem 6 ii. and iv.) are satisfied. Define $\Gamma := \mathbb{R}^2_+ \setminus (B_1 \cup B_2)$. It is easy to see that $\mathbf{0} \in \Gamma$. Now conclusions (a), (b) and (c) follow from Kulenovic and Merino (2006, Theorems 5 and 6). □

3 Discussions

Seasonal environmental change has effects on individual physiology, species growth, and strength of interactions. Alternation of seasons, a common phenomenon in nature, includes quantitative and qualitative fluctuation of environment (Hu and Tessier 1995; Schmitt and Holbrook 1986). The alternations may be fast (e.g., daily light change, Litchman and Klausmeier 2001), intermediate (e.g., tidal cycles and annual seasons, DeAngelis et al. 2009), or slow (e.g., El Nino events). In the present study, we assumed a Lotka–Voltera competition model with periodic succession of environmental forcing on species growth. We should point out that the dynamics in bad seasons is not the exponential decay in Koch (1974), although the Lotka–Volterra competition dynamics in good seasons is assumed there. Both the numerical results of Koch (1974) and our analytic results show that the alternation of good and bad seasons, implicitly defined by resource availability, can reverse the prediction made by the original Lotka–Voltera model. Below we provide detailed explanations.

Consider the following classical Lotka–Volterra two species competition model:

$$\begin{aligned}
\frac{dx_1}{dt} &= r_1 x_1 \left[1 - \frac{x_1}{K_1}\right] - \alpha x_1 x_2,\\
\frac{dx_2}{dt} &= r_2 x_2 \left[1 - \frac{x_2}{K_2}\right] - \beta x_1 x_2,\\
(x_1(0), x_2(0)) &= x^0 \in \mathbb{R}^2_+.
\end{aligned} \tag{3.1}$$

It is well-known that there are four cases of the competition outcome in model (3.1) (see, e.g., (Murray, 1989, Section 3.5)), namely:

A. If $K_1 > \frac{r_2}{\beta}$ and $K_2 < \frac{r_1}{\alpha}$, then species 1 wins the competition.
B. If $K_1 < \frac{r_2}{\beta}$ and $K_2 > \frac{r_1}{\alpha}$, then species 2 wins the competition.
C. If $K_1 < \frac{r_2}{\beta}$ and $K_2 < \frac{r_1}{\alpha}$, then two species coexist at a stable equilibrium.
D. If $K_1 > \frac{r_2}{\beta}$ and $K_2 > \frac{r_1}{\alpha}$, then the bistability occurs for two species in the sense that there exists a separatrix curve Γ connecting $(0, 0)$ to the infinity in $\mathbb{R}^2_+$ such that species 2 wins whenever the initial distribution is above Γ, while species 1 wins whenever the initial distribution is below Γ.

In this paper, we studied the Lotka–Volterra two species competition model with seasonal succession (2.4). The results can be summarized according to five cases, namely:

E. Two species go to extinction.
I. Species 1 wins the competition.
II. Species 2 wins the competition.
III. Two species coexist at a stable periodic state.
IV. Bistability occurs for two species.

From Theorem 2.1(i), we first see that if

$$r_i \phi - \lambda_i (1 - \phi) < 0, \quad \forall i = 1, 2, \tag{3.2}$$

then the outcome E occurs. By Theorem 2.1(ii) and Theorem 2.2(i), it follows that the outcome I occurs provided either

$$r_1\phi - \lambda_1(1-\phi) > 0, \;\; r_2\phi - \lambda_2(1-\phi) < 0, \tag{3.3}$$

or

$$\begin{aligned} &r_i\phi - \lambda_i(1-\phi) > 0, \quad \forall i = 1, 2,\\ &r_2\phi - \lambda_2(1-\phi) < \frac{\beta K_1}{r_1}\,(r_1\phi - \lambda_1(1-\phi)),\\ &r_1\phi - \lambda_1(1-\phi) > \frac{\alpha K_2}{r_2}\,(r_2\phi - \lambda_2(1-\phi)). \end{aligned} \tag{3.4}$$

In view of Theorem 2.1(iii) and Theorem 2.2(ii), the outcome II occurs provided either

$$r_1\phi - \lambda_1(1-\phi) < 0, \;\; r_2\phi - \lambda_2(1-\phi) > 0, \tag{3.5}$$

or

$$\begin{aligned} &r_i\phi - \lambda_i(1-\phi) > 0, \quad \forall i = 1, 2,\\ &r_2\phi - \lambda_2(1-\phi) > \frac{\beta K_1}{r_1}\,(r_1\phi - \lambda_1(1-\phi)),\\ &r_1\phi - \lambda_1(1-\phi) < \frac{\alpha K_2}{r_2}\,(r_2\phi - \lambda_2(1-\phi)). \end{aligned} \tag{3.6}$$

Theorem 2.3 implies that the outcome III occurs provided

$$\begin{aligned} &r_i\phi - \lambda_i(1-\phi) > 0, \quad \forall i = 1, 2,\\ &r_2\phi - \lambda_2(1-\phi) > \frac{\beta K_1}{r_1}\,(r_1\phi - \lambda_1(1-\phi)),\\ &r_1\phi - \lambda_1(1-\phi) > \frac{\alpha K_2}{r_2}\,(r_2\phi - \lambda_2(1-\phi)). \end{aligned} \tag{3.7}$$

Finally, we see from Theorem 2.4 that the outcome IV occurs provided

$$\begin{aligned} &r_i\phi - \lambda_i(1-\phi) > 0, \quad \forall i = 1, 2,\\ &r_2\phi - \lambda_2(1-\phi) < \frac{\beta K_1}{r_1}\,(r_1\phi - \lambda_1(1-\phi)),\\ &r_1\phi - \lambda_1(1-\phi) < \frac{\alpha K_2}{r_2}\,(r_2\phi - \lambda_2(1-\phi)). \end{aligned} \tag{3.8}$$

In order to give biological interpretations of our analytic results on periodic system (2.4) and to compare them with those on the autonomous system (3.1), we introduce the following discontinuous ω-periodic functions:

$$b_i(t) = \begin{cases} -\lambda_i, & \forall t \in [m\omega, m\omega + (1-\phi)\omega), \ m \in \mathbb{Z}, \\ r_i, & \forall t \in [m\omega + (1-\phi)\omega, (m+1)\omega), \ m \in \mathbb{Z}, \end{cases}$$
$$a_i(t) = \begin{cases} 0, & \forall t \in [m\omega, m\omega + (1-\phi)\omega), \ m \in \mathbb{Z}, \\ \frac{r_i}{K_i}, & \forall t \in [m\omega + (1-\phi)\omega, (m+1)\omega), \ m \in \mathbb{Z}, \end{cases}$$
$$\alpha(t) = \begin{cases} 0, & \forall t \in [m\omega, m\omega + (1-\phi)\omega), \ m \in \mathbb{Z}, \\ \alpha, & \forall t \in [m\omega + (1-\phi)\omega, (m+1)\omega), \ m \in \mathbb{Z}, \end{cases}$$
$$\beta(t) = \begin{cases} 0, & \forall t \in [m\omega, m\omega + (1-\phi)\omega), \ m \in \mathbb{Z}, \\ \beta, & \forall t \in [m\omega + (1-\phi)\omega, (m+1)\omega), \ m \in \mathbb{Z}, \end{cases}$$

where $i = 1, 2$. It then follows that system (2.4) can be written as the nonautonomous system with discontinuous ω-periodic coefficients:

$$\begin{aligned} \frac{dx_1}{dt} &= b_1(t)x_1 - a_1(t)x_1^2 - \alpha(t)x_1x_2, \\ \frac{dx_2}{dt} &= b_2(t)x_2 - a_2(t)x_2^2 - \beta(t)x_1x_2. \end{aligned} \tag{3.9}$$

Taking the average values of these ω-periodic coefficients on $[0, \omega]$, we then obtain the following averaged autonomous system:

$$\begin{aligned} \frac{dx_1}{dt} &= \bar{b}_1x_1 - \bar{a}_1x_1^2 - \bar{\alpha}x_1x_2, \\ \frac{dx_2}{dt} &= \bar{b}_2x_2 - \bar{a}_2x_2^2 - \bar{\beta}x_1x_2, \end{aligned} \tag{3.10}$$

where $\bar{b}_i = r_i\phi - \lambda_i(1-\phi)$, $\bar{a}_i = \frac{r_i\phi}{K_i}$, $i = 1, 2$, $\bar{\alpha} = \alpha\phi$, and $\bar{\beta} = \beta\phi$. It is easy to see that system (3.10) is of form (3.1) with r_i, K_i, α and β replaced by

$$\hat{r}_i := r_i\phi - \lambda_i(1-\phi), \qquad \hat{K}_i := \frac{r_i\phi - \lambda_i(1-\phi)}{r_i\phi}K_i,$$

$\bar{\alpha}$ and $\bar{\beta}$, respectively. Thus, $\hat{r}_i$ and $\hat{K}_i$ can be regarded as the seasonal averages of the intrinsic growth rate and the carrying capacity for the i-th species, respectively.

Under the assumption that $r_i\phi - \lambda_i(1-\phi) > 0$, $\forall i = 1, 2$, we can easily see that conditions (3.4), (3.6), (3.7) and (3.8) are equivalent to those in cases A, B, C and D, respectively, for the averaged autonomous system (3.10). In other words, we can use the averaged autonomous system (3.10) to determine the competition outcome for the model (2.4) in the case where two averaged intrinsic growth rates are positive.

We should remark that our analytic results in Sect. 2 show that the above averaged method can be employed to predict the competition outcome only for the specific periodic system (2.4). But we cannot use it to prove the existence, uniqueness and stability of the positive periodic solution. Even for continuous periodic systems, we cannot expect that the qualitative properties of solutions of the averaged autonomous system can be carried over to the given periodic system. For example, the existence of a positive equilibrium for the averaged autonomous system does not imply that of a positive periodic solution of the periodic system. Further, we cannot use the known results on periodic Lotka–Volterra competition systems with continuous periodic coefficients (see, e.g., Cushing 1980; Namba and Takahashi 1993 and references therein) to obtain the conclusions for the periodic system (3.9) with discontinuous periodic coefficients.

There are four parameters $\lambda_1, \ \lambda_2, \phi$ and ω related to the season succession. Our analytic results show that the period ω is independent of any outcome in the effect of season succession. Theorem 2.1(i)–(iii) states that if the death rate λ_i of the i-th species in the bad season is too large, i.e., $\lambda_i > \frac{r_i\phi}{1-\phi}$, then the i-th species becomes extinct as time becomes large. Thus, in the rest of this section, we always assume that $0 < \lambda_i < \frac{r_i\phi}{1-\phi}$, $\forall i = 1, 2$.

3.1 The effect of λ_1 and λ_2

In this subsection, we fix all parameters except λ_1 and λ_2, and let L_1 and L_2 represent two lines in the λ_1–λ_2 plane with their equations given, respectively, by

$$L_1 : r_2\phi - \lambda_2(1-\phi) = \frac{\beta K_1}{r_1}\left(r_1\phi - \lambda_1(1-\phi)\right),$$

and

$$L_2 : r_1\phi - \lambda_1(1-\phi) = \frac{\alpha K_2}{r_2}\left(r_2\phi - \lambda_2(1-\phi)\right).$$

Case A $r_1 > \alpha K_2$ and $r_2 < \beta K_1$. In this case, if $\phi = 1$, i.e., there is no bad season, then species 1 wins the competition. Let $0 < \phi < 1$ be given, and define

$$P_1 := \left(\frac{r_1\phi}{1-\phi}, 0\right), \quad P_2 := \left(0, \frac{r_2\phi}{1-\phi}\right), \quad R_1 := \left(\frac{r_1\phi}{1-\phi}\left[1 - \frac{r_2}{\beta K_1}\right], 0\right),$$

and

$$R_2 := \left(\frac{r_1\phi}{1-\phi}\left[1 - \frac{\alpha K_2}{r_1}\right], 0\right).$$

Then we have two subcases.

Subcase A1 $K_1K_2 > \frac{r_1r_2}{\alpha\beta}$. In some parameter regions in the λ_1–λ_2 plane, we may have bistability case, or the competition outcome may be reversed to the case where species 2 wins the competition, see Fig. 1.

Subcase A2 $K_1K_2 < \frac{r_1r_2}{\alpha\beta}$. In some parameter regions in the λ_1–λ_2 plane, we may have the stable coexistence case, or the competition outcome may be reversed to the case where species 2 wins the competition, see Fig. 2.

Fig. 1 Subcase A1

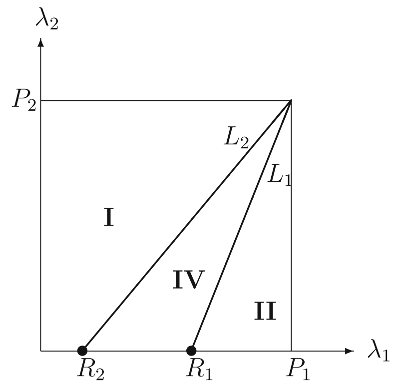
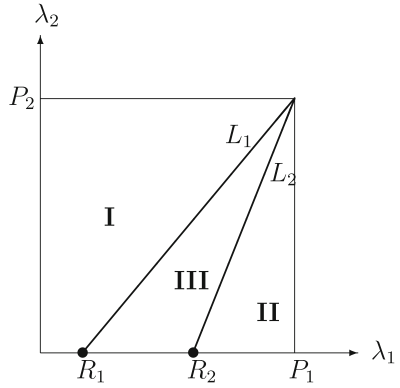


Fig. 2 Subcase A2



Case B $r_1 < \alpha K_2$ and $r_2 > \beta K_1$. In this case, if $\phi = 1$, i.e., there is no bad season, then the species 2 wins the competition. Let $0 < \phi < 1$ be given, and define

$$Q_1 := \left(0, \frac{r_2\phi}{1-\phi}\left[1 - \frac{\beta K_1}{r_2}\right]\right),$$

and

$$Q_2 := \left(0, \frac{r_2\phi}{1-\phi}\left[1 - \frac{r_1}{\alpha K_2}\right]\right).$$

Then we have two subcases.

Subcase B1 $K_1 K_2 > \frac{r_1 r_2}{\alpha\beta}$. In some parameter regions in the λ_1–λ_2 plane, the bistability may occur, or the competition outcome may be reversed to the case where the species 1 wins the competition, see Fig. 3.

Subcase B2 $K_1 K_2 < \frac{r_1 r_2}{\alpha\beta}$. In some parameter regions in the λ_1–λ_2 plane, we may have the stable coexistence for two species, or the competition outcome may be reversed to the case where the species 1 wins the competition, see Fig. 4.

Fig. 3 Subcase B1

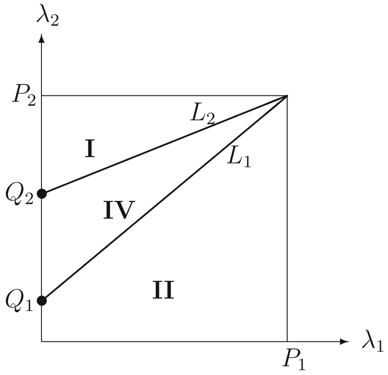


Fig. 4 Subcase B2

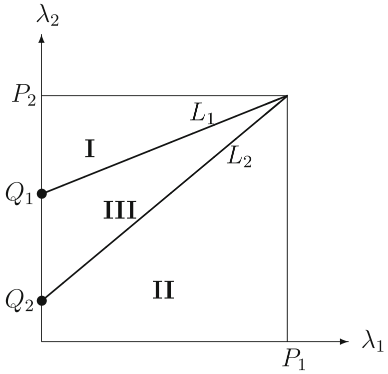
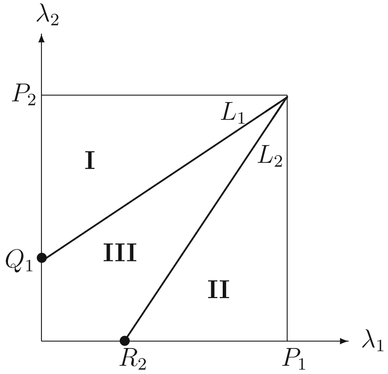


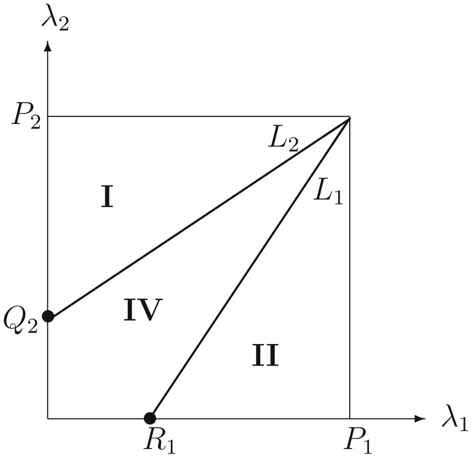
Fig. 5 Case C



Case C $r_1 > \alpha K_2$ and $r_2 > \beta K_1$. In this case, if $\phi = 1$, i.e., there is no bad season, then we have the stable coexistence for two species. For $\phi \in (0, 1)$, the competition outcome may be reversed to the case of the competitive exclusion, see Fig. 5.

Case D $r_1 < \alpha K_2$ and $r_2 < \beta K_1$. In this case, if $\phi = 1$, i.e., there is no bad season, then we have the bistability case. For $\phi \in (0, 1)$, the competition outcomes may be reversed to the case of the competitive exclusion, see Fig. 6.

Fig. 6 Case D



3.2 The effect of ϕ

In this subsection, we fix all parameters except $\phi \in (0, 1]$. Define two functions $f(\phi)$ and $g(\phi)$ by

$$f(\phi) := (r_2\phi - \lambda_2(1-\phi)) - \frac{\beta K_1}{r_1}(r_1\phi - \lambda_1(1-\phi)),$$

and

$$g(\phi) := (r_1\phi - \lambda_1(1-\phi)) - \frac{\alpha K_2}{r_2}(r_2\phi - \lambda_2(1-\phi)).$$

Without loss of generality, we assume that

$$\frac{\lambda_2}{r_2+\lambda_2} \le \frac{\lambda_1}{r_1+\lambda_1}. \tag{3.11}$$

This is because the analogous conclusions can be obtained for the reversed case of (3.11) by an exchange of the positions of two competing species x_1 and x_2. It is easy to see that the assumption (3.11) holds if and only if $\frac{\lambda_2}{r_2} \le \frac{\lambda_1}{r_1}$. Biologically, this means that the death rate λ_2 of species 2 is smaller than λ_1 in comparison with intrinsic growth rates.

We note that $r_i\phi - \lambda_i(1-\phi) > 0$ if and only $\phi > \frac{\lambda_i}{r_i+\lambda_i}$, $i = 1, 2$. It is easy to verify that the following statements are valid:

(i) If $r_2 > \beta K_1$, then $f(\phi) > 0$ for all $\phi \in \left[\frac{\lambda_1}{r_1+\lambda_1}, 1\right]$.

(ii) If $r_2 < \beta K_1$, then $f(\phi) > 0$ for all $\phi \in \left[\frac{\lambda_1}{r_1+\lambda_1}, \phi_f^*\right)$, and $f(\phi) < 0$ for all $\phi \in \left(\phi_f^*, 1\right]$, where $f(\phi_f^*) = 0$ and

$$\phi_f^* = \frac{\left(\frac{\beta K_1 \lambda_1}{r_1} - \lambda_2\right)}{(\beta K_1 - r_2) + \left(\frac{\beta K_1 \lambda_1}{r_1} - \lambda_2\right)}.$$

(iii) If $r_1 > \alpha K_2$, then $g(\phi) < 0$ for all $\phi \in \left[\frac{\lambda_1}{r_1+\lambda_1}, \phi_g^*\right)$, and $g(\phi) > 0$ for all $\phi \in (\phi_g^*, 1]$, where $g(\phi_g^*) = 0$ and

$$\phi_g^* = \frac{\left(\lambda_1 - \frac{\alpha K_2 \lambda_2}{r_2}\right)}{(r_1 - \alpha K_2) + \left(\lambda_1 - \frac{\alpha K_2 \lambda_2}{r_2}\right)}.$$

(iv) If $r_1 < \alpha K_2$, then $g(\phi) < 0$ for all $\phi \in \left[\frac{\lambda_1}{r_1+\lambda_1}, 1\right]$.

Case A $r_1 > \alpha K_2$ and $r_2 < \beta K_1$. In this case, if $\phi = 1$, i.e., there is no bad season, then species 1 wins the competition. It is easy to verify that $\phi_g^* < \phi_f^*$ if and only if $\alpha\beta K_1 K_2 < r_1 r_2$. Thus, we have two subcases.

Subcase A1 $K_1 K_2 > \frac{r_1 r_2}{\alpha\beta}$. It then follows that the following statements are valid:

1. If $\phi \in \left(\frac{\lambda_1}{r_1+\lambda_1}, \phi_f^*\right)$, then $f(\phi) > 0$ and $g(\phi) < 0$, and hence, species 2 wins the competition.
2. If $\phi \in (\phi_f^*, \phi_g^*)$, then $f(\phi) < 0$ and $g(\phi) < 0$, and hence, the bistability occurs for two species.
3. If $\phi \in (\phi_g^*, 1)$, then $f(\phi) < 0$ and $g(\phi) > 0$, and hence, species 1 wins the competition.

Subcase A2 $K_1 K_2 < \frac{r_1 r_2}{\alpha\beta}$. It then follows that the following statements are valid:

1. If $\phi \in \left(\frac{\lambda_1}{r_1+\lambda_1}, \phi_g^*\right)$, then $g(\phi) < 0$ and $f(\phi) > 0$, and hence, species 2 wins the competition.
2. If $\phi \in (\phi_g^*, \phi_f^*)$, then $g(\phi) > 0$ and $f(\phi) > 0$, and hence, two species coexist at a stable equilibrium.
3. If $\phi \in (\phi_f^*, 1)$, then $g(\phi) > 0$ and $f(\phi) < 0$, and hence, species 1 wins the competition.

Case B $r_1 < \alpha K_2$ and $r_2 > \beta K_1$. In this case, if $\phi = 1$, i.e., there is no bad season, then the species 2 wins the competition. It is easy to verify that $g(\phi) < 0$ and $f(\phi) > 0$ for all $\phi \in \left[\frac{\lambda_1}{r_1+\lambda_1}, 1\right]$. Thus, species 2 still wins the competition.

Case C $r_1 > \alpha K_2$ and $r_2 > \beta K_1$. In this case, if $\phi = 1$, i.e., there is no bad season, then we have the stable coexistence. Given $\phi \in (0, 1)$, we have $f(\phi) > 0$; and $g(\phi) < 0$ whenever $\phi \in \left(\frac{\lambda_1}{r_1+\lambda_1}, \phi_g^*\right)$, and $g(\phi) > 0$ whenever $\phi \in (\phi_g^*, 1)$. It then follows that the following statements are valid:

1. If $\phi \in \left(\frac{\lambda_1}{r_1+\lambda_1}, \phi_g^*\right)$, then species 2 wins the competition.
2. If $\phi \in (\phi_g^*, 1)$, then two species coexist at a stable equilibrium.

Case D $r_1 < \alpha K_2$ and $r_2 < \beta K_1$. In this case, if $\phi = 1$, i.e., there is no bad season, then the bistability occurs for two species. Given $\phi \in (0, 1)$, we have $g(\phi) < 0$; and $f(\phi) > 0$ whenever $\phi \in \left(\frac{\lambda_1}{r_1+\lambda_1}, \phi_f^*\right)$, and $f(\phi) < 0$ whenever $\phi \in (\phi_f^*, 1)$. It then follows that the following statements are valid:

1. If $\phi \in \left(\frac{\lambda_1}{r_1+\lambda_1}, \phi_f^*\right)$, then species 2 wins the competition.
2. If $\phi \in (\phi_f^*, 1)$, then the bistability occurs for two species.

Our study gives a consistent result with Litchman and Klausmeier (2001) that the length of good season is important for species coexistence. We also arrive at the conclusion that mortality rate in bad season affects species persistence and coexistence. We show the importance of both factors on species composition analytically. Namba and Takahashi (1993) discussed the possibility of multiple stable states in the Lotka–Volterra two species model with continuous ω-periodic coefficients. In our model (2.4), we treat the case where the Lotka–Volterra model has discontinuous ω-periodic coefficients. In contrast, we show that if system (2.4) admits a positive ω-periodic solution, then it is unique (see Lemma 2.5), and is either stable or of saddle type (see Lemma 2.4).

Our model is based on the Lotka–Volterra system and featured with no spatial context. Spatial heterogeneity is gaining more and more attention in the study of sessile organisms such as plants and reef animals and large-sized organisms in past decades. Although many studies stressed the interchangeable properties of temporal fluctuation and spatial heterogeneity, it is suggested in Chesson (2000) that temporal nonlinearity arises more easily.

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