

Stable Bifurcations in Multi-species Semelparous Population Models

Ryusuke Kon

Abstract It is known that the behavior of a nonlinear semelparous Leslie matrix model with the basic reproduction number close to one can be approximated by a solution of a Lotka-Volterra differential equation. Furthermore, even in multi-species cases, a similar approximation works as long as every species is semelparous. This paper gives a mathematical basis to this approximation and shows that Lotka-Volterra equations are helpful to study a certain bifurcation problem of multi-species semelparous population models. With the help of this approximation method, we find an example of coexistence of two biennial populations with temporal segregation. This example provides a new mechanism of producing population cycles.

Keywords Lotka-Volterra equations · Leslie matrix models · Bifurcation · Semelparity · Population cycles · Temporal segregation

1 Introduction

A species is said to be *semelparous* if it reproduces only once immediately before death. Semelparous species are often observed in insects. In order to reveal a mechanism of producing population cycles observed in insect populations, Bulmer [1] studied a nonlinear semelparous Leslie matrix model, which is an age-structured population model for a semelparous species. One of the important conclusions of this study is that population cycles occur if competition is more severe between than within age-classes. After Bulmer [1], several papers have studied the dynamics of nonlinear semelparous Leslie matrix models (e.g., see [2–6, 8, 11, 12, 15, 17]). In particular, the papers [2–5] focus on bifurcations that occur around the extinction (or population free) equilibrium and provide a clear mathematical formula expressing Bulmer’s conclusion.

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In such bifurcation studies, the basic reproduction number \mathcal{R}_0 is used as a bifurcation parameter. Since \mathcal{R}_0 represents the expected number of newborns reproduced by an individual over a lifetime, population persistence is unlikely if $\mathcal{R}_0 < 1$ and is likely if $\mathcal{R}_0 > 1$. In fact, the extinction equilibrium of a nonlinear semelparous Leslie matrix model is stable if $\mathcal{R}_0 < 1$ and is unstable if $\mathcal{R}_0 > 1$. Therefore, at the critical point $\mathcal{R}_0 = 1$, a branch of positive equilibria is expected to bifurcate from the extinction equilibrium. The papers [2–5] provide a condition for the existence and the stability of such a positive bifurcating branch. Cushing and Li [2] focus on a two-age-class semelparous Leslie matrix model and provide a condition for stable bifurcations of positive equilibria (see also Cushing [3]). Furthermore, it is also shown that if a branch of positive equilibria is unstable, a stable branch of 2-cycles bifurcates from the extinction equilibrium. Therefore, an occurrence of population cycles is predicted by the instability of bifurcating positive equilibria. These studies are extended to the case where the number of age-classes is more than two. Cushing [4] classifies the possible types of bifurcation in a three-age-class case. Furthermore, Cushing and Henson [5] provides a condition for stable bifurcations of positive equilibria that is applicable even if the number of age-classes is arbitrary large.

The purpose of this paper is to provide a simple method of dealing with such a bifurcation problem of nonlinear semelparous Leslie matrix models. The method is motivated by the study of Diekmann and van Gils [7], who showed that a solution of a nonlinear semelparous Leslie matrix model can be approximated by that of a Lotka-Volterra (differential) equation. Our method shows that the stability of bifurcating positive equilibria can be evaluated by that of positive equilibria of Lotka-Volterra equations. That is, our bifurcation problem can be reduced to a stability problem of Lotka-Volterra equations. Since a solution of a multi-species semelparous population model can also be approximated by that of a Lotka-Volterra equation [13, 14], we develop our method in the form applicable to multi-species models. With this method, we rediscover the result of Cushing and Henson [5] on a nonlinear semelparous Leslie matrix model. Furthermore, our method allows us to study high dimensional multi-species semelparous population models and to construct an example of population cycles in a competitive system of two biennial populations without assuming severe between-age-class competition. The population cycle occurs as a result of temporal segregation caused by severe age-specific species competition. This example provides a new mechanism of population cycles.

This paper is organized as follows. Section 2 introduces a multi-species semelparous population model, which is constructed by coupling multiple semelparous Leslie matrix models. Section 3 develops a bifurcation theory for a Kolmogorov difference equation, and shows that a certain bifurcation problem of Kolmogorov difference equations can be reduced to a stability problem of Lotka-Volterra equations. In order to apply the bifurcation theory to our bifurcation problem, Sect. 4 shows that a multi-species semelparous population model can be transformed to a Kolmogorov difference equation, and Sect. 5 specifies the stability problem of Lotka-Volterra equations that we need to examine. Section 6 shows that the derived stability problem of Lotka-Volterra equations can be reduced to a stability problem of lower dimensional Lotka-Volterra equations if lifespans of species, which are positive

integers, are pairwise coprime. Section 7 examines the case where such a reduction does not work and constructs an example that age-specific species interactions have an essential impact on the stability of population dynamics. The example provides a new mechanism of population cycles. Section 8 includes a concluding remark.

2 Multi-species Semelparous Population Models

Let $N \geq 1$ be the number of species. Suppose that species i has $n_i (\geq 2)$ age-classes. Then there are $n_1 + n_2 + \dots + n_N =: n$ age-classes in total. We consider the interaction among N species expressed by the following n -dimensional nonlinear difference equation

$$\begin{cases} u_{[i,1],k+1} = f_i \sigma_{[i,n_i]}(\mathbf{u}_k) u_{[i,n_i],k} \\ u_{[i,2],k+1} = s_{[i,1]} \sigma_{[i,1]}(\mathbf{u}_k) u_{[i,1],k} \\ \vdots \\ u_{[i,n_i],k+1} = s_{[i,n_i-1]} \sigma_{[i,n_i-1]}(\mathbf{u}_k) u_{[i,n_i-1],k} \end{cases} \quad i = 1, 2, \dots, N. \quad (1)$$

Here $\mathbf{u}_k = (u_{1,k}, u_{2,k}, \dots, u_{n,k})^\top$ (the symbol \top is used for vector or matrix transpose) and for $i \in \{1, 2, \dots, N\}$ the following notation is used to simplify the expression:

$$[i, j] := n_0 + n_1 + \dots + n_{i-1} + j,$$

where $n_0 = 0$ and $j \in \{1, 2, \dots, n_i\}$. Therefore, for example, \mathbf{u}_k is also written as

$$\mathbf{u}_k = \underbrace{(u_{[1,1],k}, \dots, u_{[1,n_1],k})}_{n_1}, \underbrace{(u_{[1,2],k}, \dots, u_{[2,n_2],k})}_{n_2}, \dots, \underbrace{(u_{[N,1],k}, \dots, u_{[N,n_N],k})}_{n_N}^\top.$$

The variable $u_{[i,j],k}$ denotes the number of individuals of age $j \in \{1, 2, \dots, n_i\}$ of species $i \in \{1, 2, \dots, N\}$ at time $k \in \{0, 1, 2, \dots\}$. The vital rates $f_i \sigma_{[i,n_i]}$ and $s_{[i,j]} \sigma_{[i,j]}$ denote the number of newborns produced by an individual of age n_i of species i and the probability that an individual of age j of species i survives one unit of time, respectively. It is assumed that each species has a single reproductive age-class. Thus each species is assumed to be semelparous. The ability of each individual of age j of species i is characterized by a single vital rate, either $f_i \sigma_{[i,n_i]}$ or $s_{[i,j]} \sigma_{[i,j]}$. It is assumed that f_i and $s_{[i,j]}$ are positive constants and $\sigma_{[i,j]}$ is a positive function of the population vector \mathbf{u}_k . We normalize the functions $\sigma_{[i,j]}$ by $\sigma_{[i,j]}(\mathbf{0}) = 1$. This implies that the constants f_i and $s_{[i,j]}$ represent vital rates at low population sizes, and thus the functions $\sigma_{[i,j]}$ solely determine how the vital rates depend on (both conspecific and allospecific) population sizes. Under these assumptions, the nonnegative cone

$$\mathbb{R}_+^n := \{(u_1, u_2, \dots, u_n)^\top \in \mathbb{R}^n : u_i \geq 0 \text{ for all } i \in \{1, 2, \dots, n\}\}$$

is forward invariant, i.e., $\mathbf{u}_k \in \mathbb{R}_+^n$ for all $k \geq 1$ if $\mathbf{u}_0 \in \mathbb{R}_+^n$.

If $N = 1$, then system (1) is reduced to a nonlinear semelparous Leslie matrix model, which is for instance studied in [1–6, 8, 11, 12, 15, 17].

3 Bifurcations in Kolmogorov Difference Equations

This section considers a bifurcation problem of the Kolmogorov difference equation

$$x_{i,k+1} = x_{i,k} g_i(\varepsilon, \mathbf{x}_k), \quad i = 1, 2, \dots, n, \quad (2)$$

where $\mathbf{x}_k = (x_{1,k}, x_{2,k}, \dots, x_{n,k})^\top$. This difference equation has a parameter $\varepsilon \in \mathbb{R}$. We assume that each g_i is a C^2 function defined in a neighborhood of $(0, \mathbf{0}) \in \mathbb{R} \times \mathbb{R}^n$ and satisfies $g_i(0, \mathbf{0}) = 1$. A vector is said to be *positive* (resp. *negative*) if all its components are positive (resp. negative). We are concerned with the positive equilibria of system (2), which are given by the positive vectors \mathbf{x} satisfying the equation $\mathbf{g}(\varepsilon, \mathbf{x}) = \mathbf{1}$, where $\mathbf{1}$ is a column vector whose components are all 1 and $\mathbf{g}(\varepsilon, \mathbf{x}) := (g_1(\varepsilon, \mathbf{x}), g_2(\varepsilon, \mathbf{x}), \dots, g_n(\varepsilon, \mathbf{x}))^\top$. We shall construct a positive equilibrium of system (2) near the origin $\mathbf{0}$ and show that such a positive equilibrium has the same stability property as a positive equilibrium of the Lotka-Volterra equation

$$\frac{dx_i}{dt} = x_i \left(r_i + \sum_{j=1}^n a_{ij} x_j \right), \quad i = 1, 2, \dots, n, \quad (3)$$

where

$$r_i := \frac{\partial g_i}{\partial \varepsilon}(0, \mathbf{0}), \quad a_{ij} := \frac{\partial g_i}{\partial x_j}(0, \mathbf{0}).$$

The positive equilibria of system (3) are given by the positive vectors \mathbf{x} satisfying the linear equation $\mathbf{r} + A\mathbf{x} = \mathbf{0}$, where $\mathbf{r} := (r_1, r_2, \dots, r_n)^\top$ and $A := (a_{ij})$. If A is nonsingular, i.e., $\det A \neq 0$, then the equation has the unique solution $\mathbf{x}^* := -A^{-1}\mathbf{r}$, which might not be positive. In the following theorems, the matrix A is always assumed nonsingular. Since the situation that the equality $\det A = 0$ holds is negligible, the nonsingularity assumption does not impose significant restrictions on our results.

Theorem 1 *Suppose that A is nonsingular. Then there exists a constant $\varepsilon_0 > 0$ and a unique function $\hat{\mathbf{x}} : (-\varepsilon_0, \varepsilon_0) \rightarrow \mathbb{R}^n$ satisfying $\hat{\mathbf{x}}(0) = \mathbf{0}$ and $\mathbf{g}(\varepsilon, \hat{\mathbf{x}}(\varepsilon)) = \mathbf{1}$. Furthermore, if \mathbf{g} is a C^d function ($d \geq 1$), then so is $\hat{\mathbf{x}}$.*

Proof By assumption, $\frac{\partial \mathbf{g}}{\partial \mathbf{x}}(0, \mathbf{0}) = A$ is nonsingular. Thus the conclusion of this theorem is an immediate consequence of the implicit function theorem. \square

It is clear that $\hat{\mathbf{x}}$ is an equilibrium of system (2). Furthermore, around $\varepsilon = 0$, the function $\hat{\mathbf{x}}$ is written in the form

$$\begin{aligned}\hat{\mathbf{x}}(\varepsilon) &= \hat{\mathbf{x}}(0) + \varepsilon \frac{d\hat{\mathbf{x}}}{d\varepsilon}(0) + O(\varepsilon^2) \\ &= \varepsilon \mathbf{x}^* + O(\varepsilon^2)\end{aligned}$$

since $\hat{\mathbf{x}}(0) = \mathbf{0}$ and $\frac{d\hat{\mathbf{x}}}{d\varepsilon}(0) = -(\frac{\partial \mathbf{g}}{\partial \mathbf{x}}(0, \mathbf{0}))^{-1} \frac{\partial \mathbf{g}}{\partial \varepsilon}(0, \mathbf{0}) = -A^{-1} \mathbf{r}$. Therefore, a branch of positive equilibria of system (2) bifurcates from the origin as increasing (resp. decreasing) ε through $\varepsilon = 0$ if \mathbf{x}^* is positive (resp. negative). That is, the bifurcation is to the right if $\mathbf{x}^* > \mathbf{0}$ and to the left if $\mathbf{x}^* < \mathbf{0}$.

The Jacobi matrix of system (3) evaluated at \mathbf{x}^* is given by $\text{diag}(\mathbf{x}^*)A$, where $\text{diag}(\mathbf{x}^*)$ denotes the diagonal matrix

$$\begin{pmatrix} x_1^* & 0 & \cdots & 0 \\ 0 & x_2^* & \cdots & 0 \\ \vdots & \vdots & & \vdots \\ 0 & 0 & \cdots & x_n^* \end{pmatrix}.$$

The following theorem shows that the stability of $\hat{\mathbf{x}}$ constructed in Theorem 1 can be evaluated by the stability of $\text{diag}(\mathbf{x}^*)A$. A matrix is said to be *stable* if all its eigenvalues have negative real part. For convenience, we denote the *stability modulus* of a matrix M by

$$s(M) := \max\{\Re \lambda : \lambda \text{ is an eigenvalue of } M\},$$

where $\Re \lambda$ denotes the real part of λ . Then M is stable if and only if $s(M) < 0$.

Theorem 2 *If $s(\text{diag}(\mathbf{x}^*)A) < 0$ (resp. $s(\text{diag}(\mathbf{x}^*)A) > 0$), then the equilibrium $\hat{\mathbf{x}}(\varepsilon)$ of system (2) is asymptotically stable (resp. unstable) for all sufficiently small $\varepsilon > 0$.*

Proof Since $\hat{\mathbf{x}}(\varepsilon)$ satisfies $\mathbf{g}(\varepsilon, \hat{\mathbf{x}}(\varepsilon)) = \mathbf{1}$, the Jacobi matrix of system (2) evaluated at $\hat{\mathbf{x}}(\varepsilon)$ is

$$\begin{aligned}J(\hat{\mathbf{x}}(\varepsilon)) &:= \left. \frac{\partial}{\partial \mathbf{x}} \text{diag}(\mathbf{x}) \mathbf{g}(\varepsilon, \mathbf{x}) \right|_{\mathbf{x}=\hat{\mathbf{x}}(\varepsilon)} \\ &= \left(\text{diag}(\mathbf{g}(\varepsilon, \mathbf{x})) + \text{diag}(\mathbf{x}) \frac{\partial \mathbf{g}}{\partial \mathbf{x}}(\varepsilon, \mathbf{x}) \right) \Big|_{\mathbf{x}=\hat{\mathbf{x}}(\varepsilon)} \\ &= I + \text{diag}(\hat{\mathbf{x}}(\varepsilon)) \frac{\partial \mathbf{g}}{\partial \mathbf{x}}(\varepsilon, \hat{\mathbf{x}}(\varepsilon)),\end{aligned}$$

where I is the identity matrix. Around $\varepsilon = 0$, this is written in the form

$$J(\hat{\mathbf{x}}(\varepsilon)) = I + \varepsilon (\text{diag}(\mathbf{x}^*)A + O(\varepsilon)).$$

Suppose that $s(\text{diag}(\mathbf{x}^*)A) < 0$. Then because of continuous dependence of eigenvalues of a matrix on its entries, there exists a constant $\varepsilon_s \in (0, \varepsilon_0)$ such that every eigenvalue $\lambda(\varepsilon)$ of $\text{diag}(\mathbf{x}^*)A + O(\varepsilon)$ satisfies

$$\left| \lambda(\varepsilon) + \frac{1}{\varepsilon} \right| < \frac{1}{\varepsilon}$$

for all $\varepsilon \in (0, \varepsilon_s)$. This inequality represents the situation that the disk centered at $-\frac{1}{\varepsilon}$ with radius $\frac{1}{\varepsilon}$ contains all eigenvalues of $\text{diag}(\mathbf{x}^*)A + O(\varepsilon)$ on the complex plane. Since $\varepsilon > 0$, the inequality is reduced to $|1 + \varepsilon\lambda(\varepsilon)| < 1$, which implies that the spectral radius of $J(\hat{\mathbf{x}}(\varepsilon))$ is less than one. Therefore, $\hat{\mathbf{x}}(\varepsilon)$ is asymptotically stable for all $\varepsilon \in (0, \varepsilon_s)$.

Suppose that $s(\text{diag}(\mathbf{x}^*)A) > 0$. Then $\text{diag}(\mathbf{x}^*)A$ has an eigenvalue λ_u with positive real part and $\text{diag}(\mathbf{x}^*)A + O(\varepsilon)$ has an eigenvalue $\lambda(\varepsilon)$ satisfying $\lambda(\varepsilon) \rightarrow \lambda_u$ as $\varepsilon \rightarrow 0$. Therefore, there exists a constant $\varepsilon_u \in (0, \varepsilon_0)$ such that

$$\left| \lambda(\varepsilon) + \frac{1}{\varepsilon} \right| > \frac{1}{\varepsilon}$$

holds for all $\varepsilon \in (0, \varepsilon_u)$. Since $\varepsilon > 0$, the inequality is equivalent to $|1 + \varepsilon\lambda(\varepsilon)| > 1$, which implies that the spectral radius of $J(\hat{\mathbf{x}}(\varepsilon))$ is larger than one. Therefore, $\hat{\mathbf{x}}(\varepsilon)$ is unstable for all $\varepsilon \in (0, \varepsilon_u)$. \square

4 Derivation of Kolmogorov Difference Equations from System (1)

Define the *basic reproduction number* \mathcal{R}_0^i for species i by $\mathcal{R}_0^i := s_{[i,1]}s_{[i,2]} \dots s_{[i,n_i-1]}f_i$. This number represents the expected number of newborns reproduced by an individual of species i per lifetime at low population sizes. We are concerned with a bifurcation that occurs in system (1) at $\mathcal{R}_0^1 = \mathcal{R}_0^2 = \dots = \mathcal{R}_0^N = 1$. Since it is difficult to treat $\mathcal{R}_0^1, \mathcal{R}_0^2, \dots, \mathcal{R}_0^N$ as multiple independent bifurcation parameters, we only consider the case where the vector $(\mathcal{R}_0^1, \mathcal{R}_0^2, \dots, \mathcal{R}_0^N)^\top$ changes along a certain one-dimensional manifold and treat a one-parameter bifurcation problem. More precisely, in order to make the derived Lotka-Volterra equation simple, we choose an arbitrary fixed vector $\mathbf{c} = (c_1, c_2, \dots, c_N)^\top$ and consider bifurcations by changing the parameters $\mathcal{R}_0^1, \mathcal{R}_0^2, \dots, \mathcal{R}_0^N$ with maintaining the relation

$$\left(\log(\mathcal{R}_0^1)^{\frac{v}{n_1}}, \log(\mathcal{R}_0^2)^{\frac{v}{n_2}}, \dots, \log(\mathcal{R}_0^N)^{\frac{v}{n_N}} \right)^\top = \varepsilon(c_1, c_2, \dots, c_N)^\top, \quad \varepsilon \in \mathbb{R} \quad (4)$$

where v is the least common multiple of n_1, n_2, \dots, n_N , and thus species i experiences $\frac{v}{n_i}$ generations within v time steps and $(\mathcal{R}_0^i)^{\frac{v}{n_i}}$ represents the expected number of descendants of species i per individual per v time step at low population sizes. Since

the above relation is assumed to be always satisfied when we consider a bifurcation problem of system (1), the new parameter ε instead of $\mathcal{R}_0^1, \mathcal{R}_0^2, \dots, \mathcal{R}_0^N$ shall be used as a bifurcation parameter. Although our approach is practically sufficient to examine the dynamics of system (1) with the parameters around $\mathcal{R}_0^1 = \mathcal{R}_0^2 = \dots = \mathcal{R}_0^N = 1$, there could exist exceptional cases that our approach is unable to treat (see Sect. 9). Note that increase of ε implies increase of \mathcal{R}_0^i if $c_i > 0$ and decrease of \mathcal{R}_0^i if $c_i < 0$. To include ε as an explicit parameter of system (1), we replace f_i by $\frac{e^{\frac{c_i n_i}{v} \varepsilon}}{s_{[i,1]} s_{[i,2]} \dots s_{[i, n_i - 1]}}$. Then system (1) becomes

$$\begin{cases} u_{[i,1],k+1} = \frac{e^{\frac{c_i n_i}{v} \varepsilon}}{s_{[i,1]} s_{[i,2]} \dots s_{[i, n_i - 1]}} \sigma_{[i, n_i]}(\mathbf{u}_k) u_{[i, n_i], k} \\ u_{[i,2],k+1} = s_{[i,1]} \sigma_{[i,1]}(\mathbf{u}_k) u_{[i,1], k} \\ \vdots \\ u_{[i, n_i], k+1} = s_{[i, n_i - 1]} \sigma_{[i, n_i - 1]}(\mathbf{u}_k) u_{[i, n_i - 1], k} \end{cases} \quad i = 1, 2, \dots, N. \quad (5)$$

Define

$$D_i := \text{diag}(1, s_{[i,1]}, s_{[i,1]} s_{[i,2]}, \dots, s_{[i,1]} s_{[i,2]} \dots s_{[i, n_i - 1]}), \quad i = 1, 2, \dots, N,$$

and $D := \text{diag}(D_1, D_2, \dots, D_N)$. The rescaling of system (5) with $\mathbf{x} := D^{-1} \mathbf{u}$ gives

$$\begin{cases} x_{[i,1],k+1} = e^{\frac{c_i n_i}{v} \varepsilon} \sigma_{[i, n_i]}(D \mathbf{x}_k) x_{[i, n_i], k} \\ x_{[i,2],k+1} = \sigma_{[i,1]}(D \mathbf{x}_k) x_{[i,1], k} \\ \vdots \\ x_{[i, n_i], k+1} = \sigma_{[i, n_i - 1]}(D \mathbf{x}_k) x_{[i, n_i - 1], k} \end{cases} \quad i = 1, 2, \dots, N.$$

Let $\pi_i, i = 1, 2, \dots, N$, be the cyclic permutation

$$\begin{pmatrix} [i, 1] & [i, 2] & \dots & [i, n_i] \\ [i, n_i] & [i, 1] & \dots & [i, n_i - 1] \end{pmatrix}$$

and P_{π_i} be its permutation matrix. The product of $\pi_1, \pi_2, \dots, \pi_N$ is denoted by π and its permutation matrix is denoted by P_π . Define

$$S_i(\varepsilon, \mathbf{x}) := P_{\pi_i} \text{diag}(\sigma_{[i,1]}(D \mathbf{x}), \dots, \sigma_{[i, n_i - 1]}(D \mathbf{x}), e^{\frac{c_i n_i}{v} \varepsilon} \sigma_{[i, n_i]}(D \mathbf{x})), \quad i = 1, 2, \dots, N,$$

and $S(\varepsilon, \mathbf{x}) := \text{diag}(S_1(\varepsilon, \mathbf{x}), S_2(\varepsilon, \mathbf{x}), \dots, S_N(\varepsilon, \mathbf{x}))$. Then the rescaled equation is written as

$$\mathbf{x}_{k+1} = S(\varepsilon, \mathbf{x}_k) \mathbf{x}_k.$$

Let $\xi(\mathbf{x}) := S(\varepsilon, \mathbf{x})\mathbf{x}$. Since ν is a common multiple of the periods of the cyclic permutations $\pi_1, \pi_2, \dots, \pi_N$, the matrix $G(\varepsilon, \mathbf{x}) := S(\varepsilon, \xi^{\nu-1}(\mathbf{x})) \dots S(\varepsilon, \xi(\mathbf{x}))S(\varepsilon, \mathbf{x})$ is diagonal. Thus the map ξ^ν , i.e.,

$$\mathbf{y}_{k+1} = G(\varepsilon, \mathbf{y}_k)\mathbf{y}_k \quad (6)$$

is a Kolmogorov difference equation. The behavior of \mathbf{y}_k shows the stroboscopic behavior of \mathbf{x}_k with period ν .

5 Lotka-Volterra Equations

In the previous two sections, it was shown that system (1) is reduced to a Kolmogorov difference equation and its bifurcation problem is reduced to a stability problem of a Lotka-Volterra equation. In this section, we shall identify the Lotka-Volterra equation that we need to study.

Define the $n \times n$ matrix $B = (b_{ij})$ by

$$b_{ij} := \frac{\partial \sigma_i}{\partial u_j}(\mathbf{0}),$$

i.e., $B = \frac{\partial \boldsymbol{\sigma}}{\partial \mathbf{u}}(\mathbf{0})$, where $\boldsymbol{\sigma} = (\sigma_1, \sigma_2, \dots, \sigma_n)^\top$. The parameter $b_{[i,k][j,l]}$ represents the intensity of density dependent effect from age-class l of species j to age-class k of species i at low population sizes. The interaction between age-class k of species i and age-class l of species j is competitive if $b_{[i,k][j,l]} < 0$ and $b_{[j,l][i,k]} < 0$, mutualistic if $b_{[i,k][j,l]} > 0$ and $b_{[j,l][i,k]} > 0$, and antagonistic if $b_{[i,k][j,l]}b_{[j,l][i,k]} < 0$ at low population sizes. Let $\mathbf{g} = (g_1, g_2, \dots, g_n)^\top$ be the diagonal entries of G defined in the previous section, i.e., $\text{diag}(\mathbf{g}(\varepsilon, \mathbf{x})) = G(\varepsilon, \mathbf{x})$. Then it is clear that $\mathbf{g}(\mathbf{0}, \mathbf{0}) = \mathbf{1}$ holds. Furthermore, we have

$$\frac{\partial g_{[i,1]}}{\partial \varepsilon}(\mathbf{0}, \mathbf{0}) = \frac{\partial g_{[i,2]}}{\partial \varepsilon}(\mathbf{0}, \mathbf{0}) = \dots = \frac{\partial g_{[i,n_i]}}{\partial \varepsilon}(\mathbf{0}, \mathbf{0}) = c_i, \quad i = 1, 2, \dots, N.$$

Thus g_i can be written as

$$g_i(\varepsilon, \mathbf{x}) = \exp\left(\varepsilon \frac{\partial g_i}{\partial \varepsilon}(\mathbf{0}, \mathbf{0})\right) \prod_{k=0}^{\nu-1} \sigma_{\pi^k(i)}(D\xi^k(\mathbf{x})), \quad i = 1, 2, \dots, n,$$

whose partial derivative with respect to x_j evaluated at $(\varepsilon, \mathbf{x}) = (0, \mathbf{0})$ is

$$\begin{aligned}
\frac{\partial g_i}{\partial x_j}(0, \mathbf{0}) &= \frac{\partial}{\partial x_j} \exp\left(\varepsilon \frac{\partial g_i}{\partial \varepsilon}(0, \mathbf{0})\right) \prod_{k=0}^{\nu-1} \sigma_{\pi^k(i)}(D\xi^k(\mathbf{x})) \Big|_{(\varepsilon, \mathbf{x})=(0, \mathbf{0})} \\
&= \sum_{l=0}^{\nu-1} \prod_{\substack{k=0 \\ k \neq l}}^{\nu-1} \sigma_{\pi^k(i)}(D\xi^k(\mathbf{x})) \frac{\partial}{\partial x_j} \sigma_{\pi^l(i)}(D\xi^l(\mathbf{x})) \Big|_{(\varepsilon, \mathbf{x})=(0, \mathbf{0})} \\
&= \sum_{l=0}^{\nu-1} \prod_{\substack{k=0 \\ k \neq l}}^{\nu-1} \sigma_{\pi^k(i)}(D\xi^k(\mathbf{x})) \frac{\partial}{\partial \mathbf{u}} \sigma_{\pi^l(i)}(D\xi^l(\mathbf{x})) \frac{\partial}{\partial x_j} D\xi^l(\mathbf{x}) \Big|_{(\varepsilon, \mathbf{x})=(0, \mathbf{0})} \\
&= \sum_{l=0}^{\nu-1} \prod_{\substack{k=0 \\ k \neq l}}^{\nu-1} \sigma_{\pi^k(i)}(D\xi^k(\mathbf{x})) \left(\frac{\partial \sigma}{\partial \mathbf{u}}(D\xi^l(\mathbf{x})) D \frac{\partial \xi^l}{\partial \mathbf{x}} \right)_{\pi^l(i), j} \Big|_{(\varepsilon, \mathbf{x})=(0, \mathbf{0})} \\
&= \sum_{l=0}^{\nu-1} (P_\pi^{-l} B D P_\pi^l)_{ij}.
\end{aligned}$$

This implies

$$\frac{\partial \mathbf{g}}{\partial \mathbf{x}}(0, \mathbf{0}) = B D + P_\pi^{-1} B D P_\pi + \dots + P_\pi^{-\nu+1} B D P_\pi^{\nu-1}.$$

Thus Theorems 1 and 2 suggest that the Lotka-Voterra equation (3) satisfying

$$\begin{aligned}
\mathbf{r} &= \underbrace{(c_1, c_1, \dots, c_1)}_{n_1} \underbrace{(c_2, c_2, \dots, c_2)}_{n_2} \dots \underbrace{(c_N, c_N, \dots, c_N)}_{n_N}^\top \\
A &= B D + P_\pi^{-1} B D P_\pi + \dots + P_\pi^{-\nu+1} B D P_\pi^{\nu-1}
\end{aligned} \tag{7}$$

is helpful to study our bifurcation problem of system (5).

Each parameter in (7) has an important biological meaning. The parameters c_1, c_2, \dots, c_N represent the ratio of $\log(\mathcal{R}_0^1)^{\frac{\nu}{n_1}}, \log(\mathcal{R}_0^2)^{\frac{\nu}{n_2}}, \dots, \log(\mathcal{R}_0^N)^{\frac{\nu}{n_N}}$, in which the basic reproduction numbers are compared with the same time scale. By definition, the $([i, k], [j, l])$ -entry of A is written as

$$a_{[i, k][j, l]} = \sum_{\Delta=0}^{\nu-1} (B D)_{\pi^\Delta([i, k])\pi^\Delta([j, l])}.$$

Since π is the product of the cyclic permutations $\pi_1, \pi_2, \dots, \pi_N$, every entry of B that appears in the right-hand side of this equation has the first subscript belonging to $\{[i, 1], [i, 2], \dots, [i, n_i]\}$ and the second subscript belonging to $\{[j, 1], [j, 2], \dots,$

$[j, n_j]$). Therefore, every $a_{[i,k][j,l]}$, $k = 1, 2, \dots, n_i$, $l = 1, 2, \dots, n_j$, indicates the intensity of an effect of species j on species i at low population sizes. In the subsequent sections, we shall see that age-specific effects of density dependence between species i and j intricately depend on n_i and n_j .

The rest of this section provides some basic properties of system (3) satisfying (7).

Lemma 1 *The vector \mathbf{r} and the matrix A defined by (7) satisfy $P_\pi \mathbf{r} = \mathbf{r}$ and $P_\pi A P_\pi^{-1} = A$.*

Proof It is clear that the first equality holds. Since $P_\pi^\nu = P_\pi^{-\nu} = I$, we have $P_\pi B D P_\pi^{-1} = P_\pi^{-\nu+1} B D P_\pi^{\nu-1}$. Thus

$$\begin{aligned} P_\pi A P_\pi^{-1} &= P_\pi (B D + P_\pi^{-1} B D P_\pi + \dots + P_\pi^{-\nu+1} B D P_\pi^{\nu-1}) P_\pi^{-1} \\ &= A, \end{aligned}$$

which shows that the second equality holds. \square

Define the $N \times n$ matrix $T = (t_{ij})$ by

$$t_{ij} := \begin{cases} 1, & j \in \{[i, 1], [i, 2], \dots, [i, n_i]\} \\ 0, & j \notin \{[i, 1], [i, 2], \dots, [i, n_i]\}. \end{cases}$$

For an $n \times n$ matrix $M = (m_{ij})$, define the $N \times N$ matrix $\bar{M} = (\bar{m}_{ij})$ by

$$\bar{m}_{ij} := \frac{1}{n_i n_j} \sum_{k=1}^{n_i} \sum_{l=1}^{n_j} m_{[i,k][j,l]},$$

similarly, for an n -dimensional vector $\mathbf{v} = (v_1, v_2, \dots, v_n)^\top$, define the N -dimensional vector $\bar{\mathbf{v}} = (\bar{v}_1, \bar{v}_2, \dots, \bar{v}_N)^\top$ by

$$\bar{v}_i = \frac{1}{n_i} \sum_{k=1}^{n_i} v_{[i,k]}.$$

Lemma 2 *Let \mathbf{r} and A be the vector and the matrix defined by (7). Suppose that A is nonsingular. Then $\mathbf{x}^* = -A^{-1} \mathbf{r}$ satisfies*

$$x_{[i,1]}^* = x_{[i,2]}^* = \dots = x_{[i,n_i]}^* = -\frac{1}{n_i} (\bar{A}^{-1} \bar{\mathbf{r}})_i, \quad i = 1, 2, \dots, N.$$

Thus $\bar{\mathbf{r}} + \bar{A} T \mathbf{x}^* = \mathbf{0}$ is fulfilled.

Proof Multiplying the both sides of $\mathbf{r} + A\mathbf{x}^* = \mathbf{0}$ on the left by P_π , we have $P_\pi\mathbf{r} + P_\pi A P_\pi^{-1} P_\pi\mathbf{x}^* = \mathbf{0}$. Since $P_\pi\mathbf{r} = \mathbf{r}$ and $P_\pi A P_\pi^{-1} = A$ hold, we obtain $\mathbf{r} + A P_\pi\mathbf{x}^* = \mathbf{0}$. The same argument shows that $\mathbf{r} + A\mathbf{x}^* = \mathbf{r} + A P_\pi\mathbf{x}^* = \cdots = \mathbf{r} + A P_\pi^{\nu-1}\mathbf{x}^* = \mathbf{0}$, i.e., $A\mathbf{x}^* = A P_\pi\mathbf{x}^* = \cdots = A P_\pi^{\nu-1}\mathbf{x}^* = -\mathbf{r}$. Since A is nonsingular, $\mathbf{x}^* = P_\pi\mathbf{x}^* = \cdots = P_\pi^{\nu-1}\mathbf{x}^*$. This shows that $x_{[i,1]}^* = x_{[i,2]}^* = \cdots = x_{[i,n_i]}^*$ for each $i \in \{1, 2, \dots, N\}$. Then we further obtain $\mathbf{0} = \mathbf{r} + A\mathbf{x}^* = \bar{\mathbf{r}} + \bar{A}\mathbf{x}^* = \bar{\mathbf{r}} + \bar{A}T\mathbf{x}^*$. \square

If $N = 1$, then π is a cyclic permutation of $\{1, 2, \dots, n\}$. Thus all components of \mathbf{r} are identical and A is a circulant matrix. In [10], the Lotka-Volterra equation with such \mathbf{r} and A is studied. It is called the *May-Leonard system* [16] if $n = 3$.

6 Stable Bifurcations in Multi-species Semelparous Models

By combing the results of the previous sections, we can establish theorems on bifurcations of positive equilibria of system (5). In the theorems of this section, we focus on the case $\mathbf{x}^* > \mathbf{0}$ since the case $\mathbf{x}^* < \mathbf{0}$ can be examined by changing the signs of c_1, c_2, \dots, c_N .

Theorem 3 *Assume that σ is a C^2 function. Let \mathbf{r} and A be the vector and the matrix defined by (7). Suppose that A is nonsingular and $\mathbf{x}^* = -A^{-1}\mathbf{r} > \mathbf{0}$. Then system (5) has a unique branch of positive equilibria bifurcating from the origin as increasing ε through $\varepsilon = 0$. The bifurcation is stable if $s(\text{diag}(\mathbf{x}^*)A) < 0$ and is unstable if $s(\text{diag}(\mathbf{x}^*)A) > 0$.*

Proof By Theorem 1, the map ξ^ν has a unique branch of positive equilibria written in the form $\hat{\mathbf{x}}(\varepsilon) = \varepsilon\mathbf{x}^* + O(\varepsilon^2)$. It is obvious that all of $\hat{\mathbf{x}}, \xi(\hat{\mathbf{x}}), \dots, \xi^{\nu-1}(\hat{\mathbf{x}})$ are positive equilibria of ξ^ν bifurcating from the origin. However, it is ensured that $\hat{\mathbf{x}}, \xi(\hat{\mathbf{x}}), \dots, \xi^{\nu-1}(\hat{\mathbf{x}})$ are identical since a branch of positive equilibria of ξ^ν bifurcating from the origin is unique. This implies that $\hat{\mathbf{x}}$ is a positive equilibrium of the map ξ , i.e., system (5). The other statements follow from Theorem 2. \square

In the rest of this section, we consider the sign of $s(\text{diag}(\mathbf{x}^*)A)$. To derive the following results, a certain property of the integers n_1, n_2, \dots, n_N plays an important role. Two integers are said to be *coprime* if their greatest common divisor is 1. A set of integers is said to be *pairwise coprime* if every couple of different integers in this set is coprime.

Lemma 3 *Suppose that $M = (m_{ij})$ is an $n \times n$ matrix satisfying $P_\pi M P_\pi^{-1} = M$. If n_i and n_j are coprime for some disjoint $i, j \in \{1, 2, \dots, N\}$, then there exists a constant μ such that $m_{[i,k][j,l]} = \mu$ for all $k \in \{1, 2, \dots, n_i\}$ and $l \in \{1, 2, \dots, n_j\}$.*

Proof Since π has the cycles visiting cyclically all elements of $\{[i, 1], [i, 2], \dots, [i, n_i]\}$ and $\{[j, 1], [j, 2], \dots, [j, n_j]\}$, respectively, it is sufficient to show that for every integer Δ there exists an integer k such that

$$m_{\pi^k((i,1)\pi^{k+\Delta}(j,1))} = m_{[i,1][j,1]}.$$

Let Δ be an arbitrary integer. Then there exists an integer s such that $\pi^{s+\Delta}([j, 1]) = [j, 1]$. Since n_i and n_j are coprime, $\{n_j, 2n_j, \dots, n_in_j\}$ is a complete system of incongruent residues of mod n_i (e.g., see [9, Theorem 56]). Therefore, there exists an integer t such that $\pi^{tn_j+s}([i, 1]) = [i, 1]$. For $k = tn_j + s$, the desired equation is satisfied as follows:

$$\begin{aligned} m_{\pi^k((i,1)\pi^{k+\Delta}(j,1))} &= m_{\pi^{tn_j+s}((i,1)\pi^{tn_j+s+\Delta}(j,1))} \\ &= m_{[i,1]\pi^{tn_j}([j,1])} \\ &= m_{[i,1][j,1]}. \end{aligned}$$

□

For an $n \times n$ matrix M , we denote by M_{ij} the $n_i \times n_j$ submatrix of M with $\{[i, 1], [i, 2], \dots, [i, n_i]\}$ and $\{[j, 1], [j, 2], \dots, [j, n_j]\}$ as the sets of row and column indices, respectively. Write an $n_i \times n_j$ matrix M_{ij} (possibly $i = j$) in partitioned form

$$M_{ij} = \begin{pmatrix} m_{[i,1][j,1]} & \mathbf{q}_1[M_{ij}]^\top \\ \mathbf{q}_2[M_{ij}] & Q[M_{ij}] \end{pmatrix}.$$

Then we obtain the following lemma.

Lemma 4 *Assume that $\{n_1, n_2, \dots, n_N\}$ is pairwise coprime. Suppose that $M = (m_{ij})$ is an $n \times n$ matrix satisfying $P_\pi M P_\pi^{-1} = M$. Then the characteristic equation of M is given by*

$$\det \left(\lambda I - \text{diag}(n_1, n_2, \dots, n_N) \bar{M} \right) \prod_{i=1}^N \det \left(\lambda I + \mathbf{q}_2[M_{ii}] \mathbf{1}^\top - Q[M_{ii}] \right) = 0.$$

Proof Define the $n_i \times n_i$ matrix H_i by

$$H_i := \begin{pmatrix} 1 & -\mathbf{1}^\top \\ \mathbf{0} & I \end{pmatrix},$$

which is nonsingular and its inverse is

$$H_i^{-1} = \begin{pmatrix} 1 & \mathbf{1}^\top \\ \mathbf{0} & I \end{pmatrix}.$$

Then $H_i^{-1}M_{ij}H_j$ is equivalent to

$$\begin{aligned}
& \begin{pmatrix} 1 & \mathbf{1}^\top \\ \mathbf{0} & I \end{pmatrix} \begin{pmatrix} m_{[i,1][j,1]} & \mathbf{q}_1[M_{ij}]^\top \\ \mathbf{q}_2[M_{ij}] & Q[M_{ij}] \end{pmatrix} \begin{pmatrix} 1 & -\mathbf{1}^\top \\ \mathbf{0} & I \end{pmatrix} \\
&= \begin{pmatrix} 1 & \mathbf{1}^\top \\ \mathbf{0} & I \end{pmatrix} \begin{pmatrix} m_{[i,1][j,1]} - m_{[i,1][j,1]}\mathbf{1}^\top + \mathbf{q}_1[M_{ij}]^\top \\ \mathbf{q}_2[M_{ij}] & -\mathbf{q}_2[M_{ij}]\mathbf{1}^\top + Q[M_{ij}] \end{pmatrix} \\
&= \begin{pmatrix} m_{[i,1][j,1]} + \mathbf{1}^\top \mathbf{q}_2[M_{ij}] & -m_{[i,1][j,1]}\mathbf{1}^\top + \mathbf{q}_1[M_{ij}]^\top - \mathbf{1}^\top \mathbf{q}_2[M_{ij}]\mathbf{1}^\top + \mathbf{1}^\top Q[M_{ij}] \\ \mathbf{q}_2[M_{ij}] & -\mathbf{q}_2[M_{ij}]\mathbf{1}^\top + Q[M_{ij}] \end{pmatrix} \\
&= \begin{pmatrix} m_{[i,1][j,1]} + \mathbf{1}^\top \mathbf{q}_2[M_{ij}] & \mathbf{0}^\top \\ \mathbf{q}_2[M_{ij}] & -\mathbf{q}_2[M_{ij}]\mathbf{1}^\top + Q[M_{ij}] \end{pmatrix},
\end{aligned}$$

where we used the fact that each column sum of M_{ij} is identical to obtain the last equality. By Lemma 3, if $i \neq j$, then there exists a constant μ_{ij} such that all entries of M_{ij} are equal to μ_{ij} . Thus if $i \neq j$, then

$$H_i^{-1}M_{ij}H_j = \begin{pmatrix} n_i \mu_{ij} & \mathbf{0}^\top \\ \mu_{ij} \mathbf{1} & O \end{pmatrix},$$

where O denotes the zero matrix. We define the block diagonal matrix $H := \text{diag}(H_1, H_2, \dots, H_N)$, whose inverse is $H^{-1} = \text{diag}(H_1^{-1}, H_2^{-1}, \dots, H_N^{-1})$. Then we have

$$H^{-1}HM = \begin{pmatrix} \begin{array}{cc|cc|ccc} \gamma_1 & \mathbf{0}^\top & n_1 \mu_{12} & \mathbf{0}^\top & \cdots & n_1 \mu_{1N} & \mathbf{0}^\top \\ \mathbf{q}_2(M_{11}) & \Gamma_1 & \mu_{12} \mathbf{1} & O & \cdots & \mu_{1N} \mathbf{1} & O \\ \hline n_2 \mu_{21} & \mathbf{0}^\top & \gamma_2 & \mathbf{0}^\top & \cdots & n_2 \mu_{2N} & \mathbf{0}^\top \\ \mu_{21} \mathbf{1} & O & \mathbf{q}_2(M_{22}) & \Gamma_2 & \cdots & \mu_{2N} \mathbf{1} & O \\ \hline \vdots & \vdots & \vdots & \vdots & & \vdots & \vdots \\ \hline n_N \mu_{N1} & \mathbf{0}^\top & n_N \mu_{N2} & \mathbf{0}^\top & \cdots & \gamma_N & \mathbf{0}^\top \\ \mu_{N1} \mathbf{1} & O & \mu_{N2} \mathbf{1} & O & \cdots & \mathbf{q}_2(M_{NN}) & \Gamma_N \end{array} \end{pmatrix},$$

where $\gamma_i := m_{[i,1][i,1]} + \mathbf{1}^\top \mathbf{q}_2[M_{ii}]$ and $\Gamma_i := -\mathbf{q}_2[M_{ii}]\mathbf{1}^\top + Q[M_{ii}]$. Thus it is straightforward to show that $\det(\lambda I - H^{-1}MH)$ is equivalent to

$$\det(\lambda I - \text{diag}(n_1, n_2, \dots, n_N)\bar{M}) \prod_{i=1}^N \det(\lambda I + \mathbf{q}_2[M_{ii}]\mathbf{1}^\top - Q[M_{ii}])$$

where the fact that

$$\begin{pmatrix} \gamma_1 & n_1 \mu_{12} & \cdots & n_1 \mu_{1N} \\ n_2 \mu_{21} & \gamma_2 & \cdots & n_2 \mu_{2N} \\ \vdots & \vdots & & \vdots \\ n_N \mu_{N1} & n_N \mu_{N2} & \cdots & \gamma_N \end{pmatrix} = \text{diag}(n_1, n_2, \dots, n_N)\bar{M}$$

is used. Thus we obtain the desired form of the characteristic equation of M . \square

Lemma 4 with $N = 1$ shows that the characteristic equation of M_{ii} is equivalent to

$$\det(\lambda I - n_i \bar{m}_{ii}) \det(\lambda I + \mathbf{q}_2[M_{ii}]\mathbf{1}^\top - Q[M_{ii}]) = 0.$$

Therefore, $s(M_{ii}) < 0$ (resp. $s(M_{ii}) > 0$) if and only if both $s(Q[M_{ii}] - \mathbf{q}_2[M_{ii}]\mathbf{1}^\top) < 0$ and $\bar{m}_{ii} < 0$ (resp. either $s(Q[M_{ii}] - \mathbf{q}_2[M_{ii}]\mathbf{1}^\top) > 0$ or $\bar{m}_{ii} > 0$).

The following theorem shows that the stability of $\text{diag}(\mathbf{x}^*)A$ can be evaluated by the stability of some matrices whose sizes are smaller than that of $\text{diag}(\mathbf{x}^*)A$.

Theorem 4 *Assume that $\{n_1, n_2, \dots, n_N\}$ is pairwise coprime. Let \mathbf{r} and A be the vector and the matrix defined by (7). Suppose that A is nonsingular, $\mathbf{x}^* = -A^{-1}\mathbf{r} > \mathbf{0}$, and $\bar{a}_{ii} < 0$, $i = 1, 2, \dots, N$. Then $s(\text{diag}(\mathbf{x}^*)A) < 0$ if and only if all of $s(\text{diag}(T\mathbf{x}^*)\bar{A})$ and $s(A_{ii})$, $i = 1, 2, \dots, N$, are negative, and $s(\text{diag}(\mathbf{x}^*)A) > 0$ if and only if some of $s(\text{diag}(T\mathbf{x}^*)\bar{A})$ and $s(A_{ii})$, $i = 1, 2, \dots, N$, are positive.*

Proof Since $\text{diag}(\mathbf{x}^*)A$ satisfies $P_\pi \text{diag}(\mathbf{x}^*)A P_\pi^{-1} = \text{diag}(\mathbf{x}^*)P_\pi A P_\pi^{-1} = \text{diag}(\mathbf{x}^*)A$, we can apply Lemma 4 to $\text{diag}(\mathbf{x}^*)A$. Then the characteristic equation of $\text{diag}(\mathbf{x}^*)A$ is equivalent to

$$\begin{aligned} & \det(\lambda I - \text{diag}(n_1, n_2, \dots, n_N) \overline{\text{diag}(\mathbf{x}^*)A}) \\ & \quad \times \prod_{i=1}^N \det \left(\lambda I + \mathbf{q}_2[(\text{diag}(\mathbf{x}^*)A)_{ii}]\mathbf{1}^\top - Q[(\text{diag}(\mathbf{x}^*)A)_{ii}] \right) \\ & = \det \left(\lambda I - \text{diag}(T\mathbf{x}^*)\bar{A} \right) \prod_{i=1}^N \bar{x}_i^* \det \left(\frac{\lambda}{\bar{x}_i^*} I + \mathbf{q}_2[A_{ii}]\mathbf{1}^\top - Q[A_{ii}] \right) = 0. \end{aligned}$$

This characteristic equation and the remark after Lemma 4 completes the proof. \square

As we shall see in Sect. 8, the assumption that $\{n_1, n_2, \dots, n_N\}$ is pairwise coprime is essential to derive the conclusion of Theorem 4. It is known that the probability that two integers are coprime is $6/\pi^2 \approx 0.6$ (see [9, Theorem 332]). Therefore, if a community is composed of randomly chosen two semelparous species, then the assumption of Theorem 4 is satisfied with the probability $6/\pi^2$. However, if the number of species is large, the probability becomes very small. A natural situation that Theorem 4 can apply might be found when we consider evolution of lifespans. Since consecutive integers are coprime, Theorem 4 is applicable if n_1, n_2, \dots, n_N are consecutive integers. This situation might happen if we consider an interaction among allied species that are produced by gradual evolution of lifespans.

7 Interpretation of Stability Conditions

7.1 The Sign of \bar{a}_{ii}

By definition, we obtain

$$\begin{aligned} \bar{a}_{ii} = \frac{\nu}{n_i^2} & \left(b_{[i,1][i,1]} + b_{[i,1][i,2]}s_{[i,1]} + \cdots + b_{[i,1][i,n_i]}s_{[i,1]}s_{[i,2]} \cdots s_{[i,n_i-1]} \right. \\ & + b_{[i,2][i,1]} + b_{[i,2][i,2]}s_{[i,1]} + \cdots + b_{[i,2][i,n_i]}s_{[i,1]}s_{[i,2]} \cdots s_{[i,n_i-1]} \\ & \left. + \cdots + b_{[i,n_i][i,1]} + b_{[i,n_i][i,2]}s_{[i,1]} + \cdots + b_{[i,n_i][i,n_i]}s_{[i,1]}s_{[i,2]} \cdots s_{[i,n_i-1]} \right). \end{aligned}$$

Since only the entries of the diagonal block B_{ii} of the matrix B appear in this form, \bar{a}_{ii} represents a gross effect of conspecific density dependence within species i at low population sizes. Thus the assumption $\bar{a}_{ii} < 0$ implies density-dependent self-inhibition in species i at low population sizes. On the other hand, the inequality $\bar{a}_{ii} > 0$ implies positive density dependence, i.e., Allee effect, in species i . Note that even if $\bar{a}_{ii} < 0$, some $b_{[i,j][i,k]}$, $j, k \in \{1, 2, \dots, n_i\}$, could be positive. Therefore, $\bar{a}_{ii} < 0$ does not simply imply that all interaction within species i are competitive.

7.2 The Sign of $s(A_{ii})$

Suppose that $N = 1$ and A is nonsingular. Then $n_1 = n$. Choose $c_1 = 1$. Then Lemma 2 shows that $x_1^* = x_2^* = \cdots = x_{n_1}^* = -\frac{1}{n_1 \bar{a}_{11}}$. Because of this property, if $\bar{a}_{11} < 0$ then $\mathbf{x}^* > \mathbf{0}$ and the sign of $s(\text{diag}(\mathbf{x}^*)A)$ is equivalent to that of $s(A)$. Therefore, under the assumption $\bar{a}_{11} < 0$, system (5) with $N = 1$ has a branch of positive equilibria bifurcating from the origin as increasing \mathcal{R}_0^1 through $\mathcal{R}_0^1 = 1$ and the bifurcation is stable (resp. unstable) if $s(A) < 0$ (resp. $s(A) > 0$). An application of this result to multi-species cases shows that, under the assumption $\bar{a}_{ii} < 0$, $i = 1, 2, \dots, N$, $s(A_{ii}) < 0$ implies that each single-species subsystem has a stable bifurcation of positive equilibria when all species are isolated from each other.

If all interactions within species i are competitive, i.e., $b_{[i,j][i,k]} < 0$ for every $j, k \in \{1, 2, \dots, n_i\}$, then $s(A_{ii}) < 0$ implies that, within species i , competition is more severe within than between age-classes. In fact, since the matrix A_{ii} is circulant, its eigenvalues are

$$\lambda_k = \sum_{j=0}^{n_i-1} \kappa_j e^{\frac{2\pi\sqrt{-1}}{n_i}jk} = \kappa_0 + \sum_{j=1}^{n_i-1} \kappa_j e^{\frac{2\pi\sqrt{-1}}{n_i}jk}, \quad k = 0, 1, \dots, n_i - 1,$$

where $\sqrt{-1}$ denotes the imaginary unit and $(\kappa_0, \kappa_1, \dots, \kappa_{n_i-1})$ is the first row of the matrix A_{ii} , i.e.,

$$\begin{aligned}\kappa_0 &:= \frac{\nu}{n_i} \left(b_{[i,1][i,1]} + b_{[i,2][i,2]}s_{[i,1]} + \dots + b_{[i,n_i][i,n_i]}s_{[i,1]}s_{[i,2]} \dots s_{[i,n_i-1]} \right) \\ \kappa_1 &:= \frac{\nu}{n_i} \left(b_{[i,n_i][i,1]} + b_{[i,1][i,2]}s_{[i,1]} + \dots + b_{[i,n_i-1][i,n_i]}s_{[i,1]}s_{[i,2]} \dots s_{[i,n_i-1]} \right) \\ &\vdots \\ \kappa_{n_i-1} &:= \frac{\nu}{n_i} \left(b_{[i,2][i,1]} + b_{[i,3][i,2]}s_{[i,1]} + \dots + b_{[i,1][i,n_i]}s_{[i,1]}s_{[i,2]} \dots s_{[i,n_i-1]} \right).\end{aligned}$$

By definition, $s(A_{ii}) < 0$ if and only if $\Re \lambda_k < 0$ for all $k = 0, 1, \dots, n_i - 1$. These inequalities clearly hold if competition between age-classes is weak, i.e., all $b_{[i,j][i,k]}$, $j \neq k$, are sufficiently small since $\kappa_0 < 0$ holds when all interaction within species i are competitive and κ_0 is independent of $b_{[i,j][i,k]}$, $j \neq k$. The same conclusion is obtained in [5] and its Table 1 gives exact stability criteria for $n_i = 2, 3, \dots, 6$.

7.3 The Sign of $s(\text{Diag}(T\mathbf{x}^*)\bar{A})$

We shall show that if $s(\text{diag}(T\mathbf{x}^*)\bar{A}) < 0$ (resp. $s(\text{diag}(T\mathbf{x}^*)\bar{A}) > 0$), then the N -species community in system (5) is evaluated as stable (resp. unstable) when each species is assumed to be fixed at a certain age-distribution. Define the vector \mathbf{d}_i , $i = 1, 2, \dots, N$, by $\mathbf{d}_i = (1, s_{[i,1]}, \dots, s_{[i,1]}s_{[i,2]} \dots s_{[i,n_i-1]})^\top$. Then \mathbf{d}_i is an eigenvector of the matrix

$$L_i = \begin{pmatrix} 0 & 0 \dots & 0 & \frac{1}{s_{[i,1]}s_{[i,2]} \dots s_{[i,n_i-1]}} \\ s_{[i,1]} & 0 \dots & 0 & 0 \\ \vdots & \vdots & \vdots & \vdots \\ 0 & 0 \dots & s_{[i,n_i-1]} & 0 \end{pmatrix}$$

associated with its dominant eigenvalue 1. This matrix is a Leslie matrix for a semelparous population whose basic reproduction number is 1. Let H be the plane spanned by \mathbf{d}_i , $i = 1, 2, \dots, N$. Then since each \mathbf{d}_i is an eigenvector of L_i , the plane H is invariant under the linearized system of (5) at the origin when $\varepsilon = 0$. Suppose that \mathbf{u}_k is on the plane H . Then each species i has the age-distribution parallel to \mathbf{d}_i at time k . Define $\mathbf{w}_k = (w_{1,k}, w_{2,k}, \dots, w_{N,k})^\top$ by $\mathbf{w}_k := TD^{-1}\mathbf{u}_k$. The i -th component of \mathbf{w}_k denotes a weighted total population size of species i at time k . Since \mathbf{u}_k is on the plane H , we have

$$u_{[i,1],k} = \frac{u_{[i,2],k}}{s_{[i,1]}} = \dots = \frac{u_{[i,n_i],k}}{s_{[i,1]}s_{[i,2]} \dots s_{[i,n_i-1]}} = \frac{w_{i,k}}{n_i}, \quad i = 1, 2, \dots, N.$$

By Eq.(5), the weighted total population size of species i at time $k + 1$ is given by

$$w_{i,k+1} = h_i(\varepsilon, \mathbf{w}_k)w_{i,k},$$

where

$$h_i(\varepsilon, \mathbf{w}_k) := \frac{1}{n_i} \left(\sigma_{[i,1]}(\mathbf{u}_k) + \sigma_{[i,2]}(\mathbf{u}_k) + \cdots + e^{\frac{c_i n_i}{v} \varepsilon} \sigma_{[i,n_i]}(\mathbf{u}_k) \right).$$

Since \mathbf{u}_{k+1} might not be on the plane H , \mathbf{w}_{k+2} is not given by iterating this Kolmogorov difference equation. However, it is used to estimate the average effect of species interactions when each species i has the age-distribution parallel to \mathbf{d}_i . In fact, we obtain

$$\frac{\partial h_i}{\partial \varepsilon}(0, \mathbf{0}) = \frac{c_i}{v}, \quad \frac{\partial h_i}{\partial w_j}(0, \mathbf{0}) = \frac{\bar{a}_{ij}}{v},$$

which shows that the species interactions can be modeled by the N -dimensional Lotka-Volterra equation

$$v \frac{dy_i}{dt} = y_i \left(c_i + \sum_{j=1}^N \bar{a}_{ij} y_j \right), \quad i = 1, 2, \dots, N$$

as long as $\varepsilon > 0$ is very small and each species i has the age-distribution parallel to \mathbf{d}_i . In this unstructured model, the N species coexist (resp. cannot coexist) stably at a positive equilibrium if $s(\text{diag}(T\mathbf{x}^*)\bar{A}) < 0$ (resp. $s(\text{diag}(T\mathbf{x}^*)\bar{A}) > 0$). Therefore, roughly speaking, Theorem 4 shows that the unstructured model derived above under the assumption that each species i has the fixed age-distribution parallel to \mathbf{d}_i correctly evaluates the stability of bifurcations in system (5) if all species have stable dynamics when they are isolated from each other (i.e., $s(A_{ii}) < 0$, $i = 1, 2, \dots, N$) and $\{n_1, n_2, \dots, n_N\}$ is pairwise coprime.

8 Examples of Instability

Theorem 4 shows that, under the condition that $\{n_1, n_2, \dots, n_N\}$ is pairwise coprime, $\bar{a}_{ii} < 0$, $i = 1, 2, \dots, N$, and $\mathbf{x}^* = -A^{-1}\mathbf{r} > \mathbf{0}$, the stability problem of the positive equilibrium of (5) bifurcating from the origin is reduced to that of $N + 1$ matrices, A_{ii} , $i = 1, 2, \dots, N$, and $\text{diag}(T\mathbf{x}^*)\bar{A}$. Since their sizes are usually much smaller than that of $\text{diag}(\mathbf{x}^*)A$, this reduction is useful. However, if $\{n_1, n_2, \dots, n_N\}$ is not pairwise coprime, this simple reduction does not work. This section focuses on this

point. We shall show that system (5) can possess an unstable branch of positive equilibria even if all of A_{ii} , $i = 1, 2, \dots, N$, and $\text{diag}(T\mathbf{x}^*)\bar{A}$ are stable.

To this end, we consider the case where $N = 2$ and $n_1 = n_2 = 2$. Then n_1 and n_2 are not coprime and their least common multiple is $\nu = 2$. The vector \mathbf{r} and the matrix A given by (7) can be rewritten as

$$\mathbf{r} = \begin{pmatrix} c_1 \\ c_1 \\ c_2 \\ c_2 \end{pmatrix}, \quad A = \begin{pmatrix} -k_1 & -k_2 & -\alpha_1 & -\alpha_2 \\ -k_2 & -k_1 & -\alpha_2 & -\alpha_1 \\ -\alpha_3 & -\alpha_4 & -k_3 & -k_4 \\ -\alpha_4 & -\alpha_3 & -k_4 & -k_3 \end{pmatrix},$$

where every constant is assumed to be positive. Then $\bar{a}_{11} = -\frac{k_1+k_2}{2} < 0$ and $\bar{a}_{22} = -\frac{k_3+k_4}{2} < 0$ are satisfied.

Suppose that A is nonsingular. Then the equation $\mathbf{r} + A\mathbf{x} = \mathbf{0}$ has a unique solution \mathbf{x}^* . Note that we can control the sign of \mathbf{x}^* by choosing suitable signs of c_1 and c_2 . By Lemma 2, \mathbf{x}^* is written as $(\frac{w_1}{2}, \frac{w_1}{2}, \frac{w_2}{2}, \frac{w_2}{2})^\top$, where $(w_1, w_2)^\top = T\mathbf{x}^*$. We shall show that $\text{diag}(\mathbf{x}^*)A$ can be destabilized under the following assumption:

$$(A): \quad A_{11} = \begin{pmatrix} -k_1 & -k_2 \\ -k_2 & -k_1 \end{pmatrix}, \quad A_{22} = \begin{pmatrix} -k_3 & -k_4 \\ -k_4 & -k_3 \end{pmatrix},$$

and $\text{diag}(T\mathbf{x}^*)\bar{A} = \begin{pmatrix} -\frac{k_1+k_2}{2}w_1 & -\frac{\alpha_1+\alpha_2}{2}w_1 \\ -\frac{\alpha_3+\alpha_4}{2}w_2 & -\frac{k_3+k_4}{2}w_2 \end{pmatrix}$ are stable.

Since $\text{tr } A_{11} < 0$ and $\text{tr } A_{22} < 0$ are satisfied, the stability conditions for A_{11} and A_{22} are reduced to

$$k_1 > k_2 \quad \text{and} \quad k_3 > k_4. \quad (8)$$

By the definition of A , the inequality implies that in each species competition between age-classes are more severe than within age-classes. Furthermore, since $\text{tr } \text{diag}(T\mathbf{x}^*)\bar{A} < 0$ is satisfied, the condition for $s(\text{diag}(T\mathbf{x}^*)\bar{A}) < 0$ is reduced to

$$(k_1 + k_2)(k_3 + k_4) > (\alpha_1 + \alpha_2)(\alpha_3 + \alpha_4), \quad (9)$$

which shows that competition between species is more severe than within species (see Sect. 7.3). In order to destabilize $\text{diag}(\mathbf{x}^*)A$, let us examine the characteristic polynomial $\det(\lambda I - \text{diag}(\mathbf{x}^*)A)$, which is reduced to

$$\det(\lambda I - \text{diag}(T\mathbf{x}^*)\bar{A}) \det(\lambda I - \tilde{A}),$$

where

$$\tilde{A} := \frac{1}{2} \text{diag}(T\mathbf{x}^*) \begin{pmatrix} -k_1 + k_2 & -\alpha_1 + \alpha_2 \\ -\alpha_3 + \alpha_4 & -k_3 + k_4 \end{pmatrix}.$$

Since $\text{diag}(T\mathbf{x}^*)\bar{A}$ is assumed to be stable, $\text{diag}(\mathbf{x}^*)A$ can be destabilized if \tilde{A} can be destabilized. By Eq. (8), $\text{tr } \tilde{A} < 0$ holds, but the sign of $\det \tilde{A}$ is not determined.

Therefore, if the set of parameters satisfying (8), (9) and

$$(k_1 - k_2)(k_3 - k_4) < (\alpha_1 - \alpha_2)(\alpha_3 - \alpha_4) \tag{10}$$

is nonempty, then system (5) can possess an unstable branch of a positive equilibria even if A_{11} , A_{22} and $\text{diag}(T\mathbf{x}^*)\bar{A}$ are stable.

Figures 1 and 2 give such examples. In the examples, it is assumed the nonlinearity is of Beverton-Holt type

$$\sigma_i(\mathbf{u}) = \frac{1}{1 + (B\mathbf{u})_i}, \quad i = 1, 2, \dots, n.$$

To construct an example of system (5) satisfying (8), (9), and (10), we need to determine s_1, s_2, c_1, c_2 , and B . We suppose that $s_1 = s_2 = 0.9$ and $c_1 = c_2 = 1$ (i.e., $\mathcal{R}_0^1 = \mathcal{R}_0^2 = e^\varepsilon$). Furthermore, we suppose that

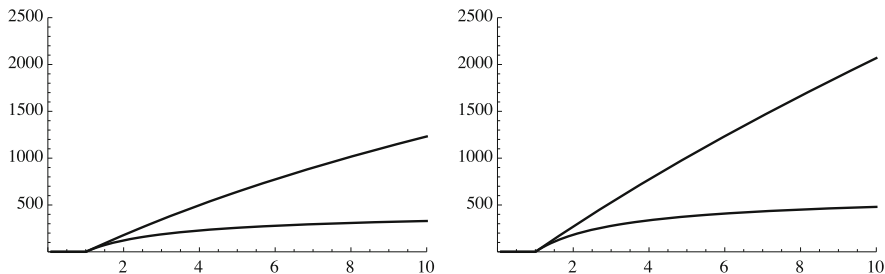


Fig. 1 Bifurcation diagram for system (5) with $N = 2$ and $n_1 = n_2 = 2$. In both panels, the horizontal axes denote e^ε ($= \mathcal{R}_0^1 = \mathcal{R}_0^2$) and the vertical axes denote $u_1 + u_2$ and $u_3 + u_4$ in the left and right panels, respectively. The parameters are $s_1 = s_3 = 0.9, c_1 = c_2 = 1, k_1 = 4K, k_2 = 3K, k_3 = 3K, k_4 = 2K, \alpha_1 = 3K, \alpha_2 = K, \alpha_3 = 3K, \alpha_4 = K$, where $K = 10^{-3}$

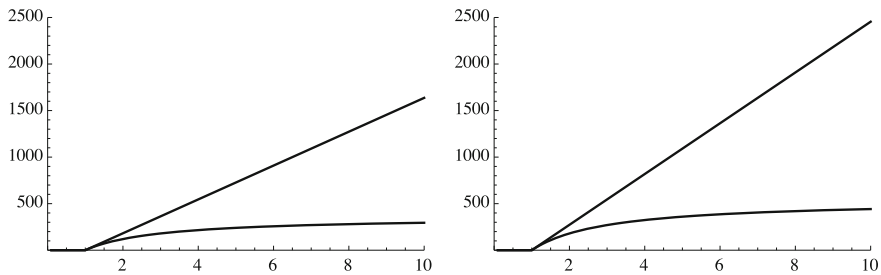


Fig. 2 Bifurcation diagram for system (5) with $N = 2$ and $n_1 = n_2 = 2$. In both panels, the horizontal axes denote e^ε ($= \mathcal{R}_0^1 = \mathcal{R}_0^2$) and the vertical axes denote $u_1 + u_2$ and $u_3 + u_4$ in the left and right panels, respectively. The parameters are $s_1 = s_3 = 0.9, c_1 = c_2 = 1, k_1 = 4K, k_2 = 3K, k_3 = 3K, k_4 = 2K, \alpha_1 = K, \alpha_2 = 3K, \alpha_3 = K, \alpha_4 = 3K$, where $K = 10^{-3}$

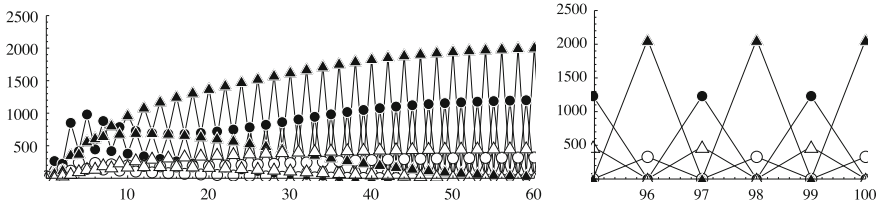


Fig. 3 Dynamics of system (5) with $N = 2$ and $n_1 = n_2 = 2$. The parameters are $s_1 = s_3 = 0.9$, $c_1 = c_2 = 1$, $e^\varepsilon = 10$ ($= \mathcal{R}_0^1 = \mathcal{R}_0^2$), $k_1 = 4K$, $k_2 = 3K$, $k_3 = 3K$, $k_4 = 2K$, $\alpha_1 = 3K$, $\alpha_2 = K$, $\alpha_3 = 3K$, $\alpha_4 = K$, where $K = 10^{-3}$. The horizontal axes denote time k . The black and white circles denote $u_{1,k}$ and $u_{2,k}$, respectively. The black and white triangles denote $u_{3,k}$ and $u_{4,k}$, respectively. The left panel shows the transient dynamics and the right panel shows the ultimate dynamics

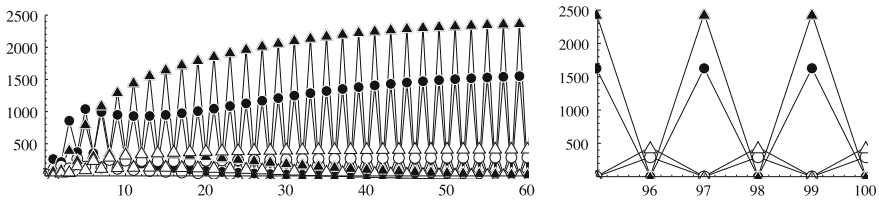


Fig. 4 Dynamics of system (5) with $N = 2$ and $n_1 = n_2 = 2$. The parameters are $s_1 = s_3 = 0.9$, $c_1 = c_2 = 1$, $e^\varepsilon = 10$ ($= \mathcal{R}_0^1 = \mathcal{R}_0^2$), $k_1 = 4K$, $k_2 = 3K$, $k_3 = 3K$, $k_4 = 2K$, $\alpha_1 = K$, $\alpha_2 = 3K$, $\alpha_3 = K$, $\alpha_4 = 3K$, where $K = 10^{-3}$. The horizontal axes denote time k . The black and white circles denote $u_{1,k}$ and $u_{2,k}$, respectively. The black and white triangles denote $u_{3,k}$ and $u_{4,k}$, respectively. The left panel shows the transient dynamics and the right panel shows the ultimate dynamics

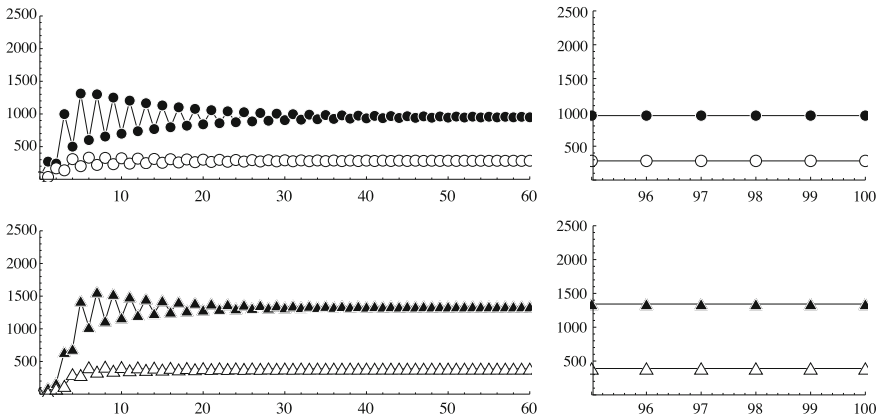


Fig. 5 Dynamics of system (5) with $N = 2$ and $n_1 = n_2 = 2$ when two species are isolated, i.e., $\alpha_1 = \alpha_2 = \alpha_3 = \alpha_4 = 0$. All other parameters are the same as in Figs. 3 and 4. The horizontal axes denote time k . The black and white circles denote $u_{1,k}$ and $u_{2,k}$, respectively. The black and white triangles denote $u_{3,k}$ and $u_{4,k}$, respectively. The left panels show the transient dynamics and the right panels shows the ultimate dynamics

$$B = \frac{1}{2} \begin{pmatrix} -k_1 & -\frac{k_2}{s_1} & -\alpha_1 & -\frac{\alpha_2}{s_3} \\ -k_2 & -\frac{k_1}{s_1} & -\alpha_2 & -\frac{\alpha_1}{s_3} \\ -\alpha_3 & -\frac{\alpha_4}{s_1} & -k_3 & -\frac{k_4}{s_3} \\ -\alpha_4 & -\frac{\alpha_3}{s_1} & -k_4 & -\frac{k_3}{s_3} \end{pmatrix}.$$

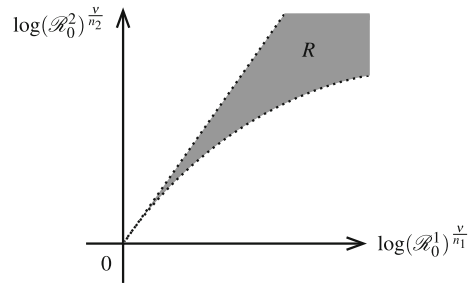
Then Eq. (7) yields the matrix A shown above. The values of $\alpha_1, \dots, \alpha_4, k_1, \dots, k_4$ are given in the figure legends of Figs. 1 and 2. They show bifurcation diagrams for system (5). In each bifurcation diagram, system (5) does not have a stable positive equilibrium bifurcating from the origin and is settled in a 2-cycle. In Fig. 1, $\alpha_1 > \alpha_2$ and $\alpha_3 > \alpha_4$ are satisfied. This condition implies that two species compete severely between the same level of age-classes. As shown in Fig. 3, this case leads to coexistence of two species with temporal segregation between the same level of age-classes. In Fig. 2, $\alpha_1 < \alpha_2$ and $\alpha_3 < \alpha_4$ are satisfied. This condition implies that two species compete severely between the different level of age-classes. As shown in Fig. 4, this case leads to coexistence of two species with temporal segregation between the different level of age-classes. Figure 5 shows the dynamics of species 1 and 2, respectively, when they are isolated from each other. All parameters are the same as in Figs. 3 and 4 except $\alpha_1, \dots, \alpha_4$. Thus this numerical simulation shows that age-specific species competition is an essential factor causing the population cycles observed in Figs. 3 and 4.

9 Concluding Remarks

This paper studied the dynamics of a multi-species semelparous population model, which is described by coupling multiple nonlinear semelparous Leslie matrix models. We focused on bifurcations of the extinction equilibrium and proposed a simple method of evaluating the stability of a branch of positive equilibria bifurcating from the extinction equilibrium. The method reduces the bifurcation problem into a stability problem of Lotka-Volterra equations. Using this reduction method, we found a population cycle in a competitive system composed of two biennial species. The mechanism of producing this population cycle is new in the sense that it is produced without either severe between-age-class competition or predator-prey like species interaction. It is a future problem to classify all possible dynamics of such a competitive system.

Our study provides a mathematical basis to some preceding studies. In [13, 14], the Lotka-Volterra equation with A and \mathbf{r} given by (7) is derived from system (1). Our study was motivated by the study by Diekmann and van Gils [7], who derived a Lotka-Volterra equation with cyclic symmetry from a nonlinear semelparous Leslie matrix model. The three preceding studies do not show how the derived Lotka-Volterra equation reflects the dynamical behavior of the original single- or multi-species semelparous population model. However our study revealed that the derived Lotka-Volterra equation can be used to examine the stability of a branch of positive

Fig. 6 The $(\log(\mathcal{R}_0^1)^{\frac{v}{n_1}}, \log(\mathcal{R}_0^2)^{\frac{v}{n_2}})$ -parameter plane with an open parameter region R with a cusp at the origin



equilibria of the original model bifurcating the extinction equilibrium. Furthermore, our result rediscovered the result by Cushing and Henson [5], who obtained a condition for stable bifurcation of positive equilibria in nonlinear semelparous Leslie matrix models (see Sect. 7.2).

In our bifurcation study, we focused on a bifurcation that occurs at the critical point $\mathcal{R}_0^1 = \mathcal{R}_0^2 = \dots = \mathcal{R}_0^N = 1$. In order to avoid treating a multi-parameter bifurcation problem, we perturb the parameters $\mathcal{R}_0^1, \mathcal{R}_0^2, \dots, \mathcal{R}_0^N$ with maintaining the relation (4). This approach is practically sufficient to examine the dynamics of system (1) with the parameter around the critical point. However there could exist exceptional cases that our approach is unable to treat. Figure 6 shows the $(\log(\mathcal{R}_0^1)^{\frac{v}{n_1}}, \log(\mathcal{R}_0^2)^{\frac{v}{n_2}})$ -parameter plane with an open parameter region R with a cusp at the origin. It is clear that any neighborhood of the origin intersects with R . However, for any vector \mathbf{c} , there exists a constant $\varepsilon_0 > 0$ such that $\varepsilon \mathbf{c} \notin R$ for all $\varepsilon \in (0, \varepsilon_0)$. This implies that our approach cannot detect the dynamics in such a region. Therefore, in order to reveal the dynamics of system (1) in a neighborhood of the origin of the parameter plane, we need to consider a multi-parameter bifurcation problem. Whether or not the region that our approach cannot detect exists remains an open question.

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