

AGE-STRUCTURED LOTKA–VOLTERRA EQUATIONS FOR MULTIPLE SEMELPAROUS POPULATIONS*

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Abstract. This paper derives a Lotka–Volterra equation with a certain symmetry from a coupled nonlinear Leslie matrix model for interacting semelparous species. The global analysis focuses on the special case where the system is composed of two species, one species having two age-classes and the other species having a single age-class. This analysis almost completely describes its global dynamics and provides examples that the age-structure changes the destiny of the system.

Key words. Leslie matrix, Lotka–Volterra equation, semelparity

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1. Introduction. One of the most important and typical models for interacting species is the Lotka–Volterra equation

$$(1.1) \quad \dot{x}_i = x_i(r_i + (A\mathbf{x})_i), \quad i = 1, 2, \dots, n,$$

where r_i , $i = 1, 2, \dots, n$, denotes the intrinsic growth rate of species i and $A = (a_{ij})$ is the interaction matrix determining the interaction between species. The variable x_i , $i = 1, 2, \dots, n$, indicates the population density of species i . From the fact that each species is represented by a single variable, it is clear that each species is assumed to consist of identical individuals. Classical approaches to community ecology have been developed on such models lacking population structure, although this simplification largely contributes mathematical tractability to models and helps to develop mathematical theories for community ecology [14, 17, 20].

The purpose of this paper is to relax this fundamental assumption of classical ecological models by taking into account a certain age-structure. This relaxation allows us to consider much more complex species interactions, such as due to a complex life history involving an abrupt ontogenetic change in an individual's morphology, physiology, and behavior (see [24, 25] for complex life histories). For example, in amphibians and insects, the habitat shifts occur at metamorphosis. The habitat shifts could change their resources, enemies, competitors, cooperators, etc. In many cases, even the sign of interaction between focal species changes. Our model framework can study such a complex species interaction due to a complex life history if metamorphosis is age-specific. Furthermore, since each species could have a distinct length of age-structure (i.e., generations could be asynchronous between species), the effect of distinct generation times between species on the population dynamics can also be explored.

The effect of age-structures on multispecies dynamics has previously been considered by several authors (e.g., see [1, 2, 3, 6, 8, 22, 23]). However, since the introduction

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of age-specific interactions usually leads to a formidable model equation, its mathematical treatment is restricted to the local stability analyses of equilibria. One of our main purposes is to overcome this problem and provide a model equation whose global dynamics is mathematically accessible. To this end, we advance the work by Diekmann and van Gils [10], who obtained a Lotka–Volterra equation with a cyclic matrix A and $\mathbf{r} = (1, 1, \dots, 1)^\top$ as a singular limit of a nonlinear Leslie matrix model for a single semelparous species (i.e, individuals are assumed to reproduce only once in their life). We advance their work and obtain a Lotka–Volterra equation for interacting age-structured species. Since a vast amount of knowledge on Lotka–Volterra equations is extremely beneficial in analyzing the model equation, we can mathematically obtain some results on the global dynamics, which clearly show the effect of age-structures on multispecies dynamics.

This paper is organized as follows. In section 2, we construct a model equation for interacting age-structured populations. This model is constructed by a coupled nonlinear Leslie matrix model. In section 3, we derive an age-structured Lotka–Volterra equation from the coupled nonlinear Leslie matrix model constructed in section 2. In section 4, we show that the age-structured Lotka–Volterra equation has a forward invariant plane, on which the system behaves as an unstructured model. In section 5, we consider three simple cases of the general age-structured Lotka–Volterra equations. The systems consist of two species: the first species has two age-classes, and the second species has a single age-class. Depending on types of age-specific interactions, the types of species interactions are classified into competitive, cooperative, and predator-prey cases. The analysis completely describes the global dynamics of these cases except in the case where the parameters satisfy certain algebraic equations. The results show that an age-structure can definitely alters the destiny of systems. The final section includes some concluding remarks.

2. Nonlinear coupled Leslie matrix models. Consider the population dynamics of N interacting species. We assume that species i consists of n_i age-classes. The population vector for species i is denoted by \mathbf{y}_i , where the j th component of \mathbf{y}_i indicates the population density of age-class j of species i . For convenience, we write

$$\mathbf{y} := \begin{pmatrix} \mathbf{y}_1 \\ \mathbf{y}_2 \\ \vdots \\ \mathbf{y}_N \end{pmatrix}.$$

Therefore the $(n_1 + \dots + n_{i-1} + j)$ th component of \mathbf{y} corresponds to the population density of age-class j of species i . Our state space is $\mathbb{R}_+^n := \{\mathbf{y} \in \mathbb{R}^n : y_i \geq 0 \text{ for all } i\}$, where $n := n_1 + n_2 + \dots + n_N$. Let $B = (b_{ij})$ be an $n \times n$ matrix. Define $(B\mathbf{y})_j^i := (B\mathbf{y})_{n_1 + \dots + n_{i-1} + j}$. The superscript and the subscript of $(B\mathbf{y})_j^i$ correspond to the indices of species and age-classes, respectively. For notational convenience, define $L[l_1, l_2, \dots, l_{n_i}]$ by

$$L[l_1, l_2, \dots, l_{n_i}] := \begin{pmatrix} 0 & 0 & \cdots & 0 & l_{n_i} \\ l_1 & 0 & \cdots & 0 & 0 \\ 0 & l_2 & \cdots & 0 & 0 \\ \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & \cdots & l_{n_i-1} & 0 \end{pmatrix}.$$

This is a special case of the Leslie matrix and reflects the age-structure of species i ; i.e., only the last age-class is reproductive.

Using this notation, we can express our coupled nonlinear Leslie matrix model as follows:

$$(2.1) \quad \mathbf{y}_i(t+1) = L[\sigma_1^i((B\mathbf{y}(t))_1^i), \sigma_2^i((B\mathbf{y}(t))_2^i), \dots, \sigma_{n_i}^i((B\mathbf{y}(t))_{n_i}^i)]\mathbf{y}_i(t), \quad i = 1, 2, \dots, N,$$

where the function σ_j^i , $j \neq n_i$, defines the survival probability of age-class j of species i and the function $\sigma_{n_i}^i$ defines the number of offspring reproduced by a single individual of species i belonging to the last age-class n_i . As the sign pattern of L reflects, it is assumed that only the last age-class is reproductive. This assumption is appropriate for semelparous organisms such as many insects and Pacific salmon. Note that if $n_i = 1$, then species i can also be seen as an iteroparous species.

Each σ_j^i is a function of the weighted total population density $(B\mathbf{y})_j^i$, where the $n \times n$ matrix $B = (b_{ij})$ may have negative entries. The matrix B determines types of age-specific species interaction. Divide the matrix B into N^2 blocks as follows:

$$B = \begin{pmatrix} B_{11} & \cdots & B_{1N} \\ \vdots & & \vdots \\ B_{N1} & \cdots & B_{NN} \end{pmatrix},$$

where the diagonal block B_{ii} is an $n_i \times n_i$ matrix. The diagonal and the off-diagonal blocks determine types of intra- and interspecific interactions, respectively. The diagonal and the off-diagonal entries of B_{ii} determine types of conspecific intra- and interclass interactions, respectively. We assume that each σ_j^i satisfies the following:

(H1) $\sigma_j^i : \mathbb{R} \rightarrow \mathbb{R}$ is continuously differentiable.

(H2) $\frac{d\sigma_j^i(x)}{dx} > 0$ for all i, j .

(H3) $\sigma_j^i(0) > 0$ and $\frac{1}{\sigma_j^i(0)} \frac{d\sigma_j^i(x)}{dx} \Big|_{x=0} = 1$ for all i, j .

Assumption (H1) is assumed to obtain ordinary differential equations from the discrete-time system (2.1). By (H2), $b_{ij} < 0$ (resp., $b_{ij} > 0$) implies that the contribution of y_i to the population growth is suppressed (resp., enhanced) by y_j . Condition (H3) is assumed to normalize the functions σ_j^i . For instance, $\sigma_j^i(x) = c_j^i \exp(x)$ with $c_j^i > 0$ satisfies (H1)–(H3).

3. Lotka–Volterra equations. Diekmann and van Gils [10] show that the Lotka–Volterra equation (1.1) with a cyclic matrix A and $\mathbf{r} = (1, 1, \dots, 1)^\top$ appears as a singular limit of (2.1) if $N = 1$. In this section, we advance their approach and obtain a Lotka–Volterra equation for interacting multiple age-structured populations.

In the derivation of Lotka–Volterra equations, basic reproduction numbers play an important role. The basic reproduction number for species i is given by $\mathcal{R}_0^i = \sigma_1^i(0)\sigma_2^i(0) \cdots \sigma_{n_i}^i(0)$ (e.g., see [3, 7]). Let m be the least common multiple of n_1, n_2, \dots, n_N . Then species i experiences m/n_i generations within m time steps. Hence, $(\mathcal{R}_0^i)^{m/n_i}$ denotes the expected number of descendants of species i per individual per m time steps when density-dependent effect is ignored. Define $s_1, s_2, \dots, s_N \in \mathbb{R}$ and $h > 0$ by

$$h = \frac{\ln(\mathcal{R}_0^1)^{m/n_1}}{s_1} = \frac{\ln(\mathcal{R}_0^2)^{m/n_2}}{s_2} = \cdots = \frac{\ln(\mathcal{R}_0^N)^{m/n_N}}{s_N} > 0.$$

Note that s_1, s_2, \dots, s_N and h are not uniquely determined, but they clearly exist. Let λ_i be the dominant real eigenvalue of $L[\sigma_1^i(0), \sigma_2^i(0), \dots, \sigma_{n_i}^i(0)]$. Then $\lambda_i =$

$(\mathcal{R}_0^i)^{1/n_i} = e^{s_i h/m}$. Let $\mathbf{u}_i = (u_1^i, u_2^i, \dots, u_{n_i}^i)^\top$ be a right eigenvector associated with λ_i (the Perron–Frobenius theorem ensures that \mathbf{u}_i is positive). We normalize it by assuming $|\mathbf{u}_i| = u_1^i + u_2^i + \dots + u_{n_i}^i = 1$. Then define the new vector $\mathbf{x}_i = (1/h)D_i^{-1}\mathbf{y}_i$, where D_i is the diagonal matrix $D_i = \text{diag}\{u_1^i, u_2^i, \dots, u_{n_i}^i\}$. For convenience, we write

$$\mathbf{x} := \begin{pmatrix} \mathbf{x}_1 \\ \mathbf{x}_2 \\ \vdots \\ \mathbf{x}_N \end{pmatrix}.$$

Hence $\mathbf{x} = (1/h)D^{-1}\mathbf{y}$, where $D = \text{diag}\{D_1, D_2, \dots, D_N\}$. Using these new vectors, (2.1) is expressed as follows:

$$\begin{aligned} \mathbf{x}_i(t+1) &= L \left[\sigma_1^i((B\mathbf{y}(t))_1^i) \frac{u_1^i}{u_2^i}, \sigma_2^i((B\mathbf{y}(t))_2^i) \frac{u_2^i}{u_3^i}, \dots, \sigma_{n_i}^i((B\mathbf{y}(t))_{n_i}^i) \frac{u_{n_i}^i}{u_1^i} \right] \mathbf{x}_i(t) \\ &= \lambda_i L \left[\frac{\sigma_1^i(h(K\mathbf{x}(t))_1^i)}{\sigma_1^i(0)}, \frac{\sigma_2^i(h(K\mathbf{x}(t))_2^i)}{\sigma_2^i(0)}, \dots, \frac{\sigma_{n_i}^i(h(K\mathbf{x}(t))_{n_i}^i)}{\sigma_{n_i}^i(0)} \right] \mathbf{x}_i(t), \end{aligned}$$

where $K = BD$. Note that K has the same sign pattern as B . We notice that $\mathbf{x}(t+j) \rightarrow P^j\mathbf{x}(t)$ as $h \rightarrow 0$, where $P = \text{diag}\{P_1, P_2, \dots, P_N\}$, whose diagonal block is the $n_i \times n_i$ permutation matrix $P_i = L[1, 1, \dots, 1]$. Because of the cyclicity of L , the system is diagonalized in the following sense:

$$(3.1) \quad \mathbf{x}_i(t+m) = e^{s_i h} \text{diag} \left\{ \prod_{j=0}^{m-1} \frac{\sigma_{j+1}^i(h(K\mathbf{x}(t+j))_{j+1}^i)}{\sigma_{j+1}^i(0)}, \prod_{j=0}^{m-1} \frac{\sigma_{j+2}^i(h(K\mathbf{x}(t+j))_{j+2}^i)}{\sigma_{j+2}^i(0)}, \dots, \prod_{j=0}^{m-1} \frac{\sigma_{j+n_i}^i(h(K\mathbf{x}(t+j))_{j+n_i}^i)}{\sigma_{j+n_i}^i(0)} \right\} \mathbf{x}_i(t),$$

where $\lambda^m = e^{s_i h}$ is used and the subscripts of σ_j^i and $(K\mathbf{x})_j^i$ are counted modulo n_i . From this equation, we can find

$$\begin{aligned} \frac{\mathbf{x}_i(t+m) - \mathbf{x}_i(t)}{h} &\rightarrow \text{diag} \left\{ s_i + \sum_{j=0}^{m-1} (KP^j\mathbf{x}(t))_{j+1}^i, \right. \\ &\quad \left. s_i + \sum_{j=0}^{m-1} (KP^j\mathbf{x}(t))_{j+2}^i, \right. \\ &\quad \left. \dots, s_i + \sum_{j=0}^{m-1} (KP^j\mathbf{x}(t))_{j+n_i}^i \right\} \mathbf{x}_i(t) \end{aligned}$$

as $h \rightarrow 0$, where (H3) is used and the subscript of $(KP^j\mathbf{x})_l^i$ is counted modulo n_i . Therefore this leads to the “age-structured” Lotka–Volterra equation (1.1) with

$$(3.2a) \quad \mathbf{r} = (s_1, \dots, s_1, s_2, \dots, s_2, \dots, s_N, \dots, s_N)^\top,$$

$$(3.2b) \quad A = K + P^{-1}KP + (P^{-1})^2KP^2 + \dots + (P^{-1})^{m-1}KP^{m-1}.$$

Note $P^{-1} = P^\top$ since P is a permutation matrix. Since this Lotka–Volterra equation is derived through the time- m map (3.1), its dynamics corresponds to that of (2.1) observed every m th unit of time. Therefore every equilibrium point of (1.1) corresponds to a periodic orbit of (2.1) whose period is a factor of m . More precisely, since $\mathbf{x}(t+j) \rightarrow P^j \mathbf{x}(t)$ as $h \rightarrow 0$, a point \mathbf{x} of (1.1) satisfying $\mathbf{x} = P^k \mathbf{x}$ and $\mathbf{x} \neq P^j \mathbf{x}$, $0 < j < k$, corresponds to a k -cycle of (2.1).

Species i has potentially n_i cohorts, and each of them is represented by one of the components of \mathbf{x}_i . If the unit of time is a year, then each component of \mathbf{x}_i corresponds to the population density of a year-class of species i . Note that the year-class of an individual is defined by its birth year, although the age-class of an individual is defined by its age.

4. Invariance and unstructured systems. Define I_1, I_2, \dots, I_N by

$$\begin{aligned} I_1 &= \{1, 2, \dots, n_1\}, \\ I_2 &= \{n_1 + 1, n_1 + 2, \dots, n_1 + n_2\}, \\ &\vdots \\ I_N &= \{n_1 + n_2 + \dots + n_{N-1} + 1, n_1 + n_2 + \dots + n_{N-1} + 2, \dots, n\}. \end{aligned}$$

Define M_i , $i = 1, 2, \dots, N$, by

$$M_i = \{\mathbf{x} \in \mathbb{R}_+^n : x_j = x_k \text{ for all } j, k \in I_i\},$$

on which the class distribution of species i is evenly distributed. This section investigates the dynamics on $M := \bigcap_{i=1}^N M_i$.

PROPOSITION 4.1. *The set M is forward invariant under (1.1) with (3.2). On M , the total population density of species i , $X_i := \sum_{j \in I_i} x_j$, $i = 1, 2, \dots, N$, is governed by the Lotka–Volterra equation*

$$(4.1) \quad \dot{X}_i = X_i(s_i + (\bar{A}\mathbf{X})_i), \quad i = 1, 2, \dots, N,$$

where $\mathbf{X} = (X_1, X_2, \dots, X_N)^\top$ and $\bar{A} = (\bar{a}_{ij})$ with $\bar{a}_{ij} = \sum_{k \in I_i} \sum_{l \in I_j} a_{kl} / (n_i n_j)$.

Proof. To prove the first statement, we show that $\mathbf{x}(0) \in M$ implies $\mathbf{x}(t) \in M$ for all $t \geq 0$. Define p_j^i by

$$p_j^i = \frac{x_j}{\sum_{k \in I_i} x_k}, \quad j \in I_i.$$

This gives the class distribution of species i . Without loss of generality, we consider only the case $\mathbf{x}(0) \in M$ with $\mathbf{x}_i(0) \neq \mathbf{0}$ for all $i \in \{1, 2, \dots, N\}$. If $\mathbf{x} \in M$, then we have

$$p_j^i = \frac{1}{n_i}, \quad j \in I_i.$$

We shall show that p_j^i does not change in time. The time derivative of p_j^i is given by

$$\begin{aligned} \dot{p}_j^i &= p_j^i \left\{ r_j + (A\mathbf{x})_j - \sum_{k \in I_i} p_k^i (r_k + (A\mathbf{x})_k) \right\}, \quad j \in I_i \\ (4.2) \quad &= p_j^i \left\{ (A\mathbf{x})_j - \sum_{k \in I_i} p_k^i (A\mathbf{x})_k \right\}, \end{aligned}$$

where we used the fact that $r_k = s_i$ for all $k \in I_i$. It is clear that $P\mathbf{x} = \mathbf{x}$ if $\mathbf{x} \in M$ since the permutation matrix P exchanges the indices only between conspecific classes (i.e., $P = \text{diag}\{P_1, P_2, \dots, P_N\}$). Furthermore, for every j and k , we have $((P^{-1})^k \mathbf{x})_j = x_{\tau^k(j)}$, where $\tau(j)$ is the permutation defined by P . Using these properties, we can show that the inside of the braces of (4.2) at $\mathbf{x} \in M$ becomes

$$\begin{aligned} & (K\mathbf{x})_j + (P^{-1}K P\mathbf{x})_j + \dots + ((P^{-1})^{m-1}K P^{m-1}\mathbf{x})_j \\ & - \frac{1}{n_i} \sum_{k \in I_i} \{ (K\mathbf{x})_k + (P^{-1}K P\mathbf{x})_k + \dots + ((P^{-1})^{m-1}K P^{m-1}\mathbf{x})_k \} \\ & = (K\mathbf{x})_j + (P^{-1}K\mathbf{x})_j + \dots + ((P^{-1})^{m-1}K\mathbf{x})_j \\ & - \frac{1}{n_i} \sum_{k \in I_i} \{ (K\mathbf{x})_k + (P^{-1}K\mathbf{x})_k + \dots + ((P^{-1})^{m-1}K\mathbf{x})_k \} \\ & = (K\mathbf{x})_j + (K\mathbf{x})_{\tau(j)} + \dots + (K\mathbf{x})_{\tau^{m-1}(j)} \\ & - \frac{1}{n_i} \sum_{k \in I_i} \{ (K\mathbf{x})_k + (K\mathbf{x})_{\tau(k)} + \dots + (K\mathbf{x})_{\tau^{m-1}(k)} \} = 0. \end{aligned}$$

Therefore, $\dot{p}_j^i(t) = 0$ holds for all $t \geq 0$ whenever $\mathbf{x}(0) = M$. This implies that M is forward invariant.

It is straightforward to prove the second statement. On the set M , $x_k = X_i/n_i$ holds for all $k \in I_i$. Therefore, if we use the fact that $r_k = s_i$ for all $k \in I_i$, then the time derivative of X_i is given by

$$\dot{X}_i = \sum_{k \in I_i} x_k(r_k + (A\mathbf{x})_k) = X_i \left(s_i + \sum_{j=1}^N \frac{\sum_{k \in I_i} \sum_{l \in I_j} a_{kl}}{n_i n_j} X_j \right).$$

This completes the proof. \square

The invariance of M is strongly related to the dynamics of the original coupled Leslie matrix model (2.1). The linearization of (2.1) at the origin leads to N linear Leslie matrix models

$$\mathbf{y}_i(t + 1) = L[\sigma_1^i(0), \sigma_2^i(0), \dots, \sigma_{n_i}^i(0)]\mathbf{y}_i(t), \quad i = 1, 2, \dots, N,$$

which are mutually decoupled. Although none of them has a stable age-distribution since L is imprimitive, they have a stationary age-distribution. The stationary age-distribution of species i is given by the right (normalized) eigenvector \mathbf{u}_i of $L[\sigma_1^i(0), \sigma_2^i(0), \dots, \sigma_{n_i}^i(0)]$ associated with the dominant eigenvalue $\lambda_i = (\mathcal{R}_0^i)^{\frac{1}{n_i}}$, namely $\mathbf{u}_i = \mathbf{w}_i/|\mathbf{w}_i|$, where

$$\begin{aligned} \mathbf{w}_i &= \left(1, \frac{\sigma_1^i(0)}{\lambda_i}, \dots, \frac{\sigma_1^i(0)\sigma_2^i(0) \cdots \sigma_{n_i-1}^i(0)}{\lambda_i^{n_i-1}} \right)^\top, \\ |\mathbf{w}_i| &= 1 + \frac{\sigma_1^i(0)}{\lambda_i} + \dots + \frac{\sigma_1^i(0)\sigma_2^i(0) \cdots \sigma_{n_i-1}^i(0)}{\lambda_i^{n_i-1}}. \end{aligned}$$

The distribution \mathbf{u}_i corresponds to the vector $\frac{1}{h}(1, 1, \dots, 1)^\top$ in the coordinate system of the Lotka–Volterra equation (1.1) with (3.2) since $\mathbf{x} = (1/h)D^{-1}\mathbf{y}$. Therefore the invariance of M implies that the age-distribution \mathbf{u}_i is still stationary in the Lotka–Volterra equation (1.1) with (3.2). Furthermore, (4.1) can be interpreted as a model

derived under the assumption that the age-distribution of each species is fixed at the stationary age-distribution. In this sense, (4.1) gives the population dynamics ignoring age-structure.

Since $\mathbf{x} = P\mathbf{x}$ if and only if $\mathbf{x} \in M$, every equilibrium $\mathbf{x} \in M$ (resp., $\mathbf{x} \notin M$) of (1.1) with (3.2) corresponds to an equilibrium (resp., a k -cycle, $k > 1$) of (2.1).

5. Three-dimensional Lotka–Volterra equations for two species. In this section, we study a simple case of (1.1) with (3.2) and show that an age-structure is influential to the population dynamics. We assume that our system is composed of two species, the first species having two age-classes and the second species having a single age-class, i.e., $N = 2$, $n_1 = 2$, $n_2 = 1$, $I_1 = \{1, 2\}$, and $I_2 = \{3\}$. In this case, the system is three-dimensional, i.e., $n = 3$. We further assume that all interactions among conspecific individuals are competitive. That is, we assume that the matrix B for (2.1) has the following sign pattern:

$$B = \begin{pmatrix} - & - & * \\ - & - & * \\ * & * & - \end{pmatrix},$$

where $*$ indicates an arbitrary sign.

The age-specific interaction matrix A defined by (3.2) can be derived as follows. Since $N = 2$, $n_1 = 2$, and $n_2 = 1$, the permutation matrix P is given by

$$P = \begin{pmatrix} 0 & 1 & 0 \\ 1 & 0 & 0 \\ 0 & 0 & 1 \end{pmatrix}.$$

Since the least common multiple of n_1 and n_2 is $m = 2$, the age-specific interaction matrix A is

$$A = K + P^{-1}KP = \begin{pmatrix} k_{11} + k_{22} & k_{12} + k_{21} & k_{13} + k_{23} \\ k_{21} + k_{12} & k_{22} + k_{11} & k_{23} + k_{13} \\ k_{31} + k_{32} & k_{32} + k_{31} & k_{33} + k_{33} \end{pmatrix},$$

where $K = BD$ or

$$K = \begin{pmatrix} b_{11} \frac{\sqrt{\sigma_2^1(0)}}{\sqrt{\sigma_1^1(0) + \sqrt{\sigma_2^1(0)}}} & b_{12} \frac{\sqrt{\sigma_1^1(0)}}{\sqrt{\sigma_1^1(0) + \sqrt{\sigma_2^1(0)}}} & b_{13} \\ b_{21} \frac{\sqrt{\sigma_2^1(0)}}{\sqrt{\sigma_1^1(0) + \sqrt{\sigma_2^1(0)}}} & b_{22} \frac{\sqrt{\sigma_1^1(0)}}{\sqrt{\sigma_1^1(0) + \sqrt{\sigma_2^1(0)}}} & b_{23} \\ b_{31} \frac{\sqrt{\sigma_2^1(0)}}{\sqrt{\sigma_1^1(0) + \sqrt{\sigma_2^1(0)}}} & b_{32} \frac{\sqrt{\sigma_1^1(0)}}{\sqrt{\sigma_1^1(0) + \sqrt{\sigma_2^1(0)}}} & b_{33} \end{pmatrix}.$$

For convenience, we write

$$(5.1) \quad A = \begin{pmatrix} -a & -b & \alpha \\ -b & -a & \alpha \\ \beta & \beta & -c \end{pmatrix},$$

where $a, b, c > 0$ and $\alpha, \beta \in \mathbb{R}$ because of the sign pattern of B .

By Proposition 4.1, the set $M = \{\mathbf{x} \in \mathbb{R}_+^3 : x_1 = x_2\}$ is forward invariant. On this set, the system is reduced to the following two-dimensional Lotka–Volterra equation:

$$(5.2) \quad \begin{cases} \dot{X}_1 &= X_1(s_1 - \frac{a+b}{2}X_1 + \alpha X_2), \\ \dot{X}_2 &= X_2(s_2 + \beta X_1 - cX_2). \end{cases}$$

By definition, α and β are given by

$$\alpha = b_{13} + b_{23}, \quad \beta = \frac{b_{31}\sqrt{\sigma_2^1(0)} + b_{32}\sqrt{\sigma_1^1(0)}}{\sqrt{\sigma_1^1(0)} + \sqrt{\sigma_2^1(0)}}.$$

Note that β is the inner product of $(b_{31}, b_{32})^\top$ and \mathbf{u}_1 , which is the stationary age-distribution of species 1 predicted by the linear Leslie matrix model (see section 4). Both α and β depend on two age-specific interactions. The parameter α , which represents the influence of species 2 on species 1, is solely determined by how each age-class of species 1 is affected by species 2. For example, if species 2 strongly reduces (resp., enhances) the activity of one of the age-classes of species 1, then α becomes negative (resp., positive). On the other hand, the parameter β , which represents the influence of species 1 on species 2, depends also on the life cycle strategy of species 1. We see that the abundant age-class of species 1 at the stationary age-distribution has a dominant effect on the sign of β . For example, if species 1 is of mass production (i.e., high fecundity and high mortality, $\sigma_1^1(0) < \sigma_2^1(0)$), then the first age-class of species 1 is more influential to species 2.

In the rest of this section, we focus on the following three typical cases: competition $(\alpha, \beta) = (-, -)$, $(s_1, s_2) = (+, +)$; cooperation $(\alpha, \beta) = (+, +)$, $(s_1, s_2) = (+, +)$; predator-prey interaction $(\alpha, \beta) = (-, +)$, $(s_1, s_2) = (+, -)$ or $(\alpha, \beta) = (+, -)$, $(s_1, s_2) = (-, +)$. By the analysis of these cases, we show how the introduction of an age-structure alters the dynamical behavior of interacting species.

5.1. Competitive species interactions. Consider the case $(\alpha, \beta) = (-, -)$, $(s_1, s_2) = (+, +)$. In this case, we can prove the following theorem.

THEOREM 5.1. *Suppose that all equilibria are isolated. Then every forward orbit in \mathbb{R}_+^3 converges to an equilibrium point.*

Proof. Since $\dot{x}_i < 0$ for all i whenever $x_1 + x_2 + x_3$ is sufficiently large, every solution is bounded for $t \geq 0$. Let $D = \text{diag}\{-\beta, -\beta, -\alpha\}$. Then DA is symmetric. Therefore $V(\mathbf{x}) = -2\mathbf{x} \cdot D\mathbf{r} - \mathbf{x} \cdot D\mathbf{A}\mathbf{x}$ is a Liapunov function [18]. In fact,

$$\dot{V}(\mathbf{x}) = -2\beta \sum_{i=1}^2 x_i (r_i + (\mathbf{A}\mathbf{x})_i)^2 - 2\alpha x_3 (r_3 + (\mathbf{A}\mathbf{x})_3)^2 \leq 0$$

holds for all $\mathbf{x} \in \mathbb{R}_+^3$. Since $\dot{V}(\mathbf{x}) = 0$ if and only if \mathbf{x} is an equilibrium point, every ω -limit set is composed of equilibrium points. Since every ω -limit set is connected, every forward orbit converges to an equilibrium point. \square

This theorem shows that the local stability analysis of equilibrium points reveals the global dynamics of the system.

The system has at most $2^3 = 8$ isolated equilibrium points: $\mathbf{0} = (0, 0, 0)$, F_1 , F_2 , F_3 , F_{12} , F_{13} , F_{23} , and F_{123} , where the subscript of F denotes the indices of the positive entries. As mentioned in section 2, some of these equilibria do not correspond to an equilibrium of the original coupled Leslie matrix model (2.1). We see that $\mathbf{0}$, F_3 , F_{12} , and F_{123} correspond to an equilibrium and $\{F_1, F_2\}$ and $\{F_{13}, F_{23}\}$ correspond to 2-cycles of (2.1). Note that on the cycles one of the classes of species 1 is always missing. More precisely, the cycles corresponding to $\{F_1, F_2\}$ and $\{F_{13}, F_{23}\}$ have the following sign patterns, respectively:

$$\begin{pmatrix} + \\ 0 \\ 0 \end{pmatrix} \rightarrow \begin{pmatrix} 0 \\ + \\ 0 \end{pmatrix} \rightarrow \begin{pmatrix} + \\ 0 \\ 0 \end{pmatrix}, \quad \begin{pmatrix} + \\ 0 \\ + \end{pmatrix} \rightarrow \begin{pmatrix} 0 \\ + \\ + \end{pmatrix} \rightarrow \begin{pmatrix} + \\ 0 \\ + \end{pmatrix}.$$

TABLE 5.1

The external eigenvalues of the boundary equilibrium points (x_1, x_2, x_3) satisfying $x_1 \geq x_2$ for the competitive case.

	\dot{x}_1/x_1	\dot{x}_2/x_2	\dot{x}_3/x_3
$\mathbf{0}$	$s_1 > 0$	$s_1 > 0$	$s_2 > 0$
F_1	0	$\frac{s_1}{a}\xi_1$	$\frac{s_2}{a}\xi_3$
F_3	$\frac{s_1}{c}\xi_2$	$\frac{s_1}{c}\xi_2$	0
F_{12}	0	0	$\frac{2s_2}{a+b}(\xi_3 - \frac{\xi_1}{2})$
F_{13}	0	$\xi_1 x_1$	0

Since the vector field is symmetric to M , we focus on the equilibrium points \mathbf{x} satisfying $x_1 \geq x_2$, i.e., $\mathbf{0}$, F_1 , F_3 , F_{12} , F_{13} , and F_{123} . Define ξ_1 , ξ_2 , and ξ_3 by

$$\xi_1 = a - b, \quad \xi_2 = c + \alpha \frac{s_2}{s_1}, \quad \xi_3 = a + \beta \frac{s_1}{s_2}.$$

Then the external eigenvalues of $\mathbf{0}$, F_1 , F_3 , F_{12} , and F_{13} can be expressed as in Table 5.1. Since the dynamics on the boundary of \mathbb{R}_+^3 is governed by a lower-dimensional Lotka–Volterra equation, it is clear that F_1 and F_3 are always internally asymptotically stable,¹ and F_{1i} , $i = 2, 3$, is internally asymptotically stable if and only if $\dot{x}_1/x_1|_{F_i} > 0$ and $\dot{x}_i/x_i|_{F_i} > 0$. The Jacobi matrix evaluated at $F_{123} = (x_1^*, x_2^*, x_3^*)$ is given by $J = \text{diag}\{x_1^*, x_1^*, x_3^*\}A$. Note that, by symmetry, $x_1^* = x_2^*$ holds. J is stable if and only if $\text{tr}J < 0$, $\det J < 0$, and $M\text{tr}J - \det J < 0$, where M is the sum of the three principal 2×2 minors of J . We have

$$\begin{aligned} \text{tr}J &= -2ax_1^* - cx_3^* < 0, \\ \det J &= -2\xi_1 \det \bar{A}x_1^{*2}x_3^*, \\ M\text{tr}J - \det J &= -2a(a+b)\xi_1x_1^{*3} - 2c(ac - \alpha\beta)x_1^*x_3^{*2} \\ &\quad - 2\{2a(ac - \alpha\beta) + \xi_1\alpha\beta\}x_1^{*2}x_3^*. \end{aligned}$$

It is straightforward to show that $ac - \alpha\beta > 0$ if $\det \bar{A} > 0$ and $\xi_1 > 0$. Therefore J is stable if $\det \bar{A} > 0$ and $\xi_1 > 0$. Conversely, if J is stable, then the Jacobi matrix of (5.2) evaluated at $(2x_1^*, x_3^*)$ must be stable; i.e., $\det \bar{A} > 0$ holds. Finally, $\det J < 0$ with $\det \bar{A} > 0$ implies $\xi_1 > 0$. Consequently, J is stable if and only if $\det \bar{A} > 0$ and $\xi_1 > 0$. Using these results, we can classify the qualitative dynamics into 12 classes if we ignore the critical cases where at least one of $\xi_1 = 0$, $\xi_2 = 0$, $\xi_3 = 0$, and $\xi_3 = \xi_1/2$ is satisfied (see Figure 5.1). In the critical cases, our system has a nonhyperbolic equilibrium. In particular, our system has a continuum of equilibria if $\xi_1 = 0$, $\xi_2 = \xi_3 = 0$, or $\xi_2 = \xi_3 - \xi_1/2 = 0$ holds. In Figure 5.1, typical phase portraits for $\mathbf{x} \neq \mathbf{0}$ are radiationally projected from $\mathbf{0}$ to the simplex $x_1 + x_2 + x_3 = 1$ since all solutions are bounded and the ω -limit set $\omega(\mathbf{x})$ with $\mathbf{x} \neq \mathbf{0}$ does not include $\mathbf{0}$.

Let us compare the dynamics on M with that on $\mathbb{R}_+^3 \setminus M$. As shown in section 4, the dynamics restricted on M shows how the system behaves if the age-structure is ignored. If $\xi_1 > 0$, then every attractor of the full system is located on M . This implies that the system reaches the same point even if the age-structure is incorporated. Therefore, in this case, the age-structure does not alter the asymptotical behavior of the system. On the other hand, if $\xi_1 < 0$, then we can find an attractor on

¹An equilibrium point \mathbf{x}^* of (1.1) is said to be *internally asymptotically stable* if it is asymptotically stable in the subsystem composed of all species $i \in \text{supp}(\mathbf{x}^*)$, where $\text{supp}(\mathbf{x}^*) = \{i : x_i^* > 0\}$.

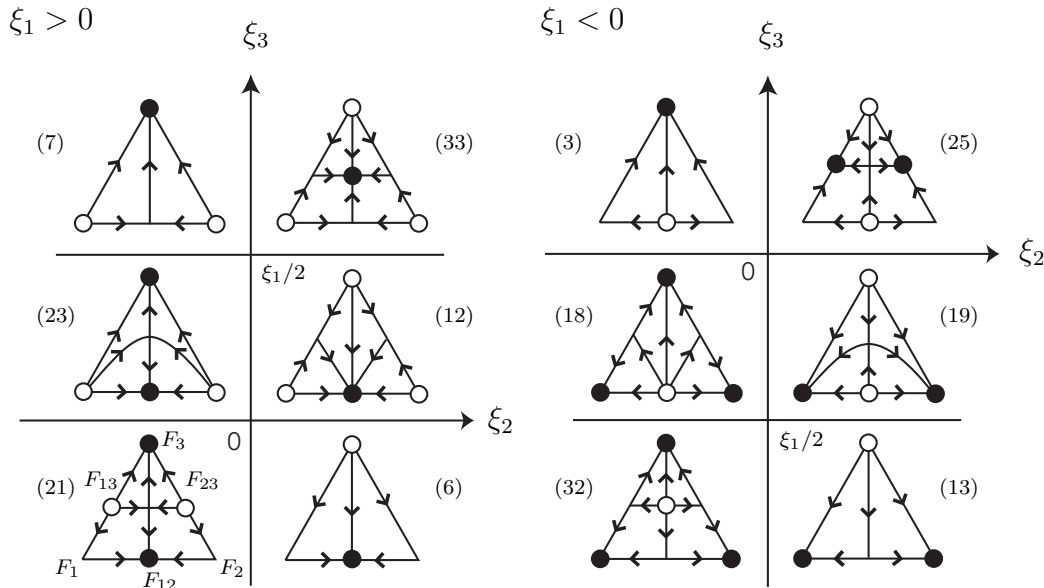


FIG. 5.1. The phase portraits for the competitive case. Each (ξ_2, ξ_3) parameter plane is subdivided into six regions, in which a typical phase portrait is shown. The vertical lines on the phase planes correspond to M . An equilibrium point is represented by a closed dot \bullet if it is asymptotically stable; by an open dot \circ if it is repelling; by an intersection of hyperbolic manifolds if it is a saddle. The numbers represented in the parentheses correspond to Zeeman's classification number [26].

$\mathbb{R}_+^3 \setminus M$. Especially, we find an interesting behavior if $\xi_1/2 < \xi_3 < 0$ is satisfied. If $\xi_1/2 < \xi_3 < 0$ and $\xi_2 < 0$, then the dynamics on M predicts that species 1 is eliminated by species 2, but the full dynamics shows that species 1 could be eliminated depending on initial conditions; i.e., the full system is bistable. If $\xi_1/2 < \xi_3 < 0$ and $\xi_2 > 0$, then the dynamics on M predicts coexistence of the two species, but the full dynamics predicts that species 2 is almost always eliminated by species 1. Therefore, if $\xi_1 < 0$, then the age-structure alters the destiny of the two species. This change of destiny can be interpreted as follows. By definition, $\xi_1 < 0$ implies that intraspecific competition of species 1 is more severe between than within classes. The severe interclass competition leads to competitive exclusion between classes (e.g., see [2, 4, 8, 9, 15, 16, 19]), and this competitive exclusion improves the environment of species 1 since severe interclass competition disappears. Furthermore, this relaxation of severe intraclass competition of species 1 increases its total population density, and this increase makes the environment of species 2 worse. That is, the age-structure of species 1 is deleterious to species 2. This suggests that a competition model without age-structures overestimates the possibility of species coexistence.

5.2. Cooperative species interaction. Consider the case $(\alpha, \beta) = (+, +)$, $(s_1, s_2) = (+, +)$. Then (5.2) is a two-dimensional Lotka–Volterra cooperative system. It is known that each orbit of such a two-dimensional cooperative system converges either to an equilibrium point or to infinity (e.g., see [14, Theorem 3.4.1]). Since $(s_1, s_2) = (+, +)$ is assumed, any positive solution of (5.2) cannot converge to a boundary equilibrium. Therefore, all positive solutions of (5.2) converge to infinity if (5.2) has no positive equilibrium, i.e., $(a + b)c/2 \leq \alpha\beta$. Conversely, if $(a + b)c/2 > \alpha\beta$ is satisfied, then (5.2) has a unique positive equilibrium point, to which all positive

solutions converge (e.g., see [14, Theorem 15.1.1]). The same argument can apply to the cooperative subsystem on the face $x_i = 0$, $i = 1, 2$. That is, all positive solutions of the subsystem converge to infinity (resp., to a positive equilibrium) if $ac \leq \alpha\beta$ (resp., $ac > \alpha\beta$).

In order to characterize not only bounded orbits but also unbounded orbits, we consider the replicator dynamics topologically equivalent to our Lotka–Volterra dynamics. The coordinate transformation $z_0 = 1/(1 + x_1 + x_2 + x_3)$ and $z_i = x_i/(1 + x_1 + x_2 + x_3)$, $i = 1, 2, 3$, proposed in [12] leads to the following replicator equation:

$$(5.3) \quad \dot{z}_i = z_i((\hat{A}\mathbf{z})_i - \mathbf{z} \cdot \hat{A}\mathbf{z}), \quad i = 0, 1, 2, 3,$$

with the payoff matrix

$$\hat{A} = \begin{pmatrix} 0 & 0 & 0 & 0 \\ s_1 & -a & -b & \alpha \\ s_1 & -b & -a & \alpha \\ s_2 & \beta & \beta & -c \end{pmatrix}.$$

This equation is defined on the simplex $S_4 := \{\mathbf{z} \in \mathbb{R}_+^4 : z_0 + z_1 + z_2 + z_3 = 1\}$, and the face $F_\infty := \{\mathbf{z} \in S_4 : z_0 = 0\}$ corresponds to the points at infinity. The replicator equation (5.3) satisfies the following theorem.

THEOREM 5.2. *Suppose that all equilibria are isolated. Then every orbit converges to an equilibrium point.*

Proof. It is known that if \hat{A} is symmetric, then $V(\mathbf{z}) = \mathbf{z} \cdot \hat{A}\mathbf{z}$ is a Liapunov function for (5.3) (see [14, Theorem 7.8.1]). In fact, $\dot{V}(\mathbf{z}) = 2 \sum_{i=1}^4 z_i [(\hat{A}\mathbf{z})_i - \mathbf{z} \cdot \hat{A}\mathbf{z}]^2 \geq 0$ for all $\mathbf{z} \in S_4$. Furthermore, $\dot{V}(\mathbf{z}) = 0$ if and only if \mathbf{z} is an equilibrium point of (5.3). This implies that every ω -limit set is composed of equilibrium points. Since each ω -limit set is connected, every orbit converges to an equilibrium point. Therefore, we shall show that our system is equivalent to (5.3) with a symmetric \hat{A} .

We use the following properties of the replicator equation: (i) the addition of a constant c_j to the j th column of \hat{A} does not change (5.3) on S_4 ; (ii) the transformation $y_i = z_i c_i / \sum_{j=1}^4 z_j c_j$ with $c_j > 0$ leads to (5.3) with the payoff matrix $(a_{ij} c_j^{-1})$ (see also [14, Exercises 7.1.2 and 7.1.3]). These properties can be derived as follows. Let C be a 4×4 matrix whose (i, j) entry is c_j . Then $(\hat{A} + C)\mathbf{z} - \mathbf{z} \cdot (\hat{A} + C)\mathbf{z} = \hat{A}\mathbf{z} - \mathbf{z} \cdot \hat{A}\mathbf{z}$ holds for $\mathbf{z} \in S_4$. Therefore, (5.3) does not change even if \hat{A} is replaced by $\hat{A} + C$. Let $y_i = z_i c_i / \sum_{j=1}^4 z_j c_j$ with $c_j > 0$. Then $\dot{y}_i = (\sum_{j=1}^4 z_j) y_i ((\tilde{A}\mathbf{y})_i - \mathbf{y} \cdot \tilde{A}\mathbf{y})$ with $\tilde{A} = (a_{ij} c_j^{-1})$. Therefore, it has the same phase portrait as (5.3) with the payoff matrix \tilde{A} .

If $s_1 \geq s_2$, then we subtract s_2 from the first column and add $s_1 - s_2 \geq 0$ to the second and the third columns. Then the multiplication of the fourth column by $(\beta + s_1 - s_2)/\alpha$ leads to a symmetric matrix. If $s_1 < s_2$, then we subtract s_1 from the first column and add $s_2 - s_1 > 0$ to the fourth column. Then the multiplication of the second and the third columns by $(\alpha + s_2 - s_1)/\beta$ leads to a symmetric matrix. \square

This theorem shows that the local stability analysis reveals the global dynamics of (5.3).

Equation (5.3) has at most $2^4 - 1 = 15$ isolated equilibrium points. Since (5.3) is symmetric with respect to the plane $z_1 = z_2$, we examine the stability of the isolated equilibrium points (z_0, z_1, z_2, z_3) satisfying $z_1 \geq z_2$, i.e., $F_0, F_1, F_3, F_{01}, F_{03}, F_{12}, F_{13}, F_{012}, F_{013}, F_{123}$, and F_{0123} . Table 5.2 gives their external eigenvalues. By this table,

TABLE 5.2

The external eigenvalues of the boundary equilibrium points (z_0, z_1, z_2, z_3) of (5.3) satisfying $z_1 \geq z_2$.

	\dot{z}_0/z_0	\dot{z}_1/z_1	\dot{z}_2/z_2	\dot{z}_3/z_3
F_0	0	$s_1 > 0$	$s_1 > 0$	$s_2 > 0$
F_1	$a > 0$	0	ξ_1	$a + \beta > 0$
F_3	$c > 0$	$c + \alpha > 0$	$c + \alpha > 0$	0
F_{01}	0	0	$\xi_1 z_1$	$\frac{s_2 \xi_3}{a + s_1} > 0$
F_{12}	$\frac{a+b}{2} > 0$	0	0	$\frac{a+b}{2} + \beta > 0$
F_{03}	0	$\frac{s_1 \xi_2}{c + s_2} > 0$	$\frac{s_1 \xi_2}{c + s_2} > 0$	0
F_{13}	$\frac{ac - \alpha\beta}{a + c + \alpha + \beta}$	0	$\xi_1 z_1$	0
F_{012}	0	0	0	$\frac{(a+b)s_2 + 2s_1\beta}{a+b+2s_1} > 0$
F_{123}	$\frac{(a+b)c - 2\alpha\beta}{a+b+2(c+\alpha+\beta)}$	0	0	0
F_{013}	0	0	$\xi_1 z_1$	0

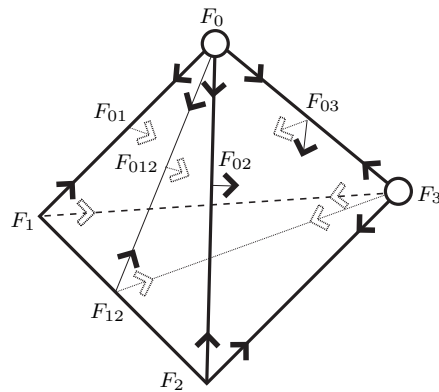


FIG. 5.2. The simplex S_4 with the information about the external eigenvalues of the boundary equilibrium points for (5.3). An equilibrium point is represented by an open dot \circ if it is a repeller.

we can depict the phase portrait given in Figure 5.2. This figure shows that F_{13} , F_{23} , F_{123} , F_{013} , F_{023} , and F_{0123} are only the candidates of the ω -limit sets of positive points. By the property of the original Lotka–Volterra cooperative system, F_{013} and F_{012} are internally asymptotically stable if and only if $ac > \alpha\beta$ and $(a + b)c/2 > \alpha\beta$, respectively. The stability analysis in the previous subsection for the competitive case shows that the Jacobi matrix evaluated at F_{0123} is stable if and only if $\xi_1 > 0$ since $\det \bar{A} > 0$ is necessary for the existence of F_{0123} . Furthermore, it is straightforward to show that F_{123} is linearly stable on the face F_∞ if and only if $\xi_1 > 0$. With this information, we can classify the qualitative dynamics into six classes if we ignore the critical cases where at least one of $\xi_1 = 0$, $\alpha\beta = ac$, and $\alpha\beta = (a + b)c/2$ is satisfied (see Figure 5.3). In the critical cases, our system has a nonhyperbolic equilibrium. In particular, our system has a continuum of equilibria if $\xi_1 = 0$. In Figure 5.3, typical phase portraits for $0 < z_3 < 1$ are radiationally projected from F_3 to the face $z_3 = 0$ since $\omega(\mathbf{z})$ with $0 < z_3 < 1$ includes neither a point on the face $z_3 = 0$ nor the point F_3 .

Let us compare the dynamics on M with that on $\mathbb{R}_+^3 \setminus M$. Similarly to the competitive case, if $\xi_1 > 0$, then every attractor of the full system is located on M , but if $\xi_1 < 0$, then we can find an attractor on $\mathbb{R}_+^3 \setminus M$. Especially, if $\xi_1 < 0$ and

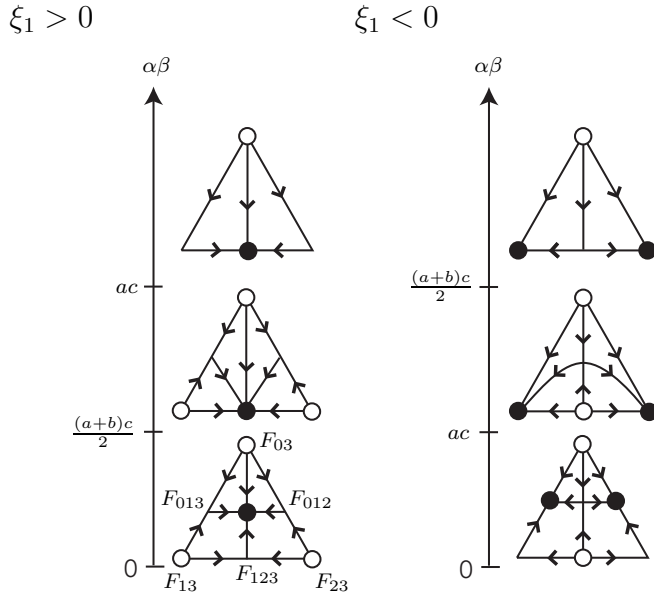


FIG. 5.3. The phase portraits for the cooperative case. Each of the $\alpha\beta$ -axes is subdivided into three intervals, in which a typical phase portrait is shown. The base lines of the triangles correspond to F_∞ . The vertical lines in the phase planes correspond to M . An equilibrium point is represented by a closed dot \bullet if it is asymptotically stable; by an open dot \circ if it is repelling; by an intersection of hyperbolic manifolds if it is a saddle.

$ac < \alpha\beta < (a + b)c/2$, then the dynamics on M does not coincide with that on $\mathbb{R}_+^3 \setminus M$. That is, the unstructured system predicts that two species coexist, but the structured system predicts that the total population densities of the two species grow without limitation. This behavior can be interpreted as follows. If $\xi_1 < 0$, then competitive exclusion between classes of species 1 leads to a better environment for species 1 in the sense that the intraspecific competition is relaxed. This relaxation enhances the total population density of species 1. Therefore species 2 obtains more cooperators, and the unbounded increase of the total population densities follows.

5.3. Predator-prey species interactions. Consider the cases where $(\alpha, \beta) = (-, +)$, $(s_1, s_2) = (+, -)$ or $(\alpha, \beta) = (+, -)$, $(s_1, s_2) = (-, +)$ is fulfilled. In these cases, the interaction between two species is predator-prey: X_1 is a prey and X_2 is a predator if $(\alpha, \beta) = (-, +)$, $(s_1, s_2) = (+, -)$; X_1 is a predator and X_2 is a prey if $(\alpha, \beta) = (+, -)$, $(s_1, s_2) = (-, +)$. The dissipativity is shown as follows.

PROPOSITION 5.3. *The system is dissipative; i.e., there exists a positive number $D > 0$ such that $\limsup_{t \rightarrow \infty} x_i(t) \leq D$ for all $\mathbf{x}(0) \in \mathbb{R}_+^3$.*

Proof. Let $V(\mathbf{x}) = |\beta|x_1 + |\beta|x_2 + |\alpha|x_3$. Then the time derivative of V satisfies

$$\dot{V}(\mathbf{x}) + V(\mathbf{x}) \leq |\beta|x_1(s_1 + 1 - ax_1) + |\beta|x_2(s_1 + 1 - ax_2) + |\alpha|x_3(s_2 + 1 - cx_3).$$

Since there exists a positive number $L > 0$ such that $\dot{V}(\mathbf{x}) + V(\mathbf{x}) < L$ for all $\mathbf{x} \in \mathbb{R}_+^3$, $\limsup_{t \rightarrow \infty} V(\mathbf{x}(t)) \leq L$ holds for all $\mathbf{x}(0) \in \mathbb{R}_+^3$. This implies that our system is dissipative. \square

5.3.1. Prey-predator: $(\alpha, \beta) = (-, +)$, $(s_1, s_2) = (+, -)$. In this case, the system has at most seven isolated equilibrium points, $\mathbf{0}$, F_1 , F_2 , F_{12} , F_{13} , F_{23} , and

F_{123} . Since the vector field is symmetric to M , we focus on the equilibrium points \mathbf{x} satisfying $x_1 \geq x_2$, i.e., $\mathbf{0}$, F_1 , F_{12} , F_{13} , and F_{123} . The external eigenvalues of $\mathbf{0}$, F_1 , F_{12} , and F_{13} are identical to those given in Table 5.1 (F_3 does not exist). Since the dynamics on the boundary of \mathbb{R}_+^3 is governed by a lower-dimensional Lotka–Volterra equation, it is clear that F_1 and F_{13} are always internally asymptotically stable, and F_{12} is internally asymptotically stable if and only if $\dot{x}_1/x_1|_{F_2} > 0$ and $\dot{x}_2/x_2|_{F_1} > 0$. Furthermore, if F_i , $i = 1, 12, 13$, is internally asymptotically stable, then it attracts all points \mathbf{x} satisfying $\text{supp}(\mathbf{x}) = \text{supp}(F_i)$, where $\text{supp}(\mathbf{x}) := \{i : x_i > 0\}$. The stability condition of the Jacobi matrix J given in section 5.1 shows that the Jacobi matrix evaluated at F_{123} is stable if and only if $\xi_1 > 0$ since $\det \bar{A} > 0$. By the linear stability of the equilibrium points, we can classify the system into six classes if we ignore the critical cases where at least one of $\xi_1 = 0$, $\xi_3 = 0$, and $\xi_3 = \xi_1/2$ is satisfied (see Figure 5.4). In the critical cases, our system has a nonhyperbolic equilibrium. In particular, our system has a continuum of equilibria if $\xi_1 = 0$. As given below, the local stability of a fixed point also ensures its global stability.

PROPOSITION 5.4. *For every $\mathbf{x}(0) \in \mathbb{R}_+^3$ with $x_1(0) + x_2(0) > 0$, there exists a positive number $\delta > 0$ such that*

$$\liminf_{t \rightarrow \infty} (x_1(t) + x_2(t)) \geq \delta.$$

Proof. Let $\mathbf{x} \in \mathbb{R}_+^3$ with $x_1 + x_2 > 0$. Since every solution on the x_3 -axis converges to $\mathbf{0}$ and $\dot{x}_1/x_1|_{\mathbf{0}} > 0$, $\dot{x}_2/x_2|_{\mathbf{0}} > 0$, and $\dot{x}_3/x_3|_{\mathbf{0}} < 0$ hold, any solution starting at \mathbf{x} cannot coverage to the hyperbolic equilibrium $\mathbf{0}$. Therefore, if $\omega(\mathbf{x})$ includes a point on the x_3 -axis, it includes a point on the x_3 -axis different from $\mathbf{0}$. But it is impossible since the ω -limit set of any bounded orbit is compact and invariant, although all nonzero points on the x_3 -axis have an unbounded backward orbit. \square

THEOREM 5.5. (i) F_{12} attracts all points $\mathbf{x} \in \mathbb{R}_+^3$ with $x_1 > 0$ and $x_2 > 0$ if $\xi_1 > 0$ and $\xi_3 > \xi_1/2$.

(ii) F_{123} attracts all positive points if $\xi_1 > 0$ and $0 < \xi_3 < \xi_1/2$.

(iii) F_1 (resp., F_2) attracts all points $\mathbf{x} \in \mathbb{R}_+^3$ with $x_1 > x_2$ (resp., $x_1 < x_2$) if $\xi_1 < 0$ and $\xi_3 > 0$.

(iv) F_{13} (resp., F_{23}) attracts all points $\mathbf{x} \in \mathbb{R}_+^3$ with $x_1 > x_2$ (resp., $x_1 < x_2$) and $x_3 > 0$ if $\xi_1 < 0$ and $\xi_3 < 0$.

Proof. Consider cases (i) and (ii). In these cases, the matrix A is VL-stable (see section A.1). In fact, $DA + A^T D$ is negative definite for $D = \text{diag}\{\beta, \beta, -\alpha\}$. The theory of VL-stability leads to statements (i) and (ii).

Consider cases (iii) and (iv). Let $\mathbf{x}(0) \in \mathbb{R}_+^3$ with $x_1(0) > x_2(0)$. If either $x_2(0) = 0$ or $x_3(0) = 0$ holds, then the conclusion is clear since the system is planar. In fact, if $x_3(0) = 0$, then Theorem 5.1 is applicable since the behavior on the face $x_3 = 0$ is independent of the signs of α and β . Therefore, in this case, $\mathbf{x}(t)$ converges to F_1 . If $x_2(0) = 0$, then the above argument of VL-stability is applicable since the principal submatrix of A with respect to the indices 1 and 3 is VL-stable. Therefore, in this case, $\mathbf{x}(t)$ converges to F_1 if $\xi_3 > 0$ and to F_{13} if $\xi_3 < 0$. Assume that $x_2(0) > 0$ and $x_3(0) > 0$. By Propositions 5.3 and 5.4, there exist positive numbers $\delta > 0$ and $D > 0$ such that $\delta \leq x_1(t) + x_2(t) \leq D$ and $0 \leq x_3(t) \leq D$ for all $t \geq 0$. Define $P(\mathbf{x}) = x_1/x_2$. Its time derivative is given by $\dot{P}(\mathbf{x}) = P(\mathbf{x})\xi_1(x_2 - x_1)$, which is positive if $x_1 > x_2 > 0$. Since $\omega(\mathbf{x}(0))$ is invariant, it must be contained in $\Omega = \{\mathbf{x} \in \mathbb{R}_+^3 : \delta \leq x_1 \leq D, x_2 = 0, 0 \leq x_3 \leq D\}$. If $\xi_3 > 0$, then $\omega(\mathbf{x}(0)) = \{F_1\}$ since all orbits in Ω converge to F_1 . If $\xi_3 < 0$, then the maximum invariant set in Ω is the closure of the connecting orbit between F_1 and F_{13} . Since the ω -limit set of any

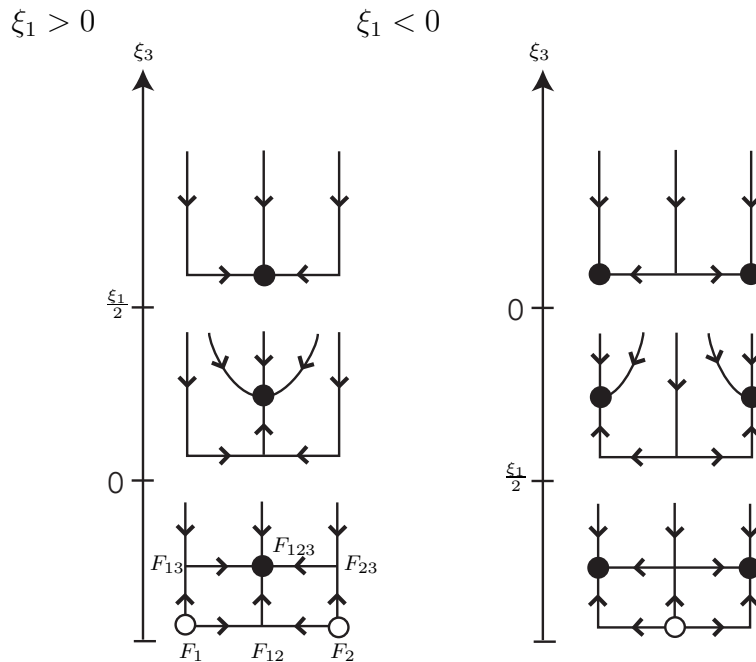


FIG. 5.4. The phase portraits for the prey-predator case. Each region contains a typical phase portrait. An equilibrium point is represented by a closed dot \bullet if it is asymptotically; by an open dot \circ if it is repelling; by an intersection of hyperbolic manifolds if it is a saddle.

bounded orbit is internally chain transitive (see section A.2), $\omega(\mathbf{x}(0)) = \{F_{13}\}$. Note that every point $\mathbf{x} \in \mathbb{R}_+^3$ with $x_1 > 0$, $x_2 = 0$, and $x_3 > 0$ is attracted by F_{13} . The same method is applicable to $\mathbf{x}(0) \in \mathbb{R}_+^3$ with $x_2(0) > x_1(0)$. \square

In Figure 5.4, typical phase portraits for $x_1 + x_2 > 0$ are projected from the x_3 -axis to the face $x_1 + x_2 = 1$ since $\omega(\mathbf{x})$ does not intersect with the x_3 -axis if $x_1 + x_2 > 0$. If $\xi_1 > 0$, then the full system behaves as predicted by the dynamics on M . On the other hand, if $\xi_1 < 0$, then the dynamics on M does not always coincide with that on $\mathbb{R}_+^3 \setminus M$. The disagreement can be observed if $\xi_1/2 < \xi_3 < 0$. In this case, the dynamics on M shows that species 2 goes extinct, but species 1 can support species 2 if the age-structure is incorporated. This coexistence occurs with the following mechanism. The condition $\xi_1 < 0$ leads to competitive exclusion between classes of species 1. Since the competition is more severe between than within classes if $\xi_1 < 0$, the competitive exclusion relaxes the intraspecific competition of species 1 and increases the total population density of species 1. Consequently, this abundant resource allows species 2 to persist.

5.3.2. Predator-prey: $(\alpha, \beta) = (+, -)$, $(s_1, s_2) = (-, +)$. In this case, the system has at most five isolated equilibrium points, $\mathbf{0}$, F_3 , F_{13} , F_{23} , and F_{123} . Since the vector field is symmetric to M , we focus on the equilibrium points \mathbf{x} satisfying $x_1 \geq x_2$, i.e., $\mathbf{0}$, F_3 , F_{13} , and F_{123} . The external eigenvalues of $\mathbf{0}$, F_3 , and F_{13} are identical to those given in Table 5.1 (F_1 and F_{12} do not exist). It is clear that F_3 and F_{13} are always internally asymptotically stable and F_i , $i = 3, 13$, attracts all points \mathbf{x} with $\text{supp}(\mathbf{x}) = \text{supp}(F_i)$. Similarly to the previous prey-predator case, the Jacobi matrix evaluated at F_{123} is stable if and only if $\xi_1 > 0$. By the linear stability of the

equilibrium points, the system is classified into four classes if we ignore the critical cases where at least one of $\xi_1 = 0$ and $\xi_2 = 0$ is satisfied (see Figure 5.5). In the critical cases, our system has a nonhyperbolic equilibrium. In particular, our system has a continuum of equilibria if $\xi_1 = 0$. As given below, the local stability of a fixed point also ensures its global stability.

PROPOSITION 5.6. *There exists a positive number $\delta > 0$ such that*

$$\liminf_{t \rightarrow \infty} x_3(t) \geq \delta$$

for all $\mathbf{x}(0) \in \mathbb{R}_+^3$ with $x_3(0) > 0$.

Proof. This is an immediate consequence of [13, Lemma 4.4] for the general Lotka–Volterra equation (1.1). The lemma shows that if (1.1) is dissipative and there exists $i \in \{1, 2, \dots, n\}$ such that $r_i + (A\mathbf{x}^*)_i > 0$ holds for all equilibrium points $\mathbf{x}^* \in \mathbb{R}_+^n$ with $x_i^* = 0$, then there exists a positive number $\delta > 0$ such that $\liminf_{t \rightarrow \infty} x_i(t) \geq \delta$ for all $\mathbf{x}(0) \in \mathbb{R}_+^n$ with $x_i(0) > 0$. Since the face $x_3 = 0$ of our specific system has no equilibrium points except $\mathbf{0}$ and $\dot{x}_3/x_3|_{\mathbf{0}} > 0$, the conclusion of this proposition follows. \square

THEOREM 5.7. (i) F_3 attracts all points $\mathbf{x} \in \mathbb{R}_+^3$ with $x_3 > 0$ if $\xi_2 > 0$.

(ii) F_{123} attracts all positive points $\mathbf{x} \in \mathbb{R}_+^3$ if $\xi_1 > 0$ and $\xi_2 < 0$.

(iii) F_{13} (resp., F_{23}) attracts all points $\mathbf{x} \in \mathbb{R}_+^3$ with $x_1 > x_2$ (resp., $x_2 > x_1$) and $x_3 > 0$ if $\xi_1 < 0$ and $\xi_2 < 0$.

Proof. Consider case (i). Then there exists a small $\epsilon > 0$ such that $\frac{s_1}{c}\xi_2 + \epsilon < 0$. Let $\mathbf{x}(0) \in \mathbb{R}_+^3$ with $x_3(0) > 0$. Since $\dot{x}_3 \leq x_3(s_2 - cx_3)$, there exists a $T > 0$ such that $x_3(t) \leq \frac{s_2}{c} + \frac{\epsilon}{\alpha}$ for all $t \geq T$. Then $\dot{x}_i \leq x_i(\frac{s_1}{c}\xi_2 + \epsilon)$, $i = 1, 2$, holds for all $t \geq T$. This implies $x_i(t) \rightarrow 0$, $i = 1, 2$, as $t \rightarrow \infty$. In case (ii), the matrix A is VL-stable (see section A.1). In fact, $DA + A^\top D$ is negative definite for $D = \text{diag}\{-\beta, -\beta, \alpha\}$. Therefore F_{123} attracts all positive points.

Consider case (iii). Let $\mathbf{x}(0) \in \mathbb{R}_+^3$ with $x_1(0) > x_2(0)$ and $x_3(0) > 0$. If $x_2(0) = 0$, then the dynamics is reduced to a two-dimensional Lotka–Volterra predator–prey system. Therefore, the conclusion clearly holds (see the proof of Theorem 5.5). Let us assume $x_2(0) > 0$. Suppose that $\omega(\mathbf{x}(0))$ intersects with the x_3 -axis. By Proposition 5.6, $\omega(\mathbf{x}(0))$ does not include $\mathbf{0}$. Furthermore, since $\dot{x}_1/x_1|_{F_3} > 0$, $\dot{x}_2/x_2|_{F_3} > 0$, and the stable manifold of F_3 is contained in the x_3 -axis, $\omega(\mathbf{x}(0))$ must include a point on the x_3 -axis different from F_3 . But it is impossible since the ω -limit set of any bounded orbit is compact and invariant. Therefore $\omega(\mathbf{x}(0))$ does not intersect with the x_3 -axis. This result with Propositions 5.3 and 5.6 implies that there exist positive numbers $\delta > 0$ and $D > 0$ such that $\delta \leq x_1(t) + x_2(t) \leq D$ and $\delta \leq x_3(t) \leq D$ for all $t \geq 0$. Using the function $P(\mathbf{x})$ defined in the proof of Theorem 5.5(iii)–(iv), we can show that $\omega(\mathbf{x}(0))$ is contained in $\Omega = \{\mathbf{x} \in \mathbb{R}_+^3 : \delta \leq x_1 \leq D, x_2 = 0, \delta \leq x_3 \leq D\}$. Since $\omega(\mathbf{x}(0))$ is invariant, we can conclude that $\omega(\mathbf{x}(0)) = \{F_{13}\}$. The same method is applicable to the case where $x_2(0) > x_1(0)$ holds. \square

In Figure 5.5, typical phase portraits for $x_3 > 0$ are projected to the face $x_3 = 0$ since $\omega(\mathbf{x})$ with $x_3 > 0$ does not intersect with the face $x_3 = 0$. In this predator–prey case, the dynamics on M is always consistent with that on $\mathbb{R}_+^3 \setminus M$. This is due to the lack of nonequilibrium dynamics of the prey species. Since the population density of species 2 equilibrates at F_3 if it is isolated from species 1, the initial increase of invading species 1 is irrespective of its age-structure. Therefore the dynamics on M predicts the survival possibility of species 1. It is worth noting that the nonequilibrium coexistence observed when $\xi_1 < 0$ is found in an analogous age-structured model in [1].

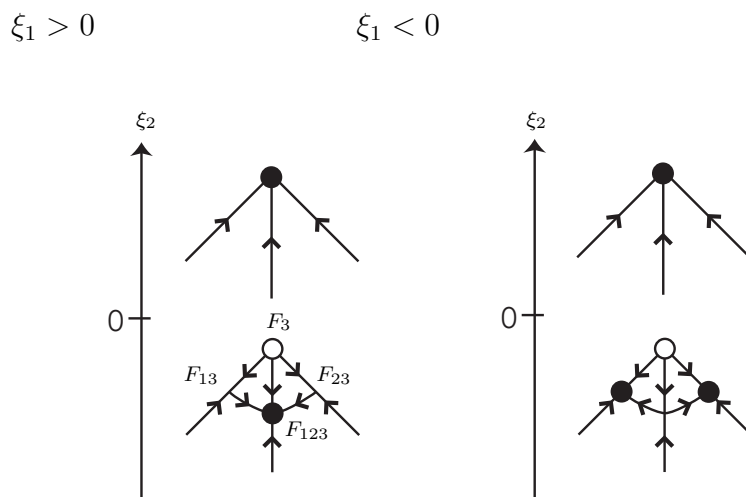


FIG. 5.5. The typical phase portraits for the predator-prey case. Each region contains a typical phase portrait. An equilibrium point is represented by a closed dot \bullet if it is asymptotically stable; by an open dot \circ if it is repelling; by an intersection of hyperbolic manifolds if it is a saddle.

5.4. Formulas in terms of the original parameters. Although all results given above are expressed in terms of the parameters of the Lotka–Volterra equations, some of them can be formulated in terms of the original parameters. In fact, as shown earlier in section 5, the parameters a, b, c, α, β are expressed by those of the original coupled Leslie matrix model. Since the Lotka–Volterra equation (1.1) with (3.2) is derived by taking the limit $h \rightarrow 0$, which implies $\mathcal{R}_0^i \rightarrow 1$, it is reasonable to assume that the parameters satisfy the constraint $\sigma_1^i(0)\sigma_2^i(0)\cdots\sigma_{n_i}^i(0) = 1$. For instance, the condition for strong interclass competition, i.e., $\xi_1 < 0$, is expressed as follows:

$$\begin{aligned} \xi_1 &= -(k_{11} + k_{22}) + k_{21} + k_{12} \\ &= \frac{\sqrt{1/\sigma_1^1(0)}}{\sqrt{\sigma_1^1(0)} + \sqrt{1/\sigma_1^1(0)}} (-b_{11} - b_{22}\sigma_1^1(0) + b_{21} + b_{12}\sigma_1^1(0)) < 0. \end{aligned}$$

If we define

$$\rho := \frac{b_{21} + b_{12}\sigma_1^1(0)}{b_{11} + b_{22}\sigma_1^1(0)},$$

then $\xi_1 < 0$ is rewritten as $\rho > 1$. ρ is introduced by Cushing [5] to measure the intensity of interclass competition relative to the intensity of intraclass competition in a semelparous population. Similarly, the parameters ξ_2 and ξ_3 are expressed as follows:

$$\begin{aligned} \xi_2 &= -2b_{33} + (b_{13} + b_{23})\frac{s_2}{s_1}, \\ \xi_3 &= \frac{\sqrt{1/\sigma_1^1(0)}}{\sqrt{\sigma_1^1(0)} + \sqrt{1/\sigma_1^1(0)}} \left\{ -b_{11} - b_{22}\sigma_1^1(0) + (b_{31} + b_{32}\sigma_1^1(0))\frac{s_1}{s_2} \right\}. \end{aligned}$$

Furthermore, by definition, the ratio s_2/s_1 is given by

$$\frac{s_2}{s_1} = \frac{\ln \sigma_1^2(0)\sigma_1^2(0)}{\ln \sigma_1^1(0)\sigma_2^1(0)}.$$

These formulas can be used to formulate coexistence conditions. As mentioned in each subsection, interesting inconsistencies of the population dynamics between unstructured and structured systems occur only when $\rho > 1$. So, we focus on the case $\rho > 1$ below. In the competitive case, Figure 5.1 shows that coexistence of two species is achieved when $\xi_2 > 0$ and $\xi_3 > 0$ are fulfilled. These conditions imply

$$(b_{13} + b_{23}) \times (b_{31} + b_{32}\sigma_1^1(0)) < (b_{11} + b_{22}\sigma_1^1(0)) \times 2b_{33}.$$

The left- and right-hand sides represent the intensities of inter- and intraspecific competitions, respectively. Note that $b_{13} + b_{23} < 0$, $b_{31} + b_{32}\sigma_1^1(0) < 0$, $b_{11} + b_{22}\sigma_1^1(0) < 0$, and $b_{33} < 0$, although all b_{ij} 's are not necessarily negative. A characteristic of this inequality is that terms corresponding to the intensity of interclass competition of species 1 do not appear in the right-hand side. This is because one of the cohorts of species 1 is eliminated if $\rho > 1$. In the cooperative case, coexistence is achieved if $ac > \alpha\beta$, which is equivalent to the above inequality. In the prey-predator case (i.e., $(\alpha, \beta) = (-, +)$, $(s_1, s_2) = (+, -)$), the predator can persist if $\xi_3 < 0$, i.e.,

$$\frac{-s_2}{s_1} < \frac{b_{31} + b_{32}\sigma_1^1(0)}{-(b_{11} + b_{22}\sigma_1^1(0))},$$

where $b_{11} + b_{22}\sigma_1^1(0) < 0$ and $b_{31} + b_{32}\sigma_1^1(0) > 0$. This inequality shows that the amount of benefit from species 1 to species 2 relative to the intensity of interspecific competition of species 1 is larger than some threshold. Similarly to the competitive case, terms corresponding to the intensity of interclass competition of species 1 do not appear in the formula.

6. Concluding remarks. We advanced the work by Diekmann and van Gils [10] and derived a Lotka–Volterra equation with a certain symmetry from a coupled nonlinear Leslie matrix model for multiple species. In [10], their n -dimensional Lotka–Volterra equation for a single species is further reduced to a replicator equation on $S_n = \{\mathbf{x} \in \mathbb{R}_+^n : x_1 + x_2 + \cdots + x_n = 1\}$, and the dynamics is reduced by one dimension. This reduction relies on the property that all intrinsic growth rates r_i are identical since their model consists of a single species (see also [14, Exercise 7.5.2]). Since our system (1.1) with (3.2) consists of multiple species, this reduction is not applicable, although the special case $s_1 = s_2 = \cdots = s_N$ leads to a replicator equation.

The multispecies model (2.1) necessarily leads us to consider not only the case $\mathcal{R}_0^i > 1$ but also the case $\mathcal{R}_0^i < 1$ since $\mathcal{R}_0^i < 1$ does not simply imply the extinction of species i . In fact, the two examples in section 5.3 show that the species with $s_i < 0$ can survive with the help of the other species. Since (1.1) with (3.2) is a valid approximation only if $\mathcal{R}_0^i \approx 1$, it is not valid for models with quick behavior such as the Nicholson–Bailey host-parasitoid model, in which the parasitoid population density becomes zero immediately if there are no host individuals. In the paper by Beddington and Free [1], we can find such a predator-prey model with an age-structure in the predator population. Furthermore, we can find that our approximate model reproduces one of the characteristic behaviors observed in [1], i.e., the 2-cycle, in which young and old predators occur in alternate time periods. This suggests that even though $\mathcal{R}_0^i \approx 1$ is a strong assumption, the classification of (1.1) with (3.2) provides a catalogue of possible behaviors of age-structured models for interacting species.

A special case of the Lotka–Volterra equation (1.1) with (3.2) was analyzed in detail. The special case assumes that the system is composed of two species, one species

having two age-classes and the other species having a single age-class. The analysis completely describes its global dynamics except in the case where the parameters satisfy certain algebraic equations. In this analysis, several mathematical theories and facts on Lotka–Volterra equations, such as the VL-stability theory, the Liapunov function for symmetric interaction matrices, and the topological equivalence to a replicator dynamics, are used. They are still applicable to our approximate system even if its dimension is more than three. Therefore, as seen in the three-dimensional examples, a vast amount of knowledge on Lotka–Volterra equations would help to understand the role of age-structures in more complex ecosystems.

Appendix A. In this appendix, we briefly introduce some general theories used in the main body of the manuscript.

A.1. VL-stability. A square matrix A is said to be *VL-stable* if there exists a positive diagonal matrix $D > 0$ such that the symmetric matrix $DA + A^T D$ is negative definite, i.e., if there exist positive numbers $d_i > 0$ such that

$$\sum_i \sum_j d_i a_{ij} x_i x_j < 0$$

for all $\mathbf{x} \neq \mathbf{0}$ [14]. The VL-stable matrix is called an S_w -matrix in [20, 21] and dissipative in [17].

THEOREM A.1 (see [21, Theorem 1]). *If A is VL-stable, then for every $r_i \in \mathbb{R}$ system (1.1) has a globally asymptotically stable equilibrium point \mathbf{x}^* ; i.e., \mathbf{x}^* is stable in \mathbb{R}_+^n and attracts all solutions with the initial conditions $\mathbf{x}(0) \in \mathbb{R}_+^n$ satisfying $x_i(0) > 0$ for all $i \in \text{supp}(\mathbf{x}^*)$.*

A.2. Internally chain transitive sets. Let X be a metric space with metric d and $\Phi(t) : X \rightarrow X$, $t \geq 0$ be a continuous semiflow. A nonempty invariant set $M \subset X$ for $\Phi(t)$ (i.e., $\Phi(t)M = M$, $t \geq 0$) is said to be *internally chain transitive* if, for any $a, b \in M$ and any $\epsilon > 0$, $t_0 > 0$, there is a finite sequence $\{x_1 = a, x_2, \dots, x_{m-1}, x_m = b; t_1, \dots, t_{m-1}\}$ with $x_i \in M$ and $t_i \geq t_0$, $1 \leq i \leq m-1$, such that $d(\Phi(t_i, x_i), x_{i+1}) < \epsilon$ for all $1 \leq i \leq m-1$.

THEOREM A.2 (see [11, Lemma 2.1]). *The ω -limit set of any precompact orbit is internally chain transitive.*

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